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Volume VI

Studies in the Life History of the Song Sparrow II

The Behavior of the Song Sparrow and Other Passerines

By Margaret Morse Nice

New York

September 1943

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To my Husband

TABLE OF CONTENTS

CHAPTER I

CHAPTER II

CHAPTER III

CHAPTER V

CHAPTER VI

CHAPTER VII

CHAPTER VIII

Chapter IX

Chapter X

Chapter XI

CHAPTER XII

CHAPTER XIII

CHAPTER XIV

CHAPTER XV

CHAPTER XVI

CHAPTER XVII

CHAPTER XVIII

CHAPTER XIX

CHAPTER XX

CHAPTER XXI

CHAPTER XXII

APPENDIX I

APPENDIX II

APPENDIX III

APPENDIX IV

APPENDIX V

LIST OF ILLUSTRATIONS

FOREWORD

This volume is primarily a treatise on the behavior of passerine birds with the Song Sparrow as the chief example. This species was chosen partly because it is a generalized type with no particular specializations except perhaps in song, and also because it is the bird with which I am most familiar. From 1929 to 1936 I carried on an intensive study of Song Sparrows in Columbus, Ohio; since then I have raised these birds during three summers and have studied them throughout the year in our home. This species offers many advantages as a subject for study, as pointed out in Volume I; it is abundant, thus affording many individuals for observation; it is widely distributed (having been available to me in Ohio, Massachusetts and Michigan); it is easily watched, since it nests at our doorsteps and its territories are small; it readily enters traps, and can be easily reared by hand and kept in captivity. Finally its individuality in song makes it of unique value for the study of the subject of song.

Without the technique of banding—both with numbered aluminum and colored celluloid rings—this research would have been impossible. Both volumes are based on intimate study of *known* individuals, on intensive campaigns of banding for seven years, and later on continuous observation of hand-raised birds. My methods of study of the Ohio Song Sparrows are given in Volume I.

The first volume, "A Population Study of the Song Sparrow",[1] dealt with the vital statistics of a group of Song Sparrows in Columbus, Ohio: their weights, migrations, territories, nesting success and failure, and the survival of adults and young. Comparisons are made with other species, but the work is chiefly concerned with a sample population of *Melospiza melodia.*

The emphasis in the present volume is somewhat different; here we are dealing with passerine behavior, with the Song Sparrow as our chief illustration; comparisons are made with many other birds, mainly, but not entirely, passerine. The book takes the bird from hatching to maturity and through its own parental activities.

Chapter II gives a detailed account of the first 4 weeks of a Song Sparrow's life, divided into 5 stages. Chapter III discusses the many activities of young passerines, arranged in 6 categories. Chapter IV is concerned with innate and learned behavior in the young bird and Chapter V with the course of development in passerines in general. Chapter VI concludes the section on the young bird with an account of behavior in the fall.

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[1] 1937. Transactions of the Linnaean Society of New York, 4:1-247.

In Chapter VII fundamental questions of social need and dominance are treated; this is of basic importance for much of the subsequent matter. Chapter VIII on awakening and roosting leads naturally to the 3 chapters on song—adult male and female, and inheritance, development and function. Territory is considered in Chapters XII and XIII, the first largely devoted to the Song Sparrow, the second to more general problems. Three chapters take up questions of mating and relations to neighbors, Chapters XIV and XV concerned mostly with Song Sparrows, Chapter XVI with problems of pair formation in general. Chapters XVII through XX on the nest, eggs, care and defense of the young, deal both with Song Sparrows and other species. Chapter XXI is on enemy recognition and XXII on innate and learned behavior in the adult. Although it was tempting to point out analogies with human behavior in many places, I refrained from doing so until the final chapter. The appendices contain detailed accounts of vocalizations, dominance, pair formation, etc., in the Song Sparrows. The gist of each chapter is given in its summary. Where quotations are made from articles or books in foreign languages, the translation is mine. Scientific names of species are given in the Index of Species.

The technique of my study was largely what Katz calls the "phenomenonological method", i.e. description of behavior. "A necessary condition for success is a continuous sympathetic observation of an animal under as natural conditions as possible. To some degree one must transfer oneself into the animal's situation and inwardly take part in its behaviour. A useful standard for determining how far one has succeeded in this is given by the certainty with which the behaviour in any concrete situation can be inwardly anticipated" (1937:49). Over 40 years ago Whitman told us we must "observe and experiment under conditions that insure *free behavior*" (1899:302).

It is all-important to *see* and *record exactly* what a bird does. Instead of saying one bird "threatens" another, we should describe precisely the notes and gestures. We need to know a bird's equipment of instinctive actions before we can judge as to what is innate and what is learned.

It is a pleasant duty to acknowledge help from many friends. For years I have benefited through correspondence from the advice of Dr. Wallace Craig. To the Lorenz family I am greatly indebted for their hospitality in June 1938 and to Dr. Konrad Lorenz for guidance and inspiration. Conversations with the late Dr. G. K. Noble emphasized a different point of view. Discusssions with Dr. Tinbergen at the meeting of the Ornithologists' Union at Washington in 1938 and with Dr. W. C. Allee and Dr. Nicholas Collias of the University of Chicago have been helpful on the theoretical points.

When I was in Austria, Dr. Lorenz and I planned to write a joint paper on "The Maturation of Some Activities in Young Redstarts and Serins", I to furnish the observations, he the theoretical discussion and sketches. I sent him my portion which he returned with comments. Although on account of his many interests and preoccupations he never found time to write his share of the article, which consequently was never published, yet his suggestions were important and some are incorporated in Chapters III and IV.

In January 1940 the first version of the first six chapters of the present volume was sent to Dr. Craig, Dr. F. A. Beach, Jr., Mr. Daniel Lehrman and Dr. A. L. Rand for criticism; their advice was helpful not only for the revision of the chapters in question, but also for the treatment of the rest of the book. I gratefully acknowledge my indebtedness to Mr. Dean Amadon, Dr. Craig, Mr. J. J. Hickey, Dr. Ernst Mayr and my daughter Constance for their great kindness in reading and criticizing the whole manuscript.

With Joost ter Pelkwyk I discussed many problems and carried out with him experiments on enemy recognition. I have to thank him for the black and white sketches in this book. Thanks are also due to the National Audubon Society for the privilege of using the illustration by Roger T. Peterson from my article in *Bird-Lore* in 1936. I am much indebted to Dr. and Mrs. Miles Pirnie for their hospitality when I spent 3 weeks in 1939 at their home at the W. K. Kellogg Bird Sanctuary, Battle Creek, Michigan, raising Song Sparrows and a Cowbird. Much information on behavior of hand-raised birds has been received by letter from Mrs. Amelia Laskey of Nashville, Tennessee, Mr. H. R. Ivor of Erindale, Ontario, Mr. W. E. Schantz of Columbus, Ohio, and the late Mr. Ernest I. Dyer of Piedmont, California. As to literature, I have benefited much from the libraries of the University of Chicago. My associate editorship of *Bird-Banding* has brought me many books and journals which otherwise would have been difficult of access for me. I must thank my daughter Janet for help in typing this manuscript. Finally I wish to express my gratitude to my husband, Dr. Leonard Blaine Nice, for his unselfish encouragement of my ornithological labors during the last 23 years.

It is my hope that this book will serve as a guide to the study of bird behavior, showing, as it does, the general pattern of development and broad outlines to be expected, and giving a viewpoint and technique which should help others to intensive observation and study.

CHAPTER I

Bird Behavior

How are we to look upon birds? Are they reflex machines, or human being in miniature? Or do they fall somewhere between these extremes? How do birds communicate with each other since they lack articulate speech? How can they carry out exceedingly complex processes, that would seem to call for foresight and planning, showing a certain amount of adaptability, yet at times fail utterly to grasp the situation when confronted with somewhat changed conditions?

In this chapter I hope to present in plain language for the bird student some of the principles of animal psychology, particularly as they relate to birds. Although the treatment is brief, an explanation is given of the terms used in the text, and references are cited to source material, books and articles, for further consultation. The point of view is fundamentally that of Lorenz, Heinroth and Tinbergen, all of whom are more conversant with and more sympathetic with wild birds and other animals than are the laboratory psychologists. However, I have read widely on the subject of animal psychology, and have attempted to give both sides in this theoretical discussion.

A. The Observations of Others

Some investigators have combined sympathy with wild birds and other animals and wide experience with them with insight into fundamental problems and an analytic and experimental point of view. Outstanding among these are Francis Herrick and Wallace Craig in America, Oskar Heinroth and Konrad Lorenz in Germany, Eliot Howard in England and Niko Tinbergen in the Netherlands.

Herrick was a pioneer in this country in the field of scientific watching of the breeding behavior of wild birds; he used the blind and camera, and studied and described the chains of reflexes involved in parental care of the young and development of the latter. One of his most detailed studies was that on the development of the Black-billed Cuckoo (1910).

Craig's works on "The Voices of Pigeons as a Means of Social Control" (1908), "Expressions of Emotion in Pigeons" (1909), "Appetites and Aversions as Constituents of Instincts" (1918), and other important papers were published in psychological journals, where they largely escaped the notice of ornithologists, whose interests, moreover, for the most part lay in other directions.

Oskar and Magdalena Heinroth accomplished the extraordinary feat of raising from the egg (or shortly thereafter) almost all the avian species of Central Europe; they studied the behavior of the young birds and took a series of remarkable photographs. Their four volumes—"Die Vögel Mitteleuropas" (1924-33)—offer a mine of information on the development of young birds of almost all orders. Heinroth has also written many valuable articles on the vocal utterances of birds (1924), the bathing of birds (1912b, 1938b), the movements of vertebrates (1930a), etc. In "Aus dem Leben der Vögel" (1938a) he has given a brief summary of salient points in bird life, a manual of biology with birds as the text. Heinroth is director of the Berlin Aquarium; he has had a wide experience with vertebrates—the whole class of birds, and fish, amphibia and reptiles; he is a keen observer and his conclusions are sound.

Gifted with an unusual sympathy for animals and insight into their ways, Lorenz makes use not only of his own varied and intimate experience with birds and animals, but also of Heinroth's results, in formulating his theoretical interpretations of bird psychology. In his brilliant exposition "Der Kumpan in der Umwelt des Vogels" (1935) Lorenz has given us a theoretical basis for the study of bird behavior with his concept of "releasers" and "companions".

Tinbergen, a careful and original investigator, co-worker with Lorenz, has published many important papers on the behavior of birds, fishes and insects, among them studies on the Northern Phalarope, Hobby, and Snow Bunting. He has also made an experimental study of gaping in young thrushes and given us several theoretical papers, particularly "The Function of Sexual Fighting in Birds" (1936a) and "On the Analysis of Social Organization among Vertebrates" (1939a).

In this country and England few studies besides those of Herrick have been made on the development of young birds. A pioneer paper by Kuhlmann (1909) appeared in a psychological journal and remained practically unknown to ornithologists. The admirable study of the Ovenbird by Hann (1937) and Rand's account of hand-raised Blue Jays (1937) and Curve-billed Thrashers (1941c) have afforded some data on this subject.

An excellent study on gaping in Starlings was done in Switzerland (Holzapfel 1939), while Strauss' (1938a, 1938b) detailed studies of tame Corvidae contain much of value.

In England the chief interest has lain in matters of territory and courtship; here Eliot Howard, Julian Huxley and David Lack have made the greatest contributions.

B. The Status of Birds in Comparison with Other Animals

"Birds," writes Huxley (1941:209) "have kept instinct as the mainstay of their behaviour," whereas "mammals have gradually perfected intelligence and the capacity for learning by experience". This is evident from an examination of the brains of birds and mammals and a comparison of the size and elaboration of the cerebral hemispheres.

According to Maier and Schneirla (1935) bird behavior is "very complex. Many of its varied modes of activity have an important emotional facilitation, and vary in close relationship with visceral condition. Learning may be responsible for the extension of a specific type of activity and may make possible its elaboration within certain limits. However, the bounds within which learning may function appear to be established by the heritably determined factors (e. g., dominance of visual control, well-ordered visceral cycles, extensive development of the striate area in the brain, etc.) which themselves are responsible for the basic stereotypy of the activity. Therefore, while the bird is enabled to live in a very *tiere*) to the highest degree with many inborn drives and little intelli- complex environment by virtue of mechanisms which have evolved to a high degree of elaboration, it is these possessions which are responsible for its psychological limitations. It is otherwise with the mammals," p. 263. "The behavior of lower animals depends largely upon their structural characteristics and the immediate stimulating conditions, but that of mammals is largely conditioned by previous responses. The study of mammalian psychology is therefore characterized by an analysis of the process of modification in behavior through experience," p. 265.

"The average bird," writes Heinroth (1938a:151), "ranks well below the average mammal in its intelligence, for with the bird, thinking to a certain degree is replaced by flight". Brain activity does not need to be so highly developed in the bird world, for the ability to fly enables this group of animals to solve problems in the matter of food, climate, enemies, etc., by changing their environments. As a result of her experiments on Corvidae, Hertz (1926) considered that these intelligent birds were on much the same level as monkeys in visual discrimination, behavior in mazes, and insight.

Huxley writes of birds, "They have raised emotion to the highest pitch found in animals; the line of mammals has done the same thing for intelligence" (1941:210). "Birds are emotional animals (*Gefühls*-gence" (Heinroth 1938a). Katz tells us, "Many animals are extraordinarily similar to human beings in their emotional and effective life, and . . . to a great extent the one essential remaining difference consists in the absence of reflectiveness in the conscious processes of animals and its presence in man" (1937:20).

The eyesight of most birds is exceedingly keen. They have been proved to have color vision (Van Eck 1939; Warden, Jenkins and Warner 1936:195). Their hearing is acute. Experiments on its range have been carried out by Brand and Kellogg (1939), and on discrimination and localization by several investigators (Warden, Jenkins and Warner 1936:179). Birds "have satisfactorily demonstrated learning ability on all the usual forms of apparatus. Their records appear to be roughly comparable to those made by the sub-primate mammals in spite of the fact that the test situations have nearly always been of a kind rather better suited to the motor capacities of the latter forms" (Warden, Jenkins and Warner 1936:256). Birds have excellent memories for many things, as places and certain experiences. A Cowbird remembered training in relation to a problem-box as long as 11 months (Porter 1910), while a hen trained to pick up only grains of a definite color retained this training after an interval of 2 years (Claparède 1926-27). My Song Sparrow Y showed evidence of memory of experiments on enemy-recognition for 18 months (See Chapter XXI). Their memory for individuals, however, in many cases is surprisingly short (Chapter XVI).

C. INNATE AND LEARNED BEHAVIOR

"The basic forms of behavior in the individual are . . . dominantly hereditary in origin" (Warden, Jenkins, and Warner 1934:51). Almost all behavior is partly natively determined and partly modified by experience.

Lorenz (1937a:246) considers instinctive action an innate coordination of movement. If we restrict the term "instinctive action" to this narrow sense, we will avoid the pitfalls of the vague generalities inherent in the discussion of "mother instinct", "homing instinct", "territorial instinct", etc.

With this definition we can understand Lorenz's insistence on the unmodifiability of instinctive action. Weiss' (1941:80) experiments on amphibia have shown "the great rigidity and unmodifiability of coordination patterns in the *lower vertebrates*. . . . Thus an amphibian can be conditioned to exhibit a certain motor reaction, e.g., alarm, preying, retreat, etc., in response to a certain set of sensory stimuli. Yet, in producing these responses, it is bound to use the existing repetoire of preformed motor mechanisms, such as they are."

"Each instinct involves an element of appetite, or aversion, or both," writes Craig (1918:91), and Lorenz agrees that instinctive action is "appeted, sought or desired" (1937a:246).

Learning is the adjustment of behavior through experience. It plays a part in the behavior of all animals, small in some, large in others. "Learning and intelligence can decide the question, whether and with what intensity in an individual case a certain instinctive act will be released, but never change in the slightest the *form* of the finally executed movements" (Lorenz 1937b:32). Flight can go off in vacuo, or as an unconditioned response when a Greylag first sees a Sea Eagle, or as a conditioned response when it sees a man with a gun, or it can be used voluntarily and with insight when the bird flies over a wire fence (Lorenz 1937b:34).

The matter of threshold should not be lost sight of. Dr. Lorenz made a chart for me illustrating this for a Greylag upon the approach of a man; there were a number of possible responses: watching the intruder, walking away, crouching, preparing to fly, flying. These different responses might depend on the nearness of the enemy, or they might illustrate the process of gradual accustoming or taming.

It often happens that the longer the interval since an instinctive action has last functioned, the lower is its threshold and the easier it is to set off. Finally a point may be reached where the action goes off without any visible stimulus, or in vacuo. On the other hand, instincts may drop out as the result of domestication, or lack of vigor in an animal.

In many chain reflexes or "interlacing of instinct and learning" (*Triebdressurverschränkung*), variation may occur at a particular point, which usually concerns the *object of the instinctive action* (Lorenz 1937b:33). Thus a shrike instinctively performs the act of attempting to impale food, but has to learn that a pointed object (in nature, a thorn) is the instrument it needs.

Sometimes an instinctive action appears to improve through practice. This may, however, be a matter of *maturation,* i.e. development. The exercising of wings by young birds is not *learning to fly;* it is merely premature appearance of the instinctive action. Many birds fly well with no previous practice whatever (Chapter IV). Improvement may also be due to *facilitation,* to a smoother working of the separate elements.

In his study of the sexual behavior of "Male Doves Reared in Isolation", Craig (1914:132) writes: "When a dove performs an instinctive act for the first time, it generally shows some surprise, hesitation, bewilderment, or even fear; and the first performance is in a mechanical, reflex style, whereas, the same act after much experience is performed with ease, skill, and intelligent adaptation. Thus even those acts which do not show improvement by the formation of associations, show improvement by *facilitation.*"

In most movements, besides the instinctive action, there is a spatially directed component or *taxis* (Kühn 1919). This has been well explained by Tinbergen in respect to a shoal of fishes (1939a:212). A taxis is an inborn form of reaction, released by an external stimulus and directed in relation to an object. Investigations on taxes in birds have been made by Tinbergen and Kuenen (1939) in respect to gaping of nestlings, and by Lorenz and Tinbergen (1938) in regard to egg rolling by the Greylag Goose. The latest theories on taxes in invertebrates are given by Fraenkel and Gunn (1940).

Lorenz stresses a certain kind of conditioning which he calls *imprinting;* it occurs early in a bird's life and determines the objects of social reactions at maturity. He states that "most birds do not recognize their own species 'instinctively', but that by far the greater part of their reactions, whose normal object is represented by a fellow-member of the species, must be conditioned to this object during the individual life of every bird" (1937a:262). "This is what we might call a super-individual conditioning of the species and certainly it is the chief biological task of imprinting to establish a sort of consciousness of species in the young bird, if we may use the term 'consciousness' in so broad a sense" (1937a:265).

D. RELEASERS, SIGNALS, AND THE "COMPANION"

Lorenz's theory of the "companion" and "releasers" may be briefly summarized as follows:

The peculiar role that the fellow-member of the species plays in the life of the bird has been designated by Jakob von Uexküll (1934) as the "companion" (*Kumpan*). Human beings perceive objects as *things,* for we combine the different stimuli from the same object, but animals may react to one stimulus from an object. "An instinctive reaction of survival value, when directed to a particular object, may be released as if through a surprisingly small choice among the large number of stimuli normally emanating from the object" (Lorenz 1937a:247). When several functions have the same thing for an object, each function corresponds to a different stimulus coming from the same object. The unity of these several functions lies in the object, not in the subject.

Characters that bring definite instinctive responses in a member of the species, Lorenz calls releasers. These may be bodily organs, or striking behavior, or a combination of both; they are compromises between simplicity and improbability. When a bird "releases" instinctive behavior in a fellow-member of the species, Lorenz calls it a "companion". He lists five such—parent-companion, child-companion, sex-companion, social-companion, and brother-and-sister-companion (Lorenz 1935, 1937c).

This conception of releasers has been criticized. From various experiments on breeding European Robins Lack (1940a) concluded:

"At least in this case, the releaser concept is too simple. The general implications are important, for they suggest that releasers are not the fundamental units of bird behaviour. Rather, the bird reacts originally to a more general situation. At a later stage (later in evolution if the releasing complex is inherited, later in the life of the individual if it is acquired: this issue is not discussed here), the bird tends to react primarily (but not necessarily exclusively) to a characteristic part of the external situation. The characteristic part or pattern may then appear to 'release' the behaviour concerned; but it is not (at least always) the sole factor which will elicit the behaviour."

Rand (1941b), citing the review by Lashley (1938) of the work of experimental psychologists, says, "Experiments based on varying the properties of the stimulus object point to the conclusion that the instinctive behavior is dependent on a complex of stimuli, and no investigator has found any single property of the stimulus object which cannot be varied within limits without disrupting the pattern."

Tinbergen (1939a:221) discusses the releaser concept thus:

"Lorenz (1935) called all movements and structures producing a response in the social companion *'Auslöser'* ('releasers'). The more general term *signal* is perhaps preferable since the activities and structures may have releasive or directive influences, or both simultaneously. The smell of unfertilized eggs of the Stickleback, for instance, releases the fertilizing movements of the male, although it certainly does not direct them; orientation is optical and tactile, but not chemical. For the Lapwing, the danger call may have primarily releasive function, whereas the white tail mark may have primarily directive function. It is quite possible, therefore, that the concept of 'signal' should be subdivided into 'releaser' and 'director', although most of the signals may have both functions."

During a discussion of this subject through letters, Joost ter Pelkwyk wrote me his definition of "signals".

"All means by which inter-relations between animals are possible. They may be visual (color, form), auditory (notes), tactile (pecking among birds), and chemical (smell) or a combination. In general a rather complicated signal is necessary for inter-reaction. However, certain characters may drop out in threshold lowering. We assume that the most 'important' characters drop out last.

"Signals may be entirely inborn(developing sooner or later); may be formed in an impressionable period (Lorenz's imprinting or *Prägung*), or may be learned through conditioning. As I see it, signals are not confined to inter-relations between the individuals of one species only, but occur also between individuals of different species which influence each other in nature (predator and prey)."

(The prey "signals" to the predator by its size, movements, perhaps lack of warning coloration—"something to eat"—; the predator "signals" to the prey by its form and movements—"danger.")

In my work the concept of the "companion" has proved useful, while that of "signals" is fundamental.

E. SUMMARY

1. The investigators whose works have been most helpful to me have been Lorenz, Tinbergen and Howard.

2. Birds "have kept instinct as the mainstay of their behavior"; they are "emotional animals", yet learning plays an appreciable role.

3. They are visual and auditory animals with excellent memories in certain fields.

4. Instinctive action is defined as an inherited type of coordinated movement. It is "appeted, sought, or desired". Its form is not modifiable through learning.

5. Learning "can decide the question, whether and with what intensity in an individual case a certain instinctive act will be released."

6. A taxis is an inborn form of reaction, released by an external stimulus and directed in relation to an object.

7. "Imprinting" is defined by Lorenz as a special conditioning process through which the objects of social reactions at maturity are determined.

8. Characters that bring definite instinctive responses in a member of the species are called "releasers" by Lorenz. When a bird "releases" instinctive behavior in a fellow-member of the species, Lorenz calls it a "companion"; as "parent-companion," "social-companion," etc.

9. Tinbergen prefers "signal" to "releaser"; ter Pelkwyk suggests that signals may be "all means by which inter-relations between animals are possible"; they may be inborn, "imprinted" or learned.

CHAPTER II

Development of the Young Song Sparrow

After a brief account of the birds observed, this chapter will be devoted to a narrative of the first 4 weeks in the life of the young Song Sparrow, which will serve as a typical passerine.

A. The Subjects of Study

There are 3 chief sources of first-hand observation on which this book is based: varied experience with birds in Massachusetts and Oklahoma; intensive study of Song Sparrows in the field in Ohio; observation of hand-raised birds in Austria and in this country.

Features contributing to my background for the study of bird behavior are: a keen interest in wild birds from childhood; experience in my teens in the care and observation of hens and chickens when many of the conclusions subsequently promulgated by Schjelderup-Ebbe (1922-1935) were commonplaces to my sister and myself; companionship with a hand-raised Bob-white at Clark University; serious study of birds in the field from 1920 on, particularly the watching of the "home life" of a number of species—Gnatcatchers, Bell Vireos, and 5 species of wood warblers—my chief interest being in the observation of parental behavior.

From 1928-1936 a Song Sparrow (*Melospiza melodia euphonia*) population on Interpont in Columbus, Ohio, was studied by means of color-banding; details of methods are given in Volume I (Nice 1937: 213-220). In the nesting season of 1929 several hours a day were spent watching the behavior of 1M and his mate K2, 4M and his mate K3; in 1935 a somewhat similar study was made of 4M and his mate K200 (Nice 1939a), while scattered observations were also made on the behavior of many other banded Song Sparrows.

In 1938 I spent a month in Altenberg, Lower Austria, at the home of Dr. Konrad Lorenz; here we raised 3 Common Redstarts (*Phoenicurus phoenicurus phoenicurus*), a species belonging to the thrush family, Turdidae, and 3 Serins (*Serinus canaria serinus*), a race of the same species as the Canary. Dr. Lorenz's advice was invaluable in pointing out to me what to look for in the development of the young birds. Since then I have raised 3 sets of Song Sparrows and several other native birds. The 24 individuals of 8 species that came under my observation are listed in **Table I.**

TABLE I
THE HAND-RAISED BIRDS
(Age in days)

Bird	Locality	Year	Sex	Date hatched	Age when taken	Time observed by me	Remarks (See key below)
Song Sparrows							
B	Mass.	1938	♂	July 24	6	3 months	1
R	Mass.	1938	♂	July 24	6	6 months	1
Y	Mass.	1938	♂	July 25	5	4 years	2
D	Mich.	1939	♂	June 15	6	8 months	3
F	Mich.	1939	♂	June 16	6	3 months	1
S	Mich.	1939	♂	June 16	6	3 months	1
N	Mich.	1939	?	June 30?	17?	4 days	1
C	Mass.	1940	♂	July 4	7	3 days	4
T	Mass.	1940	♂	July 4	7	21 days	4
A	Mass.	1940	♂	July 5	6	11 months	5
J	Ohio	1939	♀	Aug. 4?	8?	5 months	6
Common Redstarts							
RR, YR	Austria	1938	♂♂	May 27	5	3 weeks	7
BR	Austria	1938	♀	May 27	5	3 weeks	7
WR	Austria	1938	♂	May 29?	12?	2 weeks	7
Serins							
WH	Austria	1938	♂	May 26?	11?	2½ weeks	8
BL	Austria	1938	♀	May 26?	11?	2½ weeks	9
Cowbird	Mich.	1939	?	June 11	7	18 days	3
Cedar Waxwing	Mass.	1940	?	July 14?	15?	40 days	10
Goldfinches	Ohio	1939	♂, ♀	Sept.	0	8 months	11
Bobolinks	Mich.	1940	♂, ♂	July	10?	4 months	12
Ovenbird	Mass.	1940	?	July	5	4 days	13

KEY

1. Killed self against window. 2. Still with me in 1942. 3. Died through accident. 4. Died; digestive trouble. 5. Subnormal; released. 6. Raised by Schantz; given to me at 2 months; died by accident at 7 months. 7. Released at 3½ months. 8. Died. 9. Kept by Lorenz. 10. Released. 11. Raised by Schantz; with me from age of 4-12 months. 12. Raised by Pettingill; with me from age of 7-11 months. 13. Returned to parents.

Of these birds, the brood of Song Sparrows, B, R, and Y, were exceptionally vigorous, active birds; they were under almost constant observation and most of the data were obtained from them. The Redstarts were also fine examples of health. The other 2 broods of Song Sparrows had not received good starts from their parents, and, due to unfavorable weather, fresh insects were hard to procure. The feeding of the Serins also presented difficulties. The other birds were all normal individuals. The birds were caged part of the time, but much of the time most of them had their freedom in my study.

B. THE FIVE STAGES OF DEVELOPMENT

At hatching the Song Sparrow is a blind, almost cold-blooded, nearly naked creature weighing about a gram and a half. In 9 to 10 days it will increase in weight some ten-fold; it will be covered with feathers and be able to regulate its own temperature; it will be able to move about; to live independently of nest and nest mates; and to inform its parents of its whereabouts and to respond to their notes of alarm and fear. In another week it will have mastered flight. Ten days later it will be full grown and independent of its parents.

The nestling period has been divided into 3 stages by Kuhlmann (1909) who studied a number of passerine species (Chipping Sparrow, Rose-breasted Grosbeak, Robin, Red-winged Blackbird, and Brown Thrasher) from blinds. His stages were: the first 4 days when the "only coordinated movement present is the food reaction"; 5 and 6 days—"a stationary stage of development", the birds becoming "more active and vigorous, but otherwise the nature of their movements" not changing "noticeably"; from 7 days on—a period of rapid progress in motor coordinations.

This scheme fits in general the development of the Song Sparrow in the nest, the chief difference being in the characterization of Stage 2, for observation of vigorous hand-raised birds has shown the appearance of a number of activities during this period.

The young Song Sparrow may be said to pass through 3 stages in the nest and 2 stages outside the nest before it reaches independence at the age of 4 weeks. These may be briefly characterized as follows:

1. The first 4 days; coordinations mainly concerned with nutrition.
2. Five and 6 days; first appearance of new motor coordinations.
3. Seven, 8 and 9 days; rapid acquisition of motor coordinations.
4. Ten to 16 days; leaving the nest to the attainment of flight.
5. Seventeen to 28 days; attainment of independent feeding reactions.

Lists of the day-by-day appearance of the activities of the young Song Sparrows, arranged under the five stages, are given in Tables III and IV (pp. 34, 57-58).

C. THE FIRST STAGE: COORDINATIONS MAINLY CONCERNED WITH NUTRITION

At hatching black down is prominent on the dorsal, femoral and occipital regions and on the coverts. For the first two days there is little change except in increased length of down. At 3 days the sheaths of the primaries, secondaries and tertials have pierced the skin; the crural and ventral tracts are prominent; the interscapulars and head tract have become visible. At 4 days the feathers of the ventral, femoral, humeral, interscapular and occipital tracts have pierced the skin. In some individuals feathers have sprouted on the femoral tract.

The eyes begin to open at 3 or 4 days. Portmann (1938:322) points out that the delayed opening of the eyes ensures that the undeveloped organ shall be covered with a moist medium.

Observations at three nests in Ohio (Nice 1937:130) indicated brooding by the female two-thirds of the daylight hours during the first day; one-half the time during daylight during the next 3 days, and 14, 51 and 62 per cent of the time during the 5th day, the 2 high records occurring during weather 2.8° C. (5° F.) and 5° C. (9° F.) below normal.

Rand (1941c:217) points out that, "Young thrashers, shortly after hatching, assume an embryo position, resting on their belly, the tarsus on each side touching the nest only because of the curve of the bottom of the nest; the head is bent under the breast, resting on its crown." By the fifth day the "embryo attitude is abandoned."

The newly hatched Song Sparrow shows a number of reflexes—grasping, swallowing, etc.; and two chief instinctive activities—the food response and defecating reaction. It is able to crawl about to a small extent by means of uncoordinated wrigglings.

The food reaction consists in raising the head and opening the ruby colored gape to its widest extent.

This behavior in the altrix is well described by Herrick (1935:281): "Resting upon its huge pot-belly as a central pillar, the little bird raises a trembling head, rather freely at first, and, with the precarious support of undeveloped wings, opens its mouth to the widest extent, thus displaying its throat or food-target, which is often brightly colored and rimmed by the swollen commissures or 'lips' of the mandibles."

Defecation typically takes place after feeding. The nestling rises up on its legs, elevating its rump, thus facilitating removal by the parent of the anal sac which is enclosed in a mucous covering. Later the young bird turns toward the rim of the nest to defecate, turning around sometimes 90 or even 180 degrees.

The feeding note *see-sec* was first heard by me in two-day-old birds. It doubtless would be heard during the first day if the bird were not fed; this has been noted in Pigeons (as mentioned by Whitman to Craig, letter) and in Starlings (Holzapfel 1939).

As to the matter of temperature control, "if the young bird was dependent upon its own resources for heat it would be as truly a poikilothermic or 'cold-blooded' animal as are many invertebrates. Especially is this the case with the very young birds which have just broken out of the shell. This similarity is further enhanced by marked variations in behavior and activity at different degrees of temperature" (Kendeigh and Baldwin 1928:275). "With the newly hatched birds

(0 days old), the body temperature . . . was found to approach closer to air temperatures at lower than at high temperatures, and there is no control at all evident over body temperatures" (Kendeigh 1939:423).

D. THE SECOND STAGE: FIRST APPEARANCE OF NEW MOTOR COORDINATIONS

At 5 days sheaths are prominent in all the tracts, while the ventral, femoral and humeral tracts begin to feather out. At 6 days typically the interscapulars feather out. The eyes are partly open at 5 days and fully so at 6 days.

The first intimations of preening come at 5 days. The legs are growing stronger; the bird sometimes stands on his feet. The location call—*ick* or *eep*—has been given by hungry birds as early as 5 and 6 days; normally it first appears at 7 and 8 days, although little used until the bird leaves the nest. This call carries as far as 75 meters. Cowering may appear at this age in response to a strong stimulus; it was shown by two birds in Ohio which I had taken into the house for the purpose of weighing, by Y apparently in response to a scream from B, and by other birds in response to a loud hiss from the observer.

Most of the time is spent sleeping, huddled together; this was true with the Massachusetts birds even on a warm day in a large artificial nest.

Temperature control is evidently fairly well established by this stage, since brooding is practically given up in the daytime except in cold or rainy weather. Records of brooding during the 6th day, when the young were 4 and 5 days old, were 5, 42 and 48 per cent of the time watched, during the 7th day 0 and 23 per cent (Nice 1937:130).

Temperature control is fairly well developed in the Ovenbird at 3 days (Hann 1937:179, 211), and in the House Wren at 6 days (Kendeigh and Baldwin 1928), and well established in the Chickadee at 9 days (Odum 1941b), in the Phoebe (Stoner 1939) and Barn Swallow (Stoner 1935) at 9 or 10 days. These birds normally leave the nest at 8, 15, 16, 16-17, and 20 days respectively. If "we consider the young bird as an isolated individual, it develops from a cold-blooded animal into a warm-blooded one during the period in the nest" (Kendeigh and Baldwin 1928:295).

E. THE THIRD STAGE: RAPID ACQUISITION OF MOTOR COORDINATIONS

This is the period of rapid acquisition of motor coordinations in normal birds. At any time the bird is capable of leaving the nest.

At 7 days the primaries and coverts begin to unsheath, and at 8 days the birds are well covered with feathers both above and below.

1. *Seven Days*

This is the day on which cowering normally appears, and with it the scream. Stretching of the wings upwards and sidewise, scratching the head, yawning, and climbing to the edge of the nest were all seen for the first time.

I will quote from the record of July 31, 1938, when B and R were 7 days old, Y 6. Activities in italics were seen for the first time.

8:55. R stretched legs up, *then wings up.*

9:25. B *scratched his head over his wing.*

9:28. Put B in a nest by himself because of the heat.

10:10. B *gives a loud note—the location call.*

12:27. B *cowered after feeding.*

2:18. I come over very quietly; B gapes in a rather uncertain way. I make a noise with the chair, and all pop up and nearly out of the nest, *see-seeing* loudly. Then R *cowered.*

7:30. I start to take B out of his nest and return him to the others; he cowers and screams his loudest. The others cower as much as possible and for a time nothing will reassure them, neither my whistle, nor touching the nest. This scream seemed to have brought fear to the 6-day-old. B had shown a compromise between fear and gaping, gaping when cowering.

The Song Sparrows in 1940 cowered at 7 and 8 days when taken into bright light. At 8 days they cowered often in the morning, usually just after begging; by noon this type of behavior was no longer shown.

2. *Eight Days*

Three new coordinations of the wings were first noted at this age: fluttering the wing when begging (B, R, Y); stretching both wings down at once (R, Y, F, S); and fanning wings (R). There was much use of harsh *kair* feeding notes, first recorded at 7 days, and one instance of a new feeding note *tit-tit-tit* (B).

Aug. 1. Very active at feeding time; nearly leaving the nest.

11:50. R nearly steps out. B *flutters his right wing.*

12:30. R *flutters* his right wing a little.

2:45. B fluttered both wings; the first fluttering from him since 11:50.

4:37. R crouched. Now standing up, suddenly stretches up on legs, *stretches both wings down at once*, then both up. B stretches wings up, then "yawns", while lying down.

5:18. B begged, then cowered.

6:10. R *fanned his wings* twice on the edge of the nest. This excited the others and they begged.

The birds are less timid today; there has been almost no cowering.

When I was watching a Song Sparrow nest at the Kellogg Sanctuary from a blind, a Kingfisher flew near giving its rattle; the 8-day-old nestling cowered, but the two 7-day birds did not. This rattle is somewhat similar to the fear note of the adult Song Sparrow, although, of course, much louder.

3. *Nine Days*

The birds continue to be more active and alert. The only new coordination seen was that of shaking themselves. For the first time they begged from one another.

Aug. 2. 6:22. Gape for shorter periods now. Y cowers. R stretches legs up, both wings down. Then preens wings and under the wings. Y stretches sidewise; this stimulates R to gape, after which he gives the hunger or location note.

7:07. R flutters both wings when begging.

8:25. B stretches up; all three suddenly start to beg from one another.

8:58. R *shakes himself.*

11:24. They are far more alert today; much less hungry. Cowered as I walked by rather quickly.

5:15. Y flutters the right wing when begging. So each did it first at 8 days. B fanned his wings 3 times.

The other hand-raised Song Sparrow showed few of these activities the last days in the nest, yet they left the nest at the normal time—9 and 10 days.

F. THE FOURTH STAGE: THE FIRST WEEK OUT OF THE NEST

The fourth stage in the development of the Song Sparrow begins with leaving the nest at the age of 9 or 10 days and ends with coming out into the open at the age of 17 days. From a sheltered, stationary position with constant contacts with nest-mates, there is a sudden change to a solitary, somewhat wandering life out in the weeds or bushes. The chief acquirement during this stage is that of flight with its corollary, landing. The bird adopts the adult method of sleeping; it makes a start in feeding itself, it drinks and may bathe.

There is some increase in weight during the fourth stage, besides unsheathing of the feathers on the crown, growth of the wing feathers and rapid growth of the tail, which is about half grown at the age of 17 days. Parental feeding continues at much the same rate as during the last days of nest life.

The hand-raised birds were markedly inactive most of the time except at meals. This silence and immobility between feeding times is surely of survival value. Although I have searched time and time again, I have seldom been able to find a young Song Sparrow at this stage, thanks to their immobility and protective coloring.

Both sets of birds were absolutely tame and confiding, letting us pick them up at any time, seeming to enjoy being stroked, and carried about, even taking naps in our hands. All the little birds, when 11 and 12 days old persisted in flying on to my shoulder and head while I sat at the table feeding them; this may have been partly because I offered the most convenient landing spot, but it also may have shown a tendency to land on the parent-companion (Lorenz 1935).

1. *Leaving the Nest*

On Interpont undisturbed Song Sparrows left the nest at ages ranging from 8 to 12 days, the average of 163 cases being 9.85 days. No birds left normally at 8 days unless their day or two older nest mates were leaving.

TABLE II

AGE OF LEAVING THE NEST OF SONG SPARROWS ON INTERPONT

(163 birds in 52 broods)

Age in days	8	9	10	11	12	Total birds	Average age
May	2	21	64	17	3	107	10.0
June	4	17	21	6	0	48	9.6
July	0	4	3	1	0	8	9.6
Total birds	6	42	88	24	3	163	9.85
Percentage	3.7	25.7	54.0	14.7	1.8	......	......

It will be seen in Table II that more than half of the birds left at 10 days, a fourth at 9 days and about one-seventh at 11 days. There was no correlation between size of brood and age of leaving. Nor was there any tendency for birds to leave earlier from nests on the ground than from those in bushes. There is, however, a tendency for broods to leave earlier in June than in May. In May 60 per cent of the birds left at 10 days and 21 per cent at 8 and 9 days; in June 44 per cent left at 10 days and the same number at 8 and 9 days. This tendency to earlier leaving may be correlated with higher temperatures; in cool weather nestlings benefit from crowding together, but in hot weather they must be uncomfortable in such close quarters as a nest only 55 to 60 mm. in diameter.

With the hand-raised birds, B and R left the nest when 10 days old and Y 9 days, D, F and S at 10 days, T at 10 and A at 9 days. The bond to the nest was suddenly broken and the birds showed a definite urge to go to some distance. Droppings at once lost their covering. The location note, used only occasionally before this, was heard constantly at first while the little bird hopped over the floor. New coordinations were the following: hopping (before this the legs had not been used together except for standing); walking; landing; landing on brothers; bowing when begging; sleeping in the adult position, i.e. with bill in the scapulars. (Y did not show these last two coordinations until the following day; none of the Michigan birds exhibited the bowing; F and S slept in the adult manner at 10 days, D not until 14.)

Some details will be given as to the nest leaving of the Massachusetts Song Sparrows:

Aug. 3. (B and R 10 days, Y 9 days.)

5:10. B wakes me by the hunger call—location note. They are hard to feed now as they are unwilling to take food from me. They turn entirely around to defecate.

5:50. B *leaves the nest!* He hops to the edge of the strawberry box, where the others beg frantically to him; then to the dish where he takes food from me, then to my arm, then to the nest again, then falls on the floor, where I gently pick him up and he screams. Then he goes with big hops to the Morris chair and up on a rung, but slips off. All this time he is calling and the others answer him. He jumps perhaps a dozen times to the top of the floor board (about 30 cm.), always, of course, falling down.

R is on the edge of the box, preening; Y is begging to him, first on one side, then the other, fluttering one wing, then two.

6:07. R stretches sidewise, fans wings; Y begs vigorously; both refuse food from me.

R *hops out,* then back again, then to the floor, hopping and occasionally stepping. He is now on the rung of a chair, calling *yeep.*

6:10. B is still trying to get to the top of the floor board. I take him a meal worm, but he shows no interest; he hops on my arm and off again. I pick him up; he screams his loudest. I put him in the bamboo cage on the table and he tries desperately to get out. He and R answer each other with location note.

6:20. Go to gather up R. He screams and tries to get out of the cage. In the meantime Y *left the nest.* Like B he tries to get to the top of the floor board.

The two in the cage near the nest are trying madly to escape. I finally got a mealworm down B. They beg and beg to each other.

6:35. I put the cage on the floor near the door; the birds calm down at once. B even starts to preen. They are as far as they can be from each other. All three call constantly.

6:50. Took a grasshopper to Y; he paid no attention to the forceps or the food, but was not afraid of me. He hopped toward me as the others did, hopped on to my hand, then off again.

In 1940 I had an illuminating experience in this matter of nest leaving. When the 3 young Song Sparrows were 9 days old I left them for 2 hours in the care of others; on my return I found them out of the nest, which I then destroyed. It was soon evident, however, that the leaving had been premature; *psychologically they were still in the nest stage,* for they stood pressed close together; they stretched up as high as possible to beg; they turned around to defecate. That night they slept in a Towhee's nest in which I placed them. The next morning they were definitely in Stage 4.

2. *Feeding Reactions*

The young bird is still almost as dependent on its parents for nourishment throughout this stage as if it passed the time in the nest, as do so many passerines that nest in protected situations.

a. Behavior towards the Parent-Companion

In the nest each bird has to make itself conspicuous upon the arrival of food; during the last days each stands as high as it can—to heights of 11 and 14 cm.—and makes loud begging noises. After leaving the nest there is normally no longer any competition between the young birds, yet each must inform the parent of its whereabouts and stimulate it to bring it food at short intervals. The chief means is the location call. When food arrives the young bird assumes a horizontal position, its head about 4.5 cm. from the ground. Sometimes it bobs up and down with a bowing motion and it may give a soft *tit-tit-tit.*

The contrast between the technique of begging before and after leaving the nest was well shown June 24, 1939; D, 10 days old, had left the nest at 6:45 A.M., but had returned to the edge of the strawberry box holding the nest in which were F and S, 9 days old. When I fed them at 7:30 I noted, "S and F stand to their full height when begging; D merely *sits.*"

At the time of leaving the nest I have had difficulty in feeding all the birds. All begged from one another, starting at 8 and 9 days with the Massachusetts birds and 9 days with the others. It is difficult to state how long this begging lasted; it was most prominent just before and after leaving the nest; my last record with the Michigan birds was 14 days, with the Massachusetts birds in 1938 16 and 17 except for one sporadic case when Y was 25 days old (see p. . . .) while in 1940 A (a weakling) begged from T fairly regularly till 24 days old.

On Aug. 3, the day the 1938 brood left, I noted "My whistle means nothing to them, the forceps nothing. They seem bound to feed from a parent bird. They beg constantly from one another, especially from a bird higher up." From the time they left the nest—5:50-6:20—it was several hours before I could get them to eat readily. At 11:08 and 11:50 they ate fairly well; the next day they were "much easier to feed."

Aug. 4. 5:00 P.M. Y is bowing; now all three are bowing to one another; go down, then up; gape from a crouched position. Jump on one another's backs.

It was a distinct surprise to me that F, S and D, when brought to Chicago on June 28 at the age of 13 and 14 days, did not beg from the adult, Y, when he came over on their cages; it had been 7 and 8 days since they had been fed by a Song Sparrow. The Cowbird, aged 17 days, begged immediately and persistently from Y, although without success; it had been fed by Chipping Sparrows till the age of 7 days and again for 6 hours at 9 days. On June 29 the Song Sparrows begged to the swing in the cage and to a brother in it.

b. Independent Feeding Reactions

It was not until the age of 12 and 13 days that the hand-raised Song Sparrows started with exploratory pecking. Until then bills had had two uses: they were opened for the reception of provender, and they were employed for preening the feathers.

Aug. 4. (B and R 11 days, Y 10) No interest in insects in their cage.

Aug. 5. Y *wipes his bill.* The first time that Y has shown an instinctive action first.

A big buzzing fly evokes no interest in B, although I bring the little bird near it.

Aug. 6. (12 and 13 days old) 12:35. Y *pecked at a spider* on the tin can top. B pecked at a grasshopper on the end of the forceps.

1:50. (I had provided clover leaves dipped in water each day since they had left the nest, with no result.) I offer R water on my finger; he *drinks a bit.* B drinks and drinks from my finger, then wipes his bill.

2:10. B takes one drink from a bowl of water into which he had accidentally hopped.

R is distinctly interested in insects that move.

3:53. Hold B up to the window screen; he *catches small creatures* that have come from the net and *eats them. He pecks at all sorts of things*—R's and his own toes, R's cheek, my finger. Y pecked a little at screen insects, but not in earnest.

Aug. 7. (13 and 14 days) 9:20. Y pecks at motionless insects on the screen, but drops them. When satisfied, the birds nibble at the egg and bread at the end of the forceps.

10:30. B eats egg out of Janet's hand. R and Y both take water from my fingers. B pecked my ring.

Aug. 8. (14 and 15 days old) They know the net as the source of food and come to it quickly. They hurry over to where a brother is being fed. They bill pieces of grass, pulling at the heads and working at clover tops. R pecks at spots on the floor.

12:10. B *got an insect himself from the net.*

3:20. Y gets a small insect and eats it. B works at a piece of bread fastened in the cage.

5:00. B is *beating his prey.* He explores the outside of the cage, picking up tiny pieces, pecking at the cage and his own toes. He runs his bill along the water dish and thus *gets a drink.* He takes the side of the dish in his bill again and again, in this way getting a little water.

R hops into the food saucer and *eats the bread and egg.* He tries to get water from the outside of the water cup.

B cleans off the screen for me, pecking at every insect and eating many tiny beetles, all motionless. Tries a stink bug, drops it and wipes his bill. Tries two others in quick succession.

Aug. 9. (15 and 16 days) R drinks properly, bending over and getting water from the cup.

B eyes a 15 mm. beetle that walks past him.

Y is as interested in motionless objects as moving ones. Picks up grass seed-cases, bills them and drops them. His eye is caught by a diminutive beetle that flies towards him, picks it up, bites off the tiny head and drops it. Pecks at a dropping; rolls it around and around in his bill, then drops it.

R *scratched in dead grass.*

The Michigan birds were a little more precocious about feeding themselves. At 12 days D picked up a piece of bread from the forceps and ate it, at 13 days F picked up egg and at 14 he drank from the water dish. (I had given them water from my finger from the age of 10 and 11 days.)

The experiences with the hand-raised birds show that a beginning is made in this stage in responding to and capturing animal food (first instances coming at 12 days with Y, D and T), and in manipulating grasses and weed stalks.

Three records of T are of interest: at 12 days he paid no attention to quiet and moving insects on the window screen in the morning, but at 5:30 P.M. pecked at two. At 15 days he chased a bug 3 mm. in length, caught it and ate it, and also pecked at a small grasshopper. At 16 days he picked up insects from the table.

3. *Flight*

The first flights appeared at 10 days with the Massachusetts brood in 1940, 11 days with the Michigan birds and with Y, and at 12 days with B and R, the day's delay probably being due to the fact that I kept the first brood in the cage most of the time for a number of days. Y flew 60 cm. at the first trial, D 30, F and S about 60; B flew about 45 and R about 60. At 12 days D flew 120 cm. and at 13 180, while R flew 270 cm. Flying improved rapidly so that by the age of 16 to 17 days all were flying well.

At first there was some difficulty in landing. I noted on June 29, 1939 when D was 15 days and F 14 that they "flew well, but are not good at landing."

The birds showed a strong tendency to land on one another, particularly in the first days after they left the nest. They also persistently landed on me.

4. *Bathing Reactions*

Four of the hand-raised birds showed their first bathing reactions during this stage, the others at the beginning of the next.

When B and R were 13 days old I provided them with a shallow bowl of water. R happened to jump into the dish but hopped right out. B also hopped in accidentally; he crouched; beat his wings (motion 1, Chapter III, B, 8); then drank. He hopped out, shook himself, fanned his wings, wiped his bill, shook himself again, preened and fell off the table.

An hour later R went through wing movements of bathing (motion 1) although he had given no reaction to the bath itself, which at this time was 40 cm. distant.

The next day I offered the three birds the bath, but none responded, even though I stirred the water with my fingers. Results were similar the following day, except that B drank twice from the dish.

When B was 16 days old, he took 8 drinks from the dish, then climbed in and took a conventional bath (motions 2 and 1) dipping in his head and beating his wings, using them simultaneously.

The next year the young birds paid no attention to a dish of water in Michigan, but the morning after their arrival in Chicago, when D was 15 days old and F 14, D hopped into Y's bathing dish which was near the bamboo cage; at once he crouched and took a conventional bath (motions 1 and 2). I put F in the dish; he crouched and went through the bathing movements rather uncertainly. Neither bird shook and preened himself afterwards, but the next day D shook himself thoroughly.

5. *Escape Reactions*

Since I was not able to imitate the fear note (***tik-tik-tik***) of the adult Song Sparrow, escape reactions in these young birds depended on innate patterns. Situations evoking such reactions during this stage were threatened capture, movement of the immediate environment, and rarely sounds. The usual response was the scream, and if possible, fleeing. Although the scream is highly stimulating to the parents, as a rule it did not seem at this stage to bring a reaction in other young birds.

At 10 days R screamed upon catching his foot in a weed stalk. From 10 to 13 days the birds sometimes responded with a scream to my picking them up; this happened twice when I merely touched their feet. Once when T hopped on 10-day old A, A screamed. When S at 13 days was stepped on by a child, he screamed and rushed away. When I leaned down and tried to get the 15-day B from a chair rung, he flew with a scream.

From 10 to 14 days I have 6 instances of immediate response to my changing paper or moving ferns in the cage or moving the net; in each case the birds attempted to escape, 4 times screaming.

When Y was 16 days old, he froze as B nearly fell off the ridge pole of the bamboo cage, making a great scratching. Although sneezing, door slamming and scraping of chairs over the floor were ignored, the 15-day birds were disturbed by the sound of a truck.

When the Michigan birds were brought to Chicago at the age of 13 and 14 days, they liked to fly to the top of Y's cage; although Y would peck their feet and pull out their tail feathers, they did not learn to avoid the cage until over 3 weeks old.

6. *Vocalizations*

The most characteristic note of this stage is the location note—***ick*** or ***eep***—given by the bird when hungry. The soft feeding note—***tit-tit-tit***—may be much used under natural conditions. ***Weech,*** a cry of pain, was heard from the Massachusetts birds at times, from 12 days on, when jumped upon by a brother, and from the Michigan birds from 15 days when attacked by Y, but neither of these situations would be apt to occur in nature. The scream is occasionally used as mentioned above.

A note—***pit***—that seemed to have no special significance appeared at 12 days with each of the first brood of Pelham birds: it was seldom used and not heard after 15 days. At 21 days D uttered ***putt, putt,*** but this note disappeared at once.

Singing came very early: at 13 days with R, 14 with B, and 15 with F. It was whispered and warbling in nature.

G. THE FIFTH STAGE: FROM FLIGHT TO INDEPENDENCE

The fifth stage of development lasts from the age of 17 to about 28 days; during this period the young birds gradually become independent of their parents. They master the techniques of procuring their own food, both animal and vegetable; they come into contact once more with nest mates and for the first time with strange birds; they may learn from parental example something as to what to fear and what not to fear; and they acquire most of the adult notes of the species, except as regards the song.

With striking regularity the young Song Sparrows on Interpont came out of hiding one week after leaving the nest, their tails half grown and adult weight almost attained. During the fifth period the tail practically finishes its growth, while the wings do likewise, increasing from about 55 mm. at 16 days to 62-65, according to sex, at 30 days. In the previous stage the young sit and call; now they actively pursue their parents for a week or ten days, and from the age of 22 to 26 days make a practice of popping up beside their father each time he sings, often landing on top of him. The latest age at which I saw a bird fed by its father was 30 days (1M).

With the Massachusetts birds in 1938 there was some advance in flying at 17 days, and frolicking appeared on that day, but the marked change came in social behavior, for an anti-social or threat note was first heard, and antagonism, as shown by the open bill was unmistakable. At 18 days they first pecked each other.

From the age of 25 to 30 days these birds were taken by automobile from Massachusetts to Chicago, a distance of some 1,500 kilometers. All this time it was necessary to keep them confined in the small bamboo cage, whereas before they had had the freedom of a large room. Most of the time they were in the automobile, but in southern Ohio I carried them about in the fields. Here they saw and heard Song Sparrows for the first time since they had been taken from the nest; there was some singing to which they seemed indifferent. To the vigorous scolding—*tchunk*—of a parent Song Sparrow they listened with crests up and answered *tsip*. (*Tchunk* was not yet in their vocabularies.) Later the same situation brought out a few *tsips;* B raised his crest a little, but R was sunning himself on the floor of the cage.

1. *Feeding Reactions*

The young bird in this stage is much more aggressive in demanding food from its parents than in the preceding stage, although at the same time it is acquiring the ability to feed itself.

a. Behavior toward the Parent-companion

The hand-raised birds, adequately fed by me at frequent intervals (B, R and Y were given 14 full meals when 16 and 17 days old) and having egg yolk, bread and ant eggs always before them, were much less demonstrative in their begging behavior than the wild birds.

(1) The Hand-raised Birds

Aug. 10. (17 days) B and R fly to meet me and the dish of food. R bows, gapes and says *tit-tit-tit* as B returns.

Aug. 20. Y begged from B who had flown up on the side of the cage in which all three were confined.

Aug. 23. (29 and 30 days) They do not gape to each other, but do to the forceps or my hand if it holds a grasshopper. Flutter one or both wings.

Aug. 27. (33 and 34 days) They still gape and flutter wings when I give them grasshoppers.

Aug. 30. (36 and 37 days) I tested them with mealworms held in the forceps and my best whistling; only R fluttered his wing.

Wing fluttering did not last so long with the Michigan birds; D and F had given it up at 28 days and S a few days later.

On the afternoon of July 16, 1939, Dr. L. H. Walkinshaw caught for me a young Song Sparrow (N) which I judged to be about 17 days old; its tail measured 30 mm., its wing 52. At first I fed it forcibly with mealworms; at 1:00 the next day it opened its mouth and ate readily, *but only when firmly held in my hand.* On July 19 it ate from the forceps while standing in the cage, but made no attempt to pick up food. On the 20th it fed from the dish, but would still eat when held in my hand.

It was not until July 19 at 3:00 P.M. that I let it free in the study. While in the cage it gave the location call to all the Song Sparrows (D, F and S were a month old) that came near, and tried to get out to them. Soon after it was free it began to gape to the young Song Sparrows and later to pursue them with fluttering wings. The next day it continued to follow them with persistent *yeeps.*

3:30. F took a bath, then flew to Y's cage. N rushed to him, begging. He responded with a peck, but N still begged with open bill. N is fluffy and looks twice as big as the pygmy F after a bath.

(2) The Wild Birds

In 1929 as I was watching 1M and 4M busied with their fourth nestings, I had opportunity to see the activities of their young from the previous brood. Calling with the location note—about 30 times a minute—pursuing parents, landing on parents, begging with fluttering wings and loud notes, all these were prominent until the age of 28 to 30 days. At this latter time 1M's new family hatched; he may have fed the well-grown young early in the morning before he knew of the happenings in the nest. These young continued to call at intervals during that day and the next. Young birds of 33 and 34 days met their father 1M at the feeding station; each time the young bird flipped its wing, but gave no note; 1M hastily left.

Young were not always demonstrative; I once noted 4M feeding 2 young 20 days old that neither fluttered nor made any sound.

I have a number of notes on the position taken by the young when begging: 17 days, assumes horizontal position; 25 days, squats; 26 days, bows and bows, giving begging notes; 28 days, bows in a ridiculous manner. Interestingly enough, a bird of 29 days was feeding itself at the station, in the meantime *"constantly squealing and fluttering one wing."*

b. Independent Feeding Reactions

(1) The Hand-raised Birds

At 17 days hand-raised birds fed themselves readily from the egg and bread in their dish.

Aug. 10. (17 days) B and R work on canary seed; manipulate and manipulate them, then drop them. R swallows at least one whole. At length succeeds in shelling one after many attempts; eats half the kernel, then picks up the shells and eats them.

Aug. 11. A large stink bug comes towards R; he looks at it uncertainly, then moves out of its way.

Y works and works on canary and rape seeds, but doesn't succeed in shelling them. Occasionally swallows a canary seed whole after much manipulation.

Aug. 12. (18 and 19 days) R and Y are able to manage whole mealworms, pecking at them, beating them, and swallowing them. Y chases a grasshopper. Y *scratches* on the paper.

R mouths rape seeds for 12 seconds; then may drop them or eat them. B also mouths them.

Aug. 15. (21 and 22 days) Still don't shell seeds. Catch insects better. They avoid large and brightly colored ones.

Aug. 20. (26 and 27 days) They *shell seeds* for the first time; they were not offered them on the 18th and 19th. B eats gravel out of my hand.

Aug. 23. (29 and 30 days) They may take a small grasshopper by the head, then apparently by means of their tongues get it farther into their mouths so they can swallow it. They take food from each other's bills a good deal, a sizeable grasshopper changing beaks many times before finally being swallowed. They never stand on prey to hold it, and cannot cut it with their beaks. Beat it to some extent. One will take the insect out of his brother's bill, then perhaps the third will seize it and there will be a tug of war. There seems to be no resentment on the part of the robbed bird.

(32 and 33 days) They pursue hopping grasshoppers. Canary seeds are thoroughly shelled; the rape is ignored.

As for A and T at 22 and 23 days I noted: They will not touch orange and black lady beetles. They now avoid stink bugs after several trials. They seldom touch ants; if they do pick one up, they usually drop it. T pecks at a small grasshopper; it leaps; he pursues it; it leaps again; he dashes and seizes it. He starts to peck at a lady beetle, but refrains.

At 24 days T was on top of the bamboo cage and dropped a grasshopper through the bars; 3 times he tried to squeeze head foremost through the bars; then hopped down and entered the cage. The same thing happened the next day.

I first gave D, F and S canary seeds at 18 and 19 days; they mouthed them and dropped them. Gravel was ignored. They did not shell seeds until the age of 32 days.

(2) The Wild Birds

19 days. 1M's 3 young are all together. One gets a drop of water from a leaf; another finds a seed.

21 days. One tried to catch an insect, but failed.

From 23 days they came to the feeding station and fed themselves but if a parent appeared they at once started to beg.

2. *Bathing Reactions*

Bathing was first seen in the fourth period with 4 of the birds—at 13, 13, 14 and 15 days—but at the start of the fifth period with 3 others—17, 17 and 18 days. A new movement appeared in this period.

Aug. 10. (17 days) B took a thorough bath, going through the ordinary movements again and again. R tried to take a bath in the drinking cup (4 cm. square, 3 cm. deep); he wiped his bill on the edge, put it in the water and shook the water, puffed himself out and got one foot in.

Aug. 11. Both B and R take thorough baths in the bowl, R getting himself drenched.

Aug. 12. All three bathe in the bowl, this being Y's first trial; he gets himself very wet. Later R tries to get into the drinking cup for a bath, but takes a drink instead.

Aug. 13. Two crowded in together to bathe.

R (21 days) gave a *new movement* in bathing; he threw water first with one wing, then the other.

July 3, 1939. (F and S 18 days) F and S take "baths" in the water cup; F is now dipping his head into the water, while S is performing *bathing movements on the floor of the cage*—his first bath.

July 4. S on the edge of the water bowl; fell in; started to bathe, but hopped out and *went through bathing movements on the paper next the bowl;* performed them 8 times.

Later S takes a bath on the edge of the bowl; all he gets in is his head, but he goes through the movements in excellent form.

(23 days) S puts his head into the drinking cup and goes through bathing movements.

The next day I removed the bowl 12 cm. in diameter and gave them a pie pan 20 cm. in diameter. Almost at once D and S took a social bath—S's first proper bath so far as I know. D (25 days) gave the *alternate movement* with his wings. The birds were still not expert at drying themselves.

In 1940 T at 15 days paid no attention to the dish of water, even though he walked through it twice. Two days later he tried to get an ant "egg" that was in the middle of the dish; in this way he got his first real drink; he tried 16 times, each time getting a little water and drinking in proper fashion. He puffed out his feathers, stepped into the water, crouched and went through motion 1 (see Chapter III) many times, although he did not crouch enough to get his wings very wet. He dried himself skillfully, shivering his wings, shaking and preening. At 21 days he first showed the alternate movement of the wings.

3. *Sunning*

The first time I saw sunning with any of the birds was with R at 29 days. The Michigan birds at 18 and 19 days were "very contented in the sun, but didn't 'sun' "; all did so at 35 and 36 days. A first sunned at 38 days.

4. *Frolicking*

It was at 17 days that R and Y first showed this activity, while B and T did so at 18 days.

Aug. 10. R "plays", turning suddenly around, flapping his wings and jumping to another spot.

Aug. 11. Y rushes at his brothers, dashing hither and yon. B also "plays", making short and sudden turns.

Aug. 15. They are very playful now, tearing about over the floor.

This activity was often seen except during the 6 days of the journey when the birds were closely confined.

With the Michigan birds frolicking did not appear until 26 days with F and S and 33 with D; none of them indulged in it often.

5. *Escape Reactions*

It is probable that it is during this period that the young birds are conditioned by parental behavior to some extent as to what to fear and what not to fear.

a. The Hand-raised Birds

The fear note—*tik-tik*—appeared at 19 to 21 days. R and B at 21 days, Y at 20 days, gave it with compressed feathers as they stood looking out the window; the only unusual object I could see was a child walking up the path. S gave it at 20 days when I started to put newspaper where he was standing. Interestingly enough there seemed to be no external stimulus for its first appearance in T; when 19 days old he suddenly elongated himself, crouched down a little with his feathers compressed, looked up and said *tik-tik;* then he assumed a normal posture and yawned.

With the hand-raised birds the scream was not recorded during stage 5. There was only one instance in which "threatened capture" played a role: T was perched on my hand and I touched him with my thumb; he elongated himself, gave a cry and leaped off. Movement of the immediate environment—changing paper or vegetation in the cages—brought immediate fleeing responses.

As to sounds, on two occasions at the chatter of a red squirrel, R, B and Y (20-23 days) dashed to cover or froze. At the snarl of an alley cat D, S and F (19, 20 days) rushed to cover. T and Y at 18 days cowered at hearing the fluttering wings of a brother falling to the floor. T (20 days) dashed for cover when I tore a paper napkin.

A clap of thunder and the scream of a Red-shouldered Hawk brought no response from 25--26-day-old birds.

When the first brood was taken west, *large moving objects*—automobiles, horses drawing a wagon—induced attempts to escape from the cage. When small children closely approached the cage, the birds showed signs of disturbance. A half-grown chicken came within a few centimeters and the birds tried to escape. Perhaps in both these cases the *close proximity of strange objects* was the disturbing factor.

When the cage was taken into the open (B, R and Y 27-29 days), at first the birds compressed their feathers and froze at the sight of birds flying over; later they intently watched Crows and Nighthawks passing above them.

Three experiments were made with cats on this trip: a black and white cat was brought within 1½ meters without eliciting any response from the birds; later in the day another cat was eager to get at the birds, but they did not appear to notice it; 3 days later a tiger cat was ignored. No attention was paid to dogs under similar circumstances. The different reaction to the harmless chicken and predatory cat was probably due to the difference in proximity. No attention has been paid by the Song Sparrows to cats seen out of the window.

b. The Wild Birds

On May 22, 1929, I noted that 1M's and K2's baby that had just come into the open was "a wild little thing, much more timid than its parents." On June 22 4M's 18-day-old young was pursuing its father; they unexpectedly came very near me; 4M gave a prolonged ***tik-tik-tik-tik-tik***. Later the little bird was calling vigorously—36 times a minute—near me; 4M came, gave a song, then a loud fear note; ***the baby stopped its cries instantly***. 4M continued with his ***tik-tik-tik-tik-tik***, and succeeded in driving the little bird from my vicinity.

6. *Social Behavior*

In nature fledgling Song Sparrows are usually separate until the age of 17 days when they may meet their nest mates again.

a. The Hand-raised Birds

Social behavior that became apparent at the age of 17 to 19 days was predominantly anti-social.

Aug. 10. (B and R 17 days) B opens his bill at R and Y. Later B is singing with his eyes shut; greets R with a little twitter.

Aug. 11. All 3 open bills at one another. One hopped on top of another; a loud and long twitter ensued. Y gives the queer twitter. Y jumps on top of R; R pecks at him.

Aug. 12. *First fight.* B alighted on the roof of the cage where R was perched. They went for each other with *outspread wings* and *outspread tails;* pecked each other. R drove B off.

Aug. 14. Y in the cage; B dashed in after him; Y threatened him with outspread wings. A little later B goes in and Y gives the twitter.

Aug. 16. Another fight. Y was on top of the curtain and R flew there and they started to peck back and forth. R spread out his wings and tail (I couldn't see Y well); they opened bills, then bumped bills. Stood in queer threatening attitudes. Fought again, giving the twitter.

On the journey west they fought occasionally, particularly R and B.

With the Michigan Song Sparrows fighting first appeared as defence from the attacks of the adult Y. When it was evident that the little birds would not learn that it was dangerous to alight on top of Y's cage, I covered it with newspaper, so it was only when they perched on the edge that they were vulnerable. When D was 19 days old he appeared to peck at Y.

July 4. (D 20 days, F and S 19) F is sitting on top of Y's cage, giving location call. Y pulls out a bunch of feathers. They *won't learn to avoid danger!*

9:30. Y is fighting D who is above him. D *fights back*. D is now settled on one corner of Y's cage—tempting fate. Y does not give the threat note, but shows territorial behavior, puffing, wing waving and singing (see Chapter XII). Pecks D and pulls out feathers; D squeals and remains. Y pulls out more feathers; D squeals and remains. I remove him.

F and the Cowbird are resting side by side on top of the bamboo cage; have a pecking encounter; then settle down in peace.

D and S peck at each other.

F is on top of Y's cage; when Y threatens him, he threatens in turn with open bill.

July 5. D no longer alights on top of the big cage. F is there; Y slipped up and bit his foot; F *weech, weech, weech;* then *tsip, tsip,* but *stays.* Later F is napping there; Y pulls out a feather. F squeals, threatens Y, and still remains.

D and S have a fight; S says *weech.*

July 6. (22 and 23 days) S and F have only a few tail feathers left, thanks to Y. Later in the morning S has no tail at all. The two were fighting, opening bills at each other and pecking.

D was on the rim of the big cage defying Y with open bill. When D's attention was elsewhere, Y sneaked up and pecked him.

July 7. D and Y have a fight through the wire with spread tails, pecking each other. D spreading his wings.

F is fighting S.

July 8. D and Y are fighting each other. Then D turned his side and Y pulled out a tail feather.

July 9. D fights vigorously with Y.

July 12. S flies up near D (28 days); latter gives the threat note, the first time I have heard it with this set of birds.

July 13. (D 29, F and S 28 days) Up till now Y had been kept caged, but this morning I released him while F was out.

Y approaches F who seems indifferent; pecks F; F raises his wings and rushes at Y who retreats! Later F defies him and he leaves. This happens again.

Y alights on the bamboo cage: D, shut up within, gives the threat note. I let S and D out. S makes a circling flight; Y attacks him, he squeals, but defies Y from the sumach branches.

D flies and is attacked by Y. There is a fight on the curtain rods; Y hits D twice; the latter alights panting and I put him into the small cage.

Y may have had an inhibition against injuring the bob-tailed S and F when they were stationary. Movement, however, stimulated his attacking reaction. (Lack, 1939b:207, noted that European Robins chased other species only in flight.) D, who possessed a tail and looked much like an adult, received no mercy from Y. In 1940 T first pecked at A at 20 days, and first used the threat note at 21 days, A using it at 20 days.

b. The Wild Birds

As to wild Song Sparrows, at 25 days one of 4M's young was seen to drive another; at 26 days one of 1M's young was driven by 4M; while at 28, 29 and 30 days 1M's young were alternately fed and pecked by their father.

7. *Vocalizations*

Most of the notes common to the adults of both sexes appear during this fifth stage. At the same time the location note and begging notes are prominent. Instead of the loud scream, *weech* is used. The threat note appeared at 17 days with the first brood; the fear note at 19 days with T, 20 days with Y and S, 21 with B and R; the call note *tsip* at 20 days with Y and F, 21 with B and R, 25 with T; while the "ordinary" note *tchunk,* sometimes denoting a moderate amount of alarm, at other times perhaps expressing self-assertion, appeared at 28 and 29 days.

Three of the birds started to sing during this period: Y at 17 days, T at 19, D at 20.

H. SUMMARY

1. The development of the young Song Sparrow from hatching to independence can be divided into 5 stages, 3 of which are passed through in the 9 to 10 days spent in the nest.

2. The first stage embraces the first 4 days of nest life; it is characterized by rapid growth and the start of feather development; the chief motor co-

ordinations are the food response and defecation; the first food call has been heard at 2 days.

3. The second stage—5 and 6 days—is one of rapid growth in weight and feathering and the establishment of temperature control; the eyes open, and the beginnings of several motor coordinations are seen—standing, stretching up of the legs, and the first intimations of preening.

4. The third stage—7, 8 and 9 days—shows rapid development of motor coordinations; cowering typically appears; the birds are well covered with feathers and are able to leave the nest at any time. They stretch their wings up and sidewise, they scratch their heads and shake themselves, they fan their wings and flutter them when begging. New notes appear—the scream, the location call, and several new feeding notes.

5. In the 9 to 10 days of its nest life the Song Sparrow has changed from a nearly naked, blind, and practically cold-blooded creature of about 1.5 grams, absolutely dependent on parents and nest for food, warmth and shelter, to a warm-blooded, well-feathered individual of 15 to 18 grams, independent of nest and nest-mates, able to care for its feathers, to move about, to escape enemies to some extent, to inform its parents of its whereabouts so they can feed it, and to respond to its parents' notes of alarm and fear.

6. The fourth stage starts at the age of 9 to 10 days when the fledglings leave the nest. It is spent in retirement by the young bird away from its nest-mates, is characterized by silence (except when calling for food) and by general immobility. The chief advance is the acquisition of flight. A new method of begging for food appears: the birds no longer make themselves conspicuous, but call their parents and beg from a horizontal rather than vertical position. One brood was "psychologically" still in the nest for a day after leaving it. Sleeping in the adult position typically appears at 10 days. A beginning is made in independent feeding activities: wiping the bill, pecking at objects, picking up food, catching insects, working at grass heads, and scratching the ground. Bathing reactions appeared in several of the hand-raised birds. Singing appeared with 3 birds at 13, 14 and 15 days.

7. The fifth stage, starting with the attainment of flight and ending with independence, lasts about 10 days. At 17 days Song Sparrows in Ohio come out from retirement; they come into contact again with nest-mates and soon pursue their parents for food. They may beg from their parents until they are 5 weeks old, but the latest that I saw one fed was at 30 days. The Massachusetts Song Sparrows attempted to shell seeds at 17 days, but were not able to do so until the age of 25 days. The complete bathing technique, consisting of 3 chief motions, is attained during this stage. Sunning was first recorded at 29 days. Frolicking was first seen at 17 and 18 days. The fear note appears at 19 to 21 days. This fifth period may be the chief time when the young are conditioned by parental behavior with regard to what to fear and what not to fear. A note of antagonism was first noted at 17 days; pecking others at 18 days; threatening postures and fighting at 19 days. *Tsip,* denoting a social bond, first appeared at 19-20 days. The characteristic adult note *tchunk* was heard at 28 and 29 days.

8. The day by day appearance and duration of the activities of the Song Sparrow during the first month of its life are shown in Table III divided into the 5 stages.

TABLE III

APPEARANCE AND DURATION OF ACTIVITIES IN THE YOUNG SONG SPARROW

(—) = regular occurrence; (-) = occasional; (.) = exceptional

Stage	I				II		III			IV							V												
Days	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
I—																													
Gaping	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Defecating as nestling	—	—	—	—	—	—	—	—	—																				
Food calls	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-	-	-	-	-	-	-	-
II—																													
Preening					-	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Yawning					-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Standing on tarsi					-	-																							
Stretching legs up					—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Standing on feet						-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scream					.	.	-	-	-	-	-	-	-	-															
Cowering and freezing						-	—	—	-							-	-	-	-	-	-	-	-	-	-	-	-	-	-
III—																													
Location call					.	.	.	.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-	-	-	-	-
Stretching wings up							—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stretching sidewise							—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scratching head							—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fluttering wings								-	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	-	-
Both wings down								-	-																				
Fanning wings								-	-																				
Shaking self									-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IV—																													
Leaving nest								.	—	—	.																		
Hopping and walking								.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Landing on others									-	-	-	-	-	-															
Bowing when begging									-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sleeping as adult										—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wiping bill										-	-	-	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Flying										.	-	-	-	-	-	-	—	—	—	—	—	—	—	—	—	—	—	—	—
Landing										.	-	-	-	-	-	-	—	—	—	—	—	—	—	—	—	—	—	—	—
Exploratory pecking												-	-	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Picking up food												.	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Watching prey												-	-	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Catching prey													.	-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Drinking													-	-	-	-	—	—	—	—	—	—	—	—	—	—	—	—	—
Bathing													-	-	-	-	-	—	—	—	—	—	—	—	—	—	—	—	—
Singing													-	-	-	-	-	-	-	—	—	—	—	—	—	—	—	—	—
Scratching ground																-		-	-			-		-		-		-	
V—																													
Frolicking																	-	-	-	-	-	-	-	-	-	-	-	-	-
Threat note																	-	-	-	-	-	-	-	-	-	-	-	-	-
Fighting																			-	—	—	—	—	—	—	—	—	—	—
Fear note																			-	-	-	-	-	-	-	-	-	-	-
Tsip																			-	-	-	-	-	-	-	-	-	-	-
Shelling seeds																									-	—	—	—	—
Tchunk																												—	—
Sunning																													-
Days	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29

CHAPTER III

Discussion of the Activities of the Young Bird

The activities of the young bird may be grouped under 6 general headings: A, those concerned with nutrition; B, care of plumage and other motor coordinations in situ; C, locomotion; D, escape reactions; E, social behavior; and F, vocalizations. (See Table IV at the end of this chapter.)

In correlating these with the 5 stages of development, we find that activities concerned with nutrition are of paramount importance throughout all the stages, while social behavior of some sort is present continuously, being most prominent during the fifth stage, and the same is perhaps true of vocalizations. Coordinations concerned with the care of plumage, etc., are first seen in the second stage, and are most numerous in the third stage, yet new coordinations appear in the fourth and fifth stages. Coordinations concerned with locomotion appear in the third stage and are prominent in the fourth and fifth. Escape responses typically appear for the first time in the third stage.

All these activities will be described as they occurred in the Song Sparrows, and comparisons made with observations on Common Redstarts, Serins, a Cowbird and Cedar Waxwing by myself, and on many other young birds, particularly passerines, as recorded in the literature in this country and abroad. Discussion of learned behavior in connection with the activities will be reserved for Chapter IV.

A. ACTIVITIES CONCERNED WITH NUTRITION

During the first 4 stages the passerine depends on its parent-companion for food, but during the fifth stage it gradually becomes independent.

1. *Behavior toward the Parent-Companion*

The food response to the parent consists in gaping, wing movements, special body movements and a variety of notes.

a. Gaping

There is no specific word in English for this behavior, since "gaping" is often used with a connotation of yawning. The German word *sperren* also has a variety of meanings, but is employed by ornithologists in this specific sense. Rand (1941c) uses "begging", but to my mind, "begging," like "food response", may include wing movements and cries as well as the wide opening of the mouth. Gaping is characteristic of Passeriformes, Cuculiformes and Upupidae according to the Heinroths (1924). Stresemann (1927-34) includes Picidae, but Sutter (1941), working on the Wryneck, points out that here gaping is oriented much earlier than with passerines, the 3-day nestling making searching movements for the parental bill and snapping at it in a way impossible for a passerine.

There have been several studies on gaping in young birds. Kuhlmann (1909) made experiments on the reactions of Red-winged Blackbirds and Brown Thrashers to artificial stimuli; he found that they gave the "food reaction" to a hiss from the first to third day, to a whistle and hand clapping on the fourth day, to jarring and imitation of the parental *cluck* from the first to seventh day.

Herrick (1935:281-283) compares the nestling "to an electric toy of which the action is purely automatic." He tested a 20 to 30-hour old Brown Thrasher by putting it on a piece of cloth and scratching the cloth; he obtained 100 successive food reactions in 13 minutes, "each representing the entire complex of movement," each lasting from 3 to 15 seconds "according to the strength of stimulus received". He found an early association of the "food-response" with the nest, birds of 6 or 7 days refusing to beg when out of the nest.

In an experimental study on Song Thrushes and Blackbirds (*Turdus ericetorum* and *T. merula*) Tinbergen and Kuenen (1939) analyzed the releasing and directing components of gaping. For releasing gaping, gentle jarring of the nest was the most effective means, but rough shaking inhibited gaping. Touching the edge of the bill and imitating a puff of wind usually brought a response, but changing of lighting and temperature, and all sorts of sounds were ineffective. By means of ingenious cardboard models it was found that three characters were needed for the optical release of gaping: an object, larger than 3 mm., must *move* above the level of the eyes. As to orientation, although the eyes open at 9 and 10 days, gaping was still directed vertically; it was not until two or three days later that gaping was directed toward the head of the adult. The following characteristics were found necessary for directing the gaping: the head must be higher than other parts of the adult; it must be nearer; it must be a convex interruption in the contour and be divided from the body by an indentation.

Working on Starlings in Switzerland, Holzapfel (1939) concluded that gaping is an instinctive rather than reflex action, since it is released by a variety of unspecific stimuli, and since it appears spontaneously in newly hatched birds. The following releasers were most effective—touching the edge of the bill, gentle shaking, scratching sounds. Rough shaking, cold air, sudden change between light and darkness brought no result. After 11 days optical releasers were most important; from 11 to 17 days any movement brought a response, but after 20 days the birds gaped only to the forceps or objects resembling them. Hence the release of gaping in this last stage depends on a learned stimulus situation. As to orientation, although the eyes open at 10 days, it is not until 14 days that the bird will follow the forceps with its bill. With Choughs the eyes begin to open at 8-9 days, yet the birds gaped vertically until the age of 18 days (Schifferli and Lang 1940).

With the Song Sparrows touching the edge of the bill brought no reaction. All responded to uncovering of the nest and to jarring, but after 8 days they cowered at severe jarring. Movement in front of or above them brought a response from 7 days on. The Serins and Cowbird also reacted to motion above their heads, but this was not true of the hole-nesting Common Redstarts. The Ovenbird cowered at any kind of jarring.

At 7 days the Song Sparrows reacted to the sight of the forceps and to my whistle; at 8 days the Redstarts and Cowbird did so. The Cowbird responded to the approach of human beings, but the Song Sparrows did not until food was in sight. The Redstarts behaved differently; at 7 and 8 days they reacted to any sight or sound connected with people, even the shutting of a door. In the early morning my slightest movement in bed was followed by an explosion of begging calls from the nest beside it. After "fear" had appeared at 9 days, the birds became much less noisy; they did not respond to every shutting of the door, nor always to my approach, but my whistle had a definite releasing value. When the threshold was lowered by hunger, they still begged at every sight and sound connected with a human being.

With both Song Sparrows and Common Redstarts the eyes are fully open at 6 days; the former gaped vertically until 7 days, the latter until 8 days, at which time they gaped horizontally and followed the forceps. Woodpeckers beg when the light is suddenly shut off (Sherman 1910, the Heinroths 1924:312; Lehrman and Stephenson 1940).

The length of time that the mouth is held open increased during nest life with the Song Sparrows and then shortened markedly. This is shown by the following records with a stop watch: 5 days, 3 and 4 seconds; 6 days, 7 seconds; 7 days, 10; 8 days, 12; 10 days, 2; 11 days, 2. With the Redstarts the change came at about 12 days; at that time instead of gaping for an appreciable time, they darted their open mouths to the front of the nest, then closed them.

The height to which the bird raises itself when gaping increases and then suddenly decreases. With the Song Sparrows it came to 5 cm. at 5 days, 7.5 cm. at 6 days, 11 at 8 days, and 11 and 14 at 9 days; then 4.5 at 11 days. The Redstarts and Cowbird also crouched when they begged after leaving the nest. The Ovenbird begged horizontally in the open Song Sparrow nest while the Song Sparrows of the same age stretched to their full height.

When gaping for food, motion to or from the caretaker is inhibited; "the pattern of the parent-companion can indeed fly" (Lorenz 1935:195). "A shy bird in a large cage was easily caught by inducing it to beg" (Rand 1941c:221).

Heinroth points out that just before leaving the nest the young have little appetite (1924; 1930b:3); this was true of all the Song Sparrows I raised.

With birds taken before fear has developed, feeding from the forceps fits into the innate pattern, but later the bird has to be conditioned to the forceps held by the human being as the source of food. The Ovenbird, taken at 5½ days, gaped readily after 2 forcible feedings. In Chapter II the process of conditioning the Song Sparrow N, caught at about 17 days, to artificial feeding was described.

There were two similar experiences at Altenberg. The Common Redstart, WR, found in the grass one evening at the estimated age of 12 days, had to be forcibly fed the following morning. By noon when the other Redstarts began to fly about, he gaped twice. At 3:25 he gaped at one of his companions. I was then able to stimulate him by moving the forceps rapidly in front of him and by hitting him on the back, but tapping on the head was ineffective. By noon the next day he had become thoroughly conditioned to the forceps as the source of food.

A European Cuckoo about 3 weeks old, taken from the nest of a Black Redstart, responded to our attempts to feed it by defense reactions—spreading of wings and tail, shaking the body and trying to peck. As soon, however, as the Redstarts and Serins started to fly about nearby, the great mouth came open and was held open, sometimes turned toward the nearest small bird. The wings were not moved and the call was not loud, but the mouth is large and the buccal cavity red. I was able at times to get it to gape by tapping it on the head (small fosterers regularly feed this parasite by perching on its head), or by bringing a Serin perched on my hand near it. The next day it was kept on the porch; by afternoon it became fully conditioned to the forceps, opening its bill at its approach and swallowing the food. The following day I took it back into the room with the small birds, and it at once gaped in the former automatic manner.

The Cedar Waxwing (Nice 1941a) taken after it had left the nest (about 15 days old) did not gape to me; it either took the proffered food or kept its bill closed. It gaped readily to the 2 Song Sparrows a week older than it. When its gullet was filled to the brim with berries and it would take nothing more from me, its mouth would fly open in an apparently automatic manner if a Song Sparrow happened to hop up beside it. Some Starlings taken at 16 days never gaped, but from the beginning picked the food from the forceps (Holzapfel 1939:549).

The last record I have for gaping with the Song Sparrow is 37 days. Holzapfel experimented on the duration of gaping with Starlings: 14 birds aged 23 to 27 days were fed with the forceps only once a day; gaping lasted to the age of 35 days at the latest, the median age of last appearance being 27 days. Eleven birds were fed with the forceps every hour or two; one gaped typically until 77 days old, the median age at last appearance being 51 days. The author suggests that gaping is not merely a juvenile character, but that it is replaced by pecking for food and becomes latent, reappearing in adult life in those species where the male feeds his mate (see Lack 1940b). In such cases the female often begs in the same manner as a young bird with the same notes and same wing motions. Mrs. Laskey informs me that her hand-raised male Mockingbird, when 11 months old, revived his begging habit after a fledgling Robin had been installed in an adjacent cage. In California the resident race of White-crowned Sparrow spends 6 months raising 3 broods and young are cared for till 32-35 days of age; the migratory race fledges 3 broods in less than 4 months in Washington and young are independent at 25-28 days (Blanchard 1941). With a Loggerhead Shrike unnatural care prolonged begging for at least 6 months (Rand 1942).

b. Wing Fluttering

Wing movement as a releaser of the feeding reaction of the parent is seen in a great many altrices. With some species the wings are moved horizontally; with others the wings are raised vertically and moved through a large arc. Wings are sometimes used together, sometimes one at a time. Wing movement was first seen in the Ovenbird at 6 days, in the Cowbird at 7 days, in the Song Sparrows at 8 days, in the Common Redstarts at 11 days, and in a Hooded Crow at 10-11 days (Strauss 1938a). With all of my hand-raised birds wing movements were much more pronounced after leaving the nest than before.

The Cowbird begged with a lateral movement of the wings, using only the manus and carpus, except at the age of 11 to 12 days when the humerus also was involved. Examination of 3½ meters of moving picture film taken by Dr. M. D. Pirnie of this bird at 12 days showed that wing flapping occurred 18 times in the 28 seconds, each spell lasting from 3 to 6 frames, the median being 4. Since 16 frames are taken a second, this means that the wings were usually moved for a fifth to a fourth of a second, then kept quiet for perhaps twice as long before being again fluttered. The Cowbird nearly always used both wings simultaneously, whereas the Song Sparrows often used only one.

When the Redstarts were 16 days old I noted that wing fluttering well illustrates exhaustion with raising of threshold—at first much action, then less and less and finally none, all in one feeding session. Sometimes the wings are used alternately. Of the 3 elements in begging, wing action tires first, then the food call, then gaping. I fed the birds at 5:45 P.M.; for the first 3 mouthfuls all four fluttered vigorously; at the fourth three fluttered; at the fifth, two; at the sixth two to a slight extent; but the seventh mouthful no bird wanted.

With the Serins at about 18 days I noted that calling and wing action persist in full vigor throughout a feeding; gaping tires first, quite in contrast to the Redstarts.

The last wing fluttering was seen in a wild Song Sparrow at 34 days, in R at 37 days. The Redstarts "still gaped distinctly and with wing fluttering" when 24 days old, while at 40 days RR "fluttered his wing with a hint of gaping" (Lorenz, letter).

c. Bowing

The marked change in height and body attitude of the bird in the nest and out of it has already been mentioned, details being given for the Song Sparrows in Chapter II.

d. Food Notes

Begging and location notes will be discussed later in this chapter under "Vocalizations."

2. *Independent Feeding Reactions*

The acquisition of independence in feeding is a gradual process, a matter of experiment, of using the instinctive actions of pecking, seizing prey, shelling seeds, etc., on a large variety of objects.

Lorenz (1935:196) says: "Young birds which are about to begin to eat independently will at first feed themselves playfully, so to speak, when they are only slightly hungry. As soon as they become hungrier, they start to beg." The Heinroths (1924, I) and Holzapfel (1939) say much the same thing, while Rand (1937:39) notes of his Blue Jays, "Especially when very hungry they would not pick up and eat food, but continued to beg." The same was true with Curve-billed Thrashers (Rand 1941c).

a. Wiping the Bill

This activity appeared before independent feeding: at 11 and 13 days with the Song Sparrows, perhaps earlier than 11 days with the Serins, and at 14 days with the Cowbird and Redstarts. Its most common use is to clean the bill.

Wiping the bill is often a sign of distate (Mostler 1935, Steiniger 1937). Y wiped his bill after tasting ink; my hand-raised Bob-white did likewise after pecking into a drop of lather. Schantz (1939:164) writes that the adult male Robin "once ate a black swallow-tail butterfly (*Papilio polyxenes*) and evinced distaste by wiping his bill and gulping. Next day when he suddenly approached several of these butterflies congregated on the pink flowers of a prostrate *Saponaria* plant, he flung away a large mouthful of food and wiped his bill in the air and on the walk."

Parent birds typically wipe their bills after disposing of fecal sacs. An interesting observation was made on a male European Dipper (Eggebrecht 1937) on the ninth day of feeding young: the nest was kept scrupulously clean through the efforts of the female; the male would make as if to take a dropping, then draw back and run to the water and wipe his bill thoroughly, just as his mate did after carrying away excreta.

b. Exploratory Pecking

The first appearance of exploratory pecking has been noted in a number of altricial species: at 6 days in the Black-billed Cuckoo (Herrick 1910), 8 in the Ovenbird (Hann 1937), 12 in the Song Sparrow, 13 in the Common Redstart, 14 in the Cowbird and (probably) Serin, 19 in the Starling (Holzapfel 1939) and Curve-billed Thrasher, and 21 in the Blue Jay (Rand 1937). Holzapfel mentions the accuracy of this pecking from the beginning.

c. Picking up Food

Independent feeding was first noted with the Song Sparrows at 12 to 16 days, with the Serins at about 14, Bicknell's Thrush at 15 (Wallace 1939), Redstarts at 16, Cowbird at 17, Starlings at 19-21, and Blue Jays at 23 days. The Heinroths (1924) say that small passerines usually feed themselves to some extent by 23 days. Swallows do not leave the nest till over 3 weeks old; they may pick up ant "eggs" while still in the nest if these are strewn within their reach (M. Heinroth 1917).

d. Preying Reactions: Watching, Catching and Beating Prey

Detailed notes on these preying activities with the Song Sparrow are given in Chapter II. Interest in circling flies was shown at 13 days by both the Song Sparrows and Redstarts. The Redstarts, being largely fed on fresh ant pupae, had little experience with live insects, but the Song Sparrows came into constant contact with them. The first capture of an insect was noted at 13 days with the Song Sparrows, 16 with the Bicknell's Thrush, 19 with the Common Redstarts, and 29 with the Blue Jays. Beating of prey was first noted in Song Sparrows at 15 days, and at 17 days with the Redstarts (the "prey" being a flower of Norway spruce). *The Serins never showed any reaction to insects.*

e. Drinking

Although the Song Sparrows paid no attention to drops of water on weeds that had been dipped in water, they drank water eagerly from my fingers when it was first offered them—the Massachusetts birds at 12 days, the Michigan birds at 9 and 10 days. The drinking reaction in its entirety—the bill dipped into water and the head raised—appeared as a forerunner of bathing with B at 13 days, F at 14 days and T at 17 days, as well as with the Cowbird at 16 days and a Redstart at 18 days and a Serin at about 19 days. R drank at 16 days, one day before he first bathed.

f. Reaction to Seeds

Pulling at grass heads, running stems through the bill, etc., appeared at 14 and 15 days in the Massachusetts Song Sparrows. R started to mouth seeds at 17 days, S at 19 and D at 20. Y, R and B first succeeded in shelling seeds at 25 and 26 days, the other Song Sparrows at 32 days. The Serins ignored canary seed, but at about 19 days picked up ant pupae and went through shelling movements with them. *The insectivorous Redstarts showed none of these movements characteristic of the seed-eating birds.* The Heinroths (1924) give one month as the age at which the European Tree Sparrow (*Passer montanus*), Linnet and Hawfinch are able to shell seeds.

g. Scratching the Ground

The Song Sparrow, like those others of the Fringillidae that possess this instinctive coordination, scratches with both feet at once, making a little jump forwards and a larger jump backwards. Scratching is a prominent characteristic in Towhees and White-throated and Fox Sparrows; it is also seen in the American Rock Sparrow, White-crowned, Harris, Lincoln, Savannah and American Tree Sparrows and the Junco, but does not seem to occur in the Field Sparrow.

Scratching was first noted with R at 16 days, Y at 18, T at 19, D at 22, S at 36 days. During the winter, scratching did not seem to be stimulated so much by the situation of a supply of weed stalks and seeds as by the feel of various substances; the Song Sparrows scratched when they hopped onto a ball of yarn, onto a sweater, or even on a ball of steel wool. Young Honey Buzzards start to scratch at the age of one month while still in the nest (Wendland 1935).

3. *Defecation*

Young passerines from their first day raise their posterior ends when defecating. This coordination is carried to an extreme in some species as pictured by the Heinroths (1924 I) where the little bird practically stands on its head, stretching its posterior as high as it does its head when begging. Titmice have a fringe of light-colored feathers around the anus which may function in calling parental attention to the forthcoming sac. Naturally this is not present at hatching, but may be useful during the highly crowded conditions during later nest life. Blair and Tucker (1941) stress the increasing cooperation of the young in nest sanitation through the tendency to evacuate on or over the edge of the nest. Defecation normally occurs after feeding.

Changes in the matter of defecation take place as soon as a bird leaves the nest; the timing with feeding is gone and the dropping loses its membranous covering. With the Snow Bunting (Tinbergen 1939c: 38) the latter change occurs just before the young leave the nest hole. What Miller (1931b) writes of the Shrike is true in general of passerines: "concomitant with the beginning of hopping or flying, the feces lose the mucous sac and resemble the fèces of the adult. This change may occur within a few minutes after leaving the nest". Dr. Rand points out to me in correspondence that activity may bring about defecation before there has been time for the formation of a mucous sac of sufficient thickness to be noticeable. "When fledglings begin to move about, the enclosing sac is no longer formed. With the Flicker it disappears gradually" (Sherman 1910).

B. CARE OF PLUMAGE AND OTHER BODILY MOVEMENTS IN SITU, NOT CONCERNED WITH NUTRITION

Under this category those bodily movements will be discussed that are connected neither with nutritional processes nor locomotion. They are: preening, yawning, stretching, scratching the head, shaking self, sleeping in the adult posture, tail and crest movements, bathing and sunning.

1. *Preening*

The first preening movements often appear before there are any feathers to be preened. Preening movements at the age of 5 days with both the Song Sparrows and Redstarts were few and uncertain; they were directed toward the wing, under the wing and to the breast. Sometimes a bird opened its bill to preen, but did not reach the feather sheaths. Preening was well established at 8 days with the Song Sparrows and 11 days with the Redstarts. The first appearance of preening is reported at 4 days with the Ovenbird (Hann 1937), 5 days with the Black-billed Cuckoo (Herrick 1910), and 6 days with the Cowbird (Shaver 1918).

2. *Yawning*

Opening the bill as if yawning was first seen with the Song Sparrows at 5 and 6 days. Heinroth (1930a:337) does not consider that birds, reptiles or amphibia really yawn, i.e. there does not seem to be the deep intake of breath nor the inclination to stretching movements that are characteristic in mammals. Herrick, however, writes that "comparatively few [birds], of which I can now mention the pelican, the gull, and the eagle, habitually indulge in a genuine yawn. In this act the gull appears to derive the same sort of relief as dog or man, and it is no more graceful in its performance. At the close of expiration in the gull the throat expands, and the tongue, which is up-raised, draws with it the larynx and thus gives free passage to the air" (1935:279).

According to von Lucanus (1925) yawning occurs only in Parrots. Strauss (1938a:160) says that he could stimulate yawning in his Jackdaws by waking them with a noise: "They looked at me blinking and 'drunk with sleep,' and, yawning, opened wide their bills." My Song Sparrows, when wakened by the turning on of the light in the evening, often stretched, but never yawned. "Yawning" is seen comparatively seldom.

3. *Stretching*

Two types of stretching movements are shown by all carinate birds. They are illustrated in Plate 14 in Strauss' article on Corvidae (1938a) and many times in the Heinroths' volumes (1924-33), not only for passerines, but for Owls, Ducks, Shorebirds, Pigeons, Bitterns, etc. See Figure 1 for sketches of these movement in the Song Sparrow.

The first movement to appear in the birds observed by me is a stretching upwards of the intertarsal joints and of the closed wings; the leg and wing movements may follow each other or be simultaneous. Stretching up of the legs was seen at 5 days in the Song Sparrows and Redstarts and 6 in the Cowbird. Stretching up of the wings was first seen at 7 days in the Song Sparrow and Catbird, 8 in the Cowbird, 11 in the Redstarts, and was already present in the Serins when obtained at the estimated age of 11 days.

The second and more common type is a stretching down of one wing, the corresponding leg, and—in the adult—half of the tail. This was first seen at 7 days in the Song Sparrows, Ovenbird and Catbird, 8 in the Cowbird, 11 in the Redstarts and about 14 in the Serins.

Stretching down of both wings at once is a temporary stage not mentioned in the writings of Heinroth (1930a, 1938a) and Kramer (1930) on movements of vertebrates. I have noted it in 6 species: Song Sparrows (9 individuals) at 8 and 9 days, Ovenbird 8 days, Cowbird 9 and 10 days, Common Redstarts 12 and 13 days, Cedar Waxwing at about 15 and 16 days and European Cuckoo at about 3 weeks. This activity was seen for only 2 days in any individual. Schifferli and Lang (1940) observed it in Choughs at 27 days. Apparently some parrots regularly stretch both wings down at the same time; this is mentioned of Bourke's Parakeet (Hampe 1939).

4. *Scratching the Head*

In most passerines *the wing is dropped down and the leg brought* *up over it in scratching the head,* a method analogous to that in dogs and lizards. (See Figure 1.) Species that use this roundabout way (*hintenherum*) according to Heinroth (1930a, 1938a) are most passerines, also Swifts, Goatsuckers, Kingfishers, Bee-eaters, Hornbills, most Woodpeckers, and the true Sandpipers including the Avocets (see Makkink 1936) and Stilts. Birds that scratch from under the wing (*vornherum*) are Galliformes, Anseriformes, Pigeons, Snipes, Storks and Toucans. Some Parrots employ one method, others the other.

Several authors emphasize the awkardness of scratching over the wing, and mention how young birds often lose their balance in attempting it (Strauss 1938a, Kramer 1930), while Kramer tells of a Thrush with a stiff wing that exhausted itself trying to scratch its head in the instinctive way rather than simply from under the wing.

Scratching the head was first noted in Ovenbirds at 4 days (Hann 1937), in Song Sparrows at 7, 8 and 9 days, in Catbirds at 7 days, in Redstarts at 9 days and Serins at about 16. My young Ovenbird at 6 and 7 days scratched its head *from under the wing;* I do not know whether or not this is the adult method. The only other passerine that I have noted using this method is the Pekin Robin (one of the Timaliidae). Scratching the head is most frequently seen with the Song Sparrows during or directly after the bath. Many passerines, after taking fat from the oil gland, suddenly scratch the bill and then the head. I noted this first in the Common Redstarts at 12 days.

5. *Shaking*

Shaking was first seen with the Song Sparrows at 9 and 10 days, the Cowbird at 11 days, the Common Redstarts 12 and the Serins about 14 days. Heinroth (1930a) says that birds shake themselves to get their feathers in order; they will not do it if alarmed. Sometimes it is a sign of relief from tension or fear (Lorenz 1935:193, 345). The Heinroths tell of the nervousness of their birds on being taken into the new environment of the photography room; as soon as they felt at ease they shook themselves. Shaking has been noted as evidence of disgust when adult Jackdaws carried off the excrement of the young (Lorenz 1931), when a Jackdaw accidently pecked into excrement or some fell near it (Strauss 1938a), and by various birds after eating a distasteful insect (Steiniger 1937).

6. *Sleeping in the Adult Position*

This position in which the head is turned back and the bill tucked into the upper wing coverts was not assumed by 4 of the species I studied until after they left the nest: 9 of the Song Sparrows at 10 days (although some of them left at 9 days), the Ovenbird at 8 days, Cowbird at 11 days and the Redstarts at 14 days. Rand's Blue Jays slept in this manner at 20 days. Two of the Serins slept in this position when we obtained them at the estimated age of 11 days, the third not until 2 days later. House Finches were noted to sleep thus 6 days before leaving the nest, i.e. at about 10 days (Stoner 1934 and letter).

7. *Tail and Crest Movements*

Tail wagging was first noted in the Song Sparrows at 12 and 13 days, and in the Redstarts at 13 days. Spreading the tail—a sign of excitement—was first recorded with the Song Sparrows at 18 days.

Raising the crest was first noted in the Massachusetts Song Sparrows at 13 and 14 days, in F at 13 and S at 18 days. With the young birds I could not see that it was correlated with any particular psychological state, but in older birds it denotes a certain state of apprehension. In the hand-raised birds this is the characteristic pose of the underling when threatened by the despot or even when within a certain distance of him. In the White-crowned Sparrow with its conspicuously marked crest the significance of raising it is just the opposite (Blanchard 1941).

8. *Bathing Reactions*

The bathing of birds has been discussed by Heinroth in two papers (1912b, 1938b), and by Lorenz as quoted by Strauss (1938a). Typically steppe and desert forms take only dust baths, while the majority of birds take only water baths. A few species take both kinds: House Sparrow, European Rock Sparrow, some Hawks and Owls, European and House Wrens, and Snow Finch. Mr. Earl Wright informs me this is true of the Bronzed Grackle. Wren-Tits bathe in puddles and in dust, but mostly depend on "fog or rain-moistened shrubbery . . . brushing and bumping against the wet leaves . . . then shaking and preening" (Erickson 1938:309). Snow baths have been reported for a Downy Woodpecker (Merriam 1920), Junco (Forbush 1929:89) and Horned Lark (Gardner 1921). According to Heinroth birds do not bathe to get themselves clean, but to bring their feathers in order; they bathe most in hot, damp weather, but may bathe in very cold weather.

In a letter to Erich Strauss (1938a:156) Lorenz describes four chief phases in bathing shown by carinate birds; the last two are characteristic of Anseriformes, but I have not seen them in passerines. From my experience with four species in captivity, I divide their bathing into 3 chief movements (see Figure 1).

The first two constitute the conventional behavior used by the majority of birds.

(1) The bird crouches and performs a horizontal movement with both wings simultaneously, spreading them apart and then bringing them together.

(2) The bird dips its head into the water.

(3) The bird stands erect and whips the water forward, then backward, first with one wing, then the other, splashing the water far more vigorously than with motion 1.

Figuce 1. *Stretching, Scratching and Bathing Postures. From left to right (upper row); 1, stretching both wings up; 2, stretching wing and leg sidwise; 3, scratching head over the wing; 4. preliminary crouching for motion 1 in batching, wings used together; 5, dipping the head, motion 2; 6, alternate wing movement, motion 3.*

Motion 1 appeared in 5 individuals before motion 2: 2 Song Sparrows (B and R) first showed 1 at 13 days, and 2 at 16 and 17 days; a Redstart showed 1 at 15 days, 2 at 16 days; a Serin 1 at 19 (?) days and 2 at 24 (?) days; a Magpie in Austria 1 at about 22 and 2 at about 28 days. Others showed 1 and 2 at the same time: 5 of the Song Sparrows—F at 14 days, D at 15, T at 17, Y and S at 18 days; 3 of the Redstarts at 18 days, and Serin at 24 (?) days. Apparently motion 1 maturates first as shown by those birds that bathed somewhat prematurely.

Motion 3 was not seen until 20, 21 and 25 days with the Song Sparrows, 16 with the Cowbird.

The Song Sparrows always start with head dippping and simultaneous wing movement, but soon work up to the alternate wing movement, each series consisting of motions 2, 1 and 3 repeated again and again. In January 1940 I watched the Song Sparrows bathing: J.

bathed for 4 minutes going through 2, 1 four times then 2, 1, 3 twenty-seven times; D gave 2, 1 eight times, then 2, 1, 3 twenty-nine times, while Y gave 2, 1 fourteen times, followed by 2, 1, 3 thirty-eight times. Y often flirted his tail after 2, 1, but not when absorbed in 2, 1, 3.

Besides Song Sparrows and the Cowbird I have seen House Sparrows, a Java Sparrow and a Starling use motion 3. Canaries used only 1 and 2 while I watched them. How general it is among passerines I cannot say, as before I went to Altenberg I did not realize the importance of watching carefully the movements of birds, and since then I have had little opportunity to see birds bathe.

The young birds are thoroughly wet after their baths, but this was not true of the older ones, even though the latter may stay in longer. Probably the feathers of the older bird are better oiled.

Birds show a great variety in their ways of bathing; Heinroth (1912b, 1938b) enumerates a number of these. Scissor-tailed Flycatchers (Nice 1927a), Kingbirds and Swallows (Seton 1921) dip in the water on the wing. A young Black Swift, adopted at 5 weeks, would catch water in its bill from a dripping faucet and "with a flip of the head would sprinkle the water over its body and in this way obtain its morning bath" (Michael 1933). The subject is one of considerable interest; we need accurate observations on the bathing technique of even our commonest birds.

9. *Sunning*

This is a striking attitude with all feathers spread, mouth open and the body usually inclined to one side.[1] The hand-raised Song Sparrows, although they had opportunities earlier, did not show this reaction until the age of 29, 35, 36 and 38 days. The Common Redstarts first assumed this position at 23 days, the Cedar Waxwing at about 36 days. The Heinroths (1924-33) show an excellent picture of a month old Blackbird (*Turdus merula*) sunning itself, and also of Wrens at 16 days (although here only one wing seems to be outstretched) and of an Aquatic Warbler sunning itself at 17 days. Strauss (1938a) gives photographs of different attitudes of Jackdaws sunning. He says that in sunning the customary alertness appears to be lacking.

C. LOCOMOTION

Locomotion of the young bird will be considered under five topics: in the nest; the act of leaving the nest; locomotion on the ground; locomotion in the air; and "frolicking".

1. *In the Nest*

The newly hatched altrix is able to crawl about to some extent by means of uncoordinated movements. It is not until the second

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[1] Wm. Beebe (1905 Two Bird-Lovers in Mexico, N. Y.) observed 3 Mexican Motmots sunning by flinging themselves "flat upon their backs and spreading their wings." p. 203.

period that the little bird has sufficient control to stand to any extent, and at first it stands on its tarsi. Climbing and stepping and turning about appear in the third stage.

2. *Leaving the Nest*

Leaving the nest appears under normal conditions when the nestling has some power of locomotion and is well able to maintain itself in isolation without the warmth afforded by nest mates. It may be induced prematurely by fright, in which case the little birds have lessened chances of survival. It was interesting how the stunted Song Sparrows D, F and S, and one bird on Interpont, all left at the average time, while two ailing birds were bound to leave even earlier. Grohmann (1938:144) from experiments on domestic pigeons, considers that with healthy birds a certain inhibition prevents them from leaving the nest until the normal time, but that this inhibition is not present in less vigorous individuals.

The age of leaving the nest with different passerines will be discussed in Chapter V.

Besides the new coordinations of hopping and perhaps flying, there are other changes that take place with the leaving of the nest. One is the immediate use of the location call, which has only rarely been used in the nest and typically only under stress of hunger.

> I once watched a Black-throated Blue Warbler leave the nest (1930); 5 minutes later I noted: "The outsider began to call, then flew across the tiny brook, twittering and cheeping. There was the greatest difference between the quiet young in the nest and the vociferous infant outside. . . . Almost constantly he clamored *tiderdée, tidderdée* as he wandered about over the dead leaves."

As already noted, defecation is no longer timed with feeding; it is not accompanied by backing nor turning around; nor are the excreta enclosed in a sac. With many fledglings there is also a definite tendency to get away from nest mates.

3. *Hopping, Walking, Running*

Hopping was the main mode of progression shown by the Song Sparrows upon leaving the nest, but a few walking steps were taken and a little running done. Although adult Song Sparrows progress over the ground chiefly by hopping, they also walk to some extent, especially where the going is rough.

Many birds whose adult mode of progression is entirely or largely walking, hop when they first leave the nest. This is true of the Cowbird (Nice 1939e), Prairie Horned Lark (Pickwell 1931:193), and Ovenbird (Hann 1937). The Heinroths (1924-33) give information on this subject on a number of species that normally walk as adults. Six hop at first: Skylark, Crested Lark, Savi's Warbler, Magpie, Hooded

Crow and Raven. In two species, however, the young walked from leaving the nest—Grasshopper Warbler and European Rock Sparrow (*Petronia petronia*). Lorenz (1937c) adds Pipits to the list of birds that hop before they walk.

4. *Flight*

Under flight we will consider wing fanning, flight, and landing.

a. Wing Fanning

Fanning consists of beating of the wings through a large arc, sometimes with the claws attached to the nest or other support. It was first seen at 8 and 9 days with 6 of the Song Sparrows, but not noted with the others. The Cowbird first indulged in this activity at 8 days; the next afternoon it went into an explosion of wing fanning that carried it out of the nest. The Common Redstarts fanned their wings from the age of 10 days till they left the nest at 14 days; it was seldom seen after that except in "frolicking" at 17 to 19 days. Herrick's films of the young Bald Eagles show much of this activity, in later stages the birds rising from the nest with sticks held in their claws.

b. Flight

Flight was first seen with the Song Sparrows at 10 and 11 days, with the Cowbird at 11 days, with the Redstarts at 14. It may appear as early as 8 days in the Black-throated Green Warbler (the Nices 1932). At 16 days the Redstarts flew skillfully and this was true of the Song Sparrows at 17 days.

c. Landing

The young Song Sparrows tried to land on top of the floor board, the young Redstarts on the wall moldings, i.e., the boundary line between the wall paper and plaster. Both tried to land on the lower length of picture frames. At 17 and 18 days they made no more mistakes in landing. Rand's Blue Jays at 28 days—they started to fly at 18 days—"discriminated against perches on which they could not land."

Landing on brothers and sisters was a definite instinctive action with the Song Sparrows and Redstarts during the first few days out of the nest. Usually the bird aimed at was knocked from the perch, but gave no sign of resentment. I have not been able to watch Song Sparrows in the wild at this age; as a rule they are well separated. But when about 3 weeks old they often land on their fathers, apparently eliciting no resentment on the part of their victims. Lorenz (1931:69) describes this behavior with young Jackdaws, stating that he has seen it with many other recently fledged passerines. He suggests that the instinctive activity is aimed at the parent-companion, the parents in this way showing the young suitable perches.

A case that may have some bearing here has been reported to me by my daughter Constance: when a hand-raised Caspian Tern at the University of Michigan Biological Station took its first flight, it appeared to be afraid to alight, flying about screaming for a long time. Was it looking for a parent to show it where to land? Dr. Lorenz wrote me: "Young Greylags (when hand-raised) are quite terribly afraid to land for lack of the releasing stimuli emanating from the landing of their mother before them." He describes (1936) the first flight of his pet Raven and his successful efforts to get it to land on his arm, thus preventing the bird from flying away and becoming lost.

5. *Frolicking*

The chief form of play which occurs in young Song Sparrows I have called "frolicking." This behavior first appeared with R and Y at 17 days, with B and T at 18. I have seen it in nature with Song Sparrows about 40 days old in July and also with young birds in September. J occasionally showed it. The Pelham birds frolicked all fall, while Y does so at intervals in a mild manner even though 3 years old.

Frolicking is characterized by sudden, rapid runs or flights with sharp turns. One of the Redstarts at 17 days rushed about on the floor of the cage flapping his wings; the next day another suddenly flew madly about the cage. My hand-raised Bob-white (1939a) used to make little flights flapping his wings, then crouch and suddenly fly.

"If one young dove begins to play, by flapping its wings and skipping, the others are apt to be incited to join in" (Whitman 1919:156). Rand (1941a) writes, "Young birds I have raised by hand frequently dashed about in various directions in their cages for no obvious reason, apparently as a release for surplus nervous energy that could be assuaged only by rapid motion."

Sedge Warblers are described by Howard (1907-1914) as very playful just after leaving the nest; they lower their heads, spring into the air and dart at one another, dodging and changing places. Young Turacos were "exceedingly playful in a monkey-like fashion," sparring with each other and making "mock attacks" upon their master and mistress (Moreau 1938:647). The Redstarts chased one another apparently in a spirit of play from the age of 21 days, and the early quarreling of the Song Sparrows is certainly not in earnest. Everyone is familiar with the play fights of young chickens.

Herrick (1934:159-62) describes " 'hunting plays' " of the young Bald Eagle "when the animal is dealing with lifeless or mock prey," and "perhaps 'fighting plays,' in which the rivalry and tilts between the opponents are of a friendly nature." This play-hunting is mentioned with several other raptors—Marsh Hawk (Sumner 1931), Goshawk (Bond 1942), Eagle Owl (the Heinroths 1924-33), Screech Owl (Sanborn 1932b).

The matter of play will be discussed further in Chapter IV.

D. ESCAPE REACTIONS

Escape reactions in young Song Sparrows and many other passerines may be classified under hiding, screaming, and fleeing.

Hiding first appears as cowering in the nest; later as "freezing." The loud scream of the nestling brings the parents to the scene where they put on a demonstration which draws the attention of the enemy to themselves. Later *weech* is a cry of pain, either experienced or anticipated. Fleeing may be on foot or on wing. Fluttering was seen in the captive birds, but would seldom appear in the wild. With the Song Sparrows from the age of 3 weeks the escape reaction might be fleeing to a protected spot followed by freezing.

1. *Age at Which "Fear" Appears*

Kuhlmann (1909) recognizes 5 stages in the development of fear in passerine nestlings :(a) "cessation of giving the food reaction to stimuli that at first aroused it"; (b) a "sudden shrinking or shiver to a stimulus"; (c) crouching to a stimulus; (d) no crouching, but an "alert" attitude in which objects are followed "in an attitude . . . of alarm"; (e) escape with hiding and crouching. A variety of (c) is designated "fighting fear" when a nestling crouches and opens its bill. "Fear in these birds is, therefore, not long delayed, and its development is in one sense quite gradual rather than abrupt," p. 71. Rand (1941c) does not mention Kuhlmann, but these 5 stages may be dated in the account of development of the Curve-billed Thrashers in the nest: (a) by the fifth day, (b) on the seventh and eighth, (d) on the tenth, (c) and (e) on the twelfth. It is a question whether "cessation of giving the food reaction to stimuli that at first aroused it" should be considered a manifestation of "fear"; I would be inclined to call it a matter perhaps both of maturation and conditioning. Crouching is what is commonly recognized as the manifestation of "fear," and this appearance is abrupt. (Kuhlmann nowhere mentions the role of the parent in inciting escape reactions in the young.)

"Fear," as shown by cowering, usually appears at the beginning of the third stage, i.e. *at the time when the young bird is first able to leave the nest*. This occurs from one to several days after the eyes are fully open. Fear appeared at 5½ days with the Ovenbird, 6½-7 days with the Song Sparrows, 6 days with the Catbird, 7 with the Cowbird, 7½ with the Rose-breasted Grosbeak (Ivor, letter), and 9 days with the Common Redstart. With the Black-billed Cuckoo the "instinct of fear commonly matures at the beginning or close of the sixth day," the bird usually leaving the nest at the age of 6 to 8 days (Herrick 1910). As to the American Tree Sparrow, "Fear was acquired quite suddenly between seven and one-half and eight days, correlating perfectly with the development of physical independence" (Baumgartner 1938a). With the Chickadee fear appears at 12 days at the time the eyes are fully open and temperature control is attained (Odum 1941b:530).

The Blond Ring Dove (Craig 1909:55) shows fear earlier, as soon as it has the full use of its eyes. At first it cowers, later in nest life it squats, erects its feathers, points its bill at the approaching hand and snaps at it; when it leaves the nest at the age of 9 to 10 days it flies instead of making a show of resistance. It gives an alarm note at 11 to 13 days; the "inflection" is "exactly like that of the adults' alarm-note, although its tone is that of the baby voice."

Intimidation behavior ("fighting fear") is shown by a number of nestlings when they are in reality helpless: Robin (Kuhlmann), Mourning Dove, Ring Dove, Nighthawk (Pickwell and Smith 1938, Tompkins 1942), European Cuckoo, Owls, Hawks, Boobies, Herons, Bitterns, etc. Once I saw it in a Song Sparrow—A at 8 days crouched with open bill after some rapid movement of mine.

Many nestlings that are normally raised in sheltered nests show much uneasiness when brought into bright light: Song Sparrows, Common Redstarts, Bluebirds, Shell Parakeets (Lorenz) and Jackdaws (Strauss 1938a). Cowering disappears when the birds become positively phototactic upon leaving the nest.

Escape reactions were practically absent in the Serins, while the nestling Michigan Song Sparrows cowered only when taken out-of-doors. *This dropping out of escape reactions is typical of less vigorous individuals.*

E. Social Behavior

The young Song Sparrow shows both social and anti-social behavior.

1. *Social Bond*

The first evidence of a response to a fellow member of the species is given by the tendency of the small young to lie in a heap; when separated, they crawl together again. The bond to nest-mates remains in force with most passerines until the birds leave the nest. (See the account in Chapter II of the 1940 brood that accidentally left a day early.) At this time some species—Chats (*Saxicola*), Wheatears, Nightingales and Thrushes—completely lose this bond, each seeking a separate perch and showing hostility to any of its nest-mates that approaches (the Heinroths, 1924, I). The same is true of Snow Buntings. Tinbergen (1939c:39) says of this behavior, "Its function is obvious: it decreases the chance of the destruction of the whole brood when a predator discovers one of them." However, "as soon as the young become independent, they collect in large flocks."

The Song Sparrows lost their bond to each other at leaving the nest, but showed no hostility until the age of 17 days, the time at which they might normally meet their nest-mates again. With the Common Redstarts, on the contrary, a strong bond persisted between the birds; on leaving the nest, RR made his way to the cage where BR was *tchipping,* and YR followed shortly after. They customarily sat close to one another. There seemed to be no discrimination against the wild Redstart added to their group the day after they left the nest.

At the age of 21 days the Redstarts started to chase one another occasionally in the air, apparently in a spirit of play. The day before they had shown some hostility to the Serins. When the Redstarts were 7½ weeks old, Dr. Lorenz wrote me, "No pecking order has developed; save for occasional bickerings they are absolutely peaceful and sleep close together, though not squeezing against each other as they did formerly." The adult Redstart is territorial.

On July 31 when Song Sparrow A was 27 days old, his brother T suddenly died, leaving A alone except for the Cedar Waxwing. The next day A sat in front of the mirror and chipped for some minutes; this behavior was repeated on August 4, 5, 6 and 7. There was a bond between him and the Waxwing; they lay in the sun together, preened at the same time, visited the lunch counter together, and slept side by side on a picture frame.

The call note *tsip* appeared at 3 weeks with the Song Sparrows; this is expressive of a social bond.

2. *Fighting Reactions*

A note of antagonism was first heard from the Massachusetts Song Sparrows at 17 days; pecking one another appeared at 18 days; threatening with outspread wings and fighting at 19 days. It was at this age that the Michigan Song Sparrows began to defend themselves from the attacks of Y. At 20 days T was first seen to peck A. At about 16 days the Waxwing attacked T who had suddenly hopped up beside it. At 20 days the Redstarts began to chase and peck the Serins; the next day RR threatened YR and BR with open bill and pecked WR; YR pecked RR. At about 23 days the Serins gave a loud, new note of hostility against the Redstarts; this and their open bills bluffed the much larger Redstarts and induced them to give way. At 18 days the Cowbird delivered its first peck.

Some Woodpeckers become very antagonistic to one another before leaving the nest, as the Heinroths note. Sherman (1910:146) describes how young Flickers "fight like little demons at times." The Heinroths found that in the majority of passerines which they raised the brothers and sisters fought one another after they became independent at about 4 weeks of age. In nature the members of the brood would scatter.

F. VOCALIZATIONS

The vocal utterances of the Song Sparrow during the first month of its life may be divided into six classes: food notes, location notes, fear notes, threat notes, self-assertion note, and song.

1. *Food Notes*

The earliest age at which I have noted a faint *see-see* with the Song Sparrows was at 2 days, but it probably would be given the first day if the bird were hungry. The first food call appears on the day of hatching with the Ovenbird and Cowbird (Hann), Robin (6 minutes after hatching—Schantz 1939), Starling (Holzapfel), Chickadee (Odum 1941b:530), Black-billed Cuckoo (Herrick 1910), Alpine Swift (Bartels 1931), and Blond Ring Dove (Craig 1909). The food call grows stronger, being conspicuous near the end of nest life. With the Song Sparrows the *see-see* reaches its maximum at about 7 days, after which it is largely replaced by harsher notes of considerable variety. A rather musical *tit-tit-tit* appeared at 8 to 13 days. Begging notes are used as long as the bird is dependent on its parent.

It has often been noted that young birds in protected sites—either through the situation or the nature of the nest, or because of living in colonies—are much more noisy in their begging than those in open, unprotected situations. The Snow Bunting, nesting in holes inaccessible to the only likely predator, the Arctic Fox, has very noisy young, their nest call carrying 150 yards, in contrast to "its open-breeding relatives, the Reed Bunting and the Yellow Bunting" which "have rather silent young" (Tinbergen 1939c:35-36). The young of the colony-nesting Rook are noisy, those of the solitary Carrion Crow silent, while in North America young Orioles are notorious for their clamor. Young Starlings are also noisy.

2. *Location Notes*

The location call of the young bird that has left the nest is, of course, also a hunger note. It normally appears late in the nest life, but with ailing Song Sparrows was heard as early as 6 and even 5 days. This is used until independence. See C, 2 in this chapter for a description of its sudden appearance after leaving the nest.

Tsip—the specific call note—appeared at 3 weeks. To human ears it is indistinguishable from the call note of some other American Sparrows with which Song Sparrows sometimes associate in winter.

3. *Fear Notes*

The earliest note of fear is the scream given at 6 or 7 days upon capture by an enemy, specifically, the bird-bander. *Weech* is first given by young birds when landed on by companions, and later when pecked or when there seems to be danger of being pecked.

The specific fear note of the adult *tik-tik* was heard at 3 weeks; this is longer or shorter according to the degree of fear.

The "ordinary" note *tchunk* is often used by adults upon occasions of moderate alarm.

4. *Threat Note*

A note of antagonism which gradually developed into one of threat was first heard at 17 days. A corresponding note was first heard from the Cowbird at 21 days and from the Serins at about 23 days.

5. *Self-Assertion*

The "ordinary" note *tchunk,* diagnostic of the species, appeared at 28 days in three of the Song Sparrows, later in the others. It is used in a large variety of situations, but seems often to express self-assertion. In the fall it is usually heard from a male on his territory. It often expresses anxiety in the nesting season at the approach of Cowbird, cat or person. Here it might be interpreted as protest against the intruder. This note would appear to function at times as a form of substitute behavior.

In August 1939 D used it a great deal, Y being confined in the large cage and D dominating F and S. I never heard it from F or S until my return August 31 after a 2½ weeks absence, at which time S had become despot over D and F, Y being confined in a large cage. In October Y and D had the freedom of the study; Y often used it, but D did not. It was not until December, when D became despot, that he again said *tchunk*. I never heard it from the female—J.

The Song Sparrow's *tchunk* seems to be somewhat analogous to the "Rain-call" or *Rülschen* of the Chaffinch as described by Sick (1939).

6. *Song*

Many young birds start to sing at a very early age. The Massachusetts Song Sparrows began with their whispered warbles at 13, 14, 17, and 19 days; two of the Michigan birds at 15 and 20 days, while the third, S, never sang to my knowledge. The ages at which 31 species have been recorded as starting to sing are given in Chapter XI.

A list of 21 vocalizations of the Song Sparrow, both young and adult, is given in Appendix I.

G. MATURATION OF ACTIVITIES IN THE YOUNG PASSERINE

In Chapter II and Table III the maturation of activities in the hand-raised Song Sparrows has been given in some detail. It is of interest to compare the Song Sparrow with other passerines in this matter.

A summary of the activities is given in Table IV. A column is devoted to each of the 3 Song Sparrows, B, R and Y, and another to the other hand-raised birds of this species, while data are given on 4 other species of 4 different families. The Ovenbird is one of the most precocious of passerines; its adult weight of 19 grams almost equals that of the Song Sparrow at 22 grams. The information comes from Hann's study (1937) and also from my experience with a nestling in 1940. The Cowbird is about twice as large as the Song Sparrow, adult females weighing about 40 grams, males about 50; its rate of development closely parallels that of the Song Sparrow. The Common Redstart weighs about 15 grams, but does not leave its protected nest until the age of some 14 days. Data for the Cowbird are based largely on my own observation; those for the Redstart entirely. The Catbirds (adult weight about 40 grams) were raised from the egg by W. E. Schantz, who gave me information on them by letter.

TABLE IV

MATURATION OF ACTIVITIES IN SONG SPARROWS AND FOUR OTHER PASSERINES

The letters (A-F) refer to the 6 categories under which the activities have been treated in this chapter. Numbers refer to age in days; h means at hatching; ( ) the day the bird was taken from the nest; (H) refers to Hann 1937. The 5 stages into which the table is divided apply primarily to the Song Sparrow. Age at left is typical of vigorous Song Sparrows.

	Song Sparrow				Oven-bird	Cow-bird	Cat-bird	Red-start
	B	R	Y	Others				
Stage I								
0 days								
Gaping (A)	h	h	h	h h	h	h	h	h
Defecating (A)	h	h	h	h h	h	h	h	h
See-see food call (A, F)	h?	h?	h?	2	h(H)	h		
Stage II								
5 days								
Preening (B)	(6)	(6)	(5)	5, 6	4(H)	8	6	5
Yawning (B)	7		5	6, 6, 7			8	
Standing on tarsi (C)	(6)	(6)	5	5				
Stretching legs up (C)	(6)		5	5, 7		8	7	5
6 days								
Standing on feet (C)	6	6				8		7
Cowering (E)	7	7	6	6, 6, 6	5	7	6	9
Scream (D, F)	7			5, 6, 7				
Stage III								
7 days								
Stretching wings up (B)	8	7	7	7, 8, 8	8	8	7	11
Stretching sidewise (B)	7	8	7	8, 8	7	8	7	11
Scratching head (C)	7	9	8	8	4(H)		7	9
Climbing (C)	7		9	7, 7	7			
Location note (A, F)	7	7	8	5, 5, 6		6		12
8 days								
Fluttering wings (begging) (A)	8	8	8	9, 9, 10	6	7	9	11
Stretching both wings down (B)	9	8	8	8, 8, 9	8	9	7-8	12

TABLE IV—(Continued)

	Song Sparrow B	Song Sparrow R	Song Sparrow Y	Song Sparrow Others	Oven-bird	Cow-bird	Cat-bird	Red-start
Fanning wings (C) (Flight maturation)	9	8	9	8, 9, 9		8	11	10
Harsh feeing note (A, F)..	8	8		8, 8, 8				
Tit-tit-tit feeding note (A, F)	8	10		7, 7, 13				
9 days								
Shaking self (B)...............	9	9	10	9, 9, 10	7	11	8	12
Stage IV								
10 days								
Leaving nest (C)...............	10	10	9	7-12	7, 8	9-11	11, 12	14
Hopping (C)	10	10	9	7-12	7	11		12
Jumping (C)	10	10	9	7-12				14
Landing (C)	10	10	9	7-12				14
Walking (C)	10	10	9	9, 10	11(H)	15		
Running (C)	10	10	10	10, 10	11(H)			
Perching (B)	10	10	9	9, 10				14
Landing on others (C)......	10	10		10, 10			11, 12	14
Bowing when begging (A)	10	10	10	10, 10, 11				
Sleeping with bill in scapulars (B)	10	10	10	10, 10, 14	8	11		13, 14
11 days								
Flying (C)	12	12	11	11, 11, 11	11(H)	11		14
Wiping bill (A)...................	13	13	11	10, 11, 12		14		14
Raising crest (B)...............	14	14	13	9, 10, 11				
12 days								
Pecking at objects (A)......	13	13	12	12, 12		14	9	13
Wagging tail (B)...............	13	13	12	11, 12, 13				13
Weech (F)	12	12	12	15				
Fluttering to escape (D)..	13	13	12					18
13 days								
Watching prey (A)...........	13	13		12				13
Catching prey (A)............	13	15	14	15				19
14 days								
Picking up food (A)...........	14	14	14	12, 13, 16		17		16
Drinking (A)	13	16		14, 17		16	13, 14	18
Bathing (B)	13	13	18	14, 15, 17		16	13	15, 18
Singing (F)	14	13	17	15, 19, 20			60	18, 19
Pulling at grass (A)..........	15	15	14	17				
15 days								
Beating prey (A).	15							17
16 days								
Scratching on ground (A)		16	18	19, 22				
"Freezing" (D)			16	19, 19, 20				14
Stage V								
17 days								
Mouthing seeds (A)...........	17	17						
Frolicking (C)	18	17	17	18, 26, 33				17
Antagonism note (E, F)....	17	17	17	20, 28		21	13, 14	
18 days								
Spreading tail (B).............	18			25				
Pecking others (E)	18	18		19, 19, 20		13		
19 days								
Threatening with outspread wings (E)...........	19	19	21	23				21
Fighting (E)	19	19	22	20, 20, 20			13, 14	
20 days								
Tik-tik fear note (D, F)..	21	21	20	19, 20				
Alternate wing movement in bathing (B)		20		21, 25		16		
Tsip call note (E, F).......	21	19	20	20, 24, 25				
26 days								
Shelling seeds (A).............	26	26	25	32, 32, 32				
28 days								
Tchunk note (F)...............	28		29	28, 32				
29 days								
Sunning (B)		29		35, 35, 36				22

The arrangement of the activities under 5 days, 6 days, etc., represents what I consider the norm with vigorous Song Sparrows. Usually it corresponds with the earliest age recorded, but certain activities may appear prematurely under an especially strong stimulus—the scream, the location call, leaving the nest and associated phenomena. (Ages for this group of activities and the earliest food call are based on wild birds as well as on the hand-raised ones.)

The regularity of appearance of almost every activity in young Song Sparrows is remarkable. Bathing and singing are almost the only instances where much spread is shown except with the birds that were below par. The suddenness of appearance of almost every activity should also be emphasized.

The table deals with 5 species whose adult weights average from 15 to 45 grams. Five families are represented: Fringillidae, Compsothlypidae, Icteridae, Mimidae and Turdidae. In comparing the Song Sparrow with the others, we find the Ovenbird the most precocious, as would be expected from its habit of leaving the nest at 8 days. The Cowbird and the Catbird are slightly slower than the Song Sparrow. The Redstart is appreciably slower than any of the others, the period of rapid development of motor coordinations coming some 4 days later than with the other birds. This is evidently correlated with the date of nest-leaving, *stage 3 starting some 3 days before this event in all the birds.*

H. SUMMARY

1. The activities of the young passerine from hatching to the age of 4 weeks are grouped under 6 headings: A, nutrition; B, care of plumage and other bodily movements in situ; C, locomotion; D, escape reactions; E, social behavior; F, vocalizations.

2. Table IV shows the order of maturation of activities of 5 species of hand-raised birds: 59 activities for the Song Sparrow, 37 for the Common Redstart, 27 for the Cowbird, 21 for the Catbird and 18 for the Ovenbird. The regularity in the order of appearance of most of the activities in healthy young Song Sparrows is striking. Much the same order of appearance of activities was found in representatives of 5 passerine families.

CHAPTER IV

Innate and Learned Behavior in the Young Bird

"In the case of most supposedly innate chain reflexes," writes Craig (1918:92), "the reactions of the beginning or middle part of the series are not innate, or not completely innate, but must be learned by trial. The end action of the series, the consummatory action, is always innate." As Lorenz points out (1935), it is often *the object of the instinctive reactions that has to be learned.*

A. INSTINCTIVE ACTIVITIES

All the activities in Tables III and IV are examples of innate modes of behavior, although some of them cannot function effectively without conditioning. The majority of them must occur in all passerines, although there will be differences in times of appearance, and an absence of certain motor coordinations and presence of others, especially in the fourth and fifth stages. Insectivorous species respond to prey, granivorous species attempt to shell seeds. Some coordinations were shown by only one of the 4 species observed by me: scratching on the ground by the Song Sparrows, pointing of the bill in the air by the Cowbird, a side-to-side movement by the Serins. The Redstarts did not walk nor run nor pull at grass stalks nor mouth seeds, while the Serins showed no interest in insects.

B. CONDITIONED ACTIONS

Learning with the young passerines raised by hand and observed in the wild concerns itself chiefly with responses to food and water, with orientation in space, choice of social-companions, escape reactions, and song. *The activity is innate, but its object is often learned.*

1. *Responses to Food*

In general during the first few days the altricial nestling responds to any change—tactile, auditory or visual—by begging; the utter lack of discrimination is strikingly shown by the case of the young Minahs clamoring to be fed by a predator in the shape of a land crab (Northwood 1940). Is the gradual elimination of responses to unfruitful stimuli a matter of maturation or conditioning?

Kuhlmann (1909), Herrick (1935), Holzapfel (1939) and Rand (1941c) say that learning is involved. Tinbergen and Kuenen (1939:58), however, contend that this is a matter of maturation. They say that when newly caught young birds cower in the presence of people, this cowering inhibits gaping, but when they are adapted to the new situation, the inhibition disappears. Instead of the birds having learned to gape to the forceps, they suggest that the forceps fit the innate pattern releasing the gaping response. This might have been true with 2 Song Sparrows I took at 7 days (and later returned to their parents) and the Ovenbird at 5½ days where gaping was first inhibited through cowering. It was not the case with the older birds—the Song Sparrow N, the Redstart WR, and the Cedar Waxwing; the last two were entirely tame, but the birds had been so thoroughly conditioned to parental feeding that the forceps no longer matched the innate pattern for the gaping response. WR and N learned to gape to them, while the Waxwing and Cuckoo did not gape, but, like Holzapfel's Starlings taken at 17 days, took food from them, although both my birds gaped "automatically" to small birds hopping about near them. Moreover, the fact that D, F and S at 13 and 14 days failed to beg from Y seems to show that they had so definitely learned to associate food with forceps and a human being that the approach of an adult Song Sparrow meant nothing to them. Rand cites as evidence of "learning", the fact that young thrashers begged "at the approach of a human being while still twenty feet or more away", and also begged "at a lump of food lying on the floor of the cage."

Learning is prominent in the matter of self-feeding. This has been noted in the account of exploratory pecking with the Song Sparrows at 13, 14 and 15 days and later experiences with insects (Chapter II). Rand's Thrashers behaved in a similar manner so far as pecking went; from 19 days on they "approached, pecked at or seized twigs, pebbles, bits of paper, small cracks, small holes, edges of boards, tins, marks or color bands on other thashers' legs. The only requisite of the stimulus causing exploratory pecking was some visual difference in the uniformity of the environment. Anything that looked small and different was pecked at. . . . Moving objects, such as a wind-moved feather, or piece of paper, were much more quickly responded to. . . . The young thrashers frequently picked up and swallowed non-food objects, pebbles, bits of wood, or paper, and it is probable that trial-and-error learning is responsible for determining just what a thrasher eats of what it finds" (1941c:222). The thrashers were found to "quickly discriminate against ill-tasting objects."

I once watched a Downy Woodpecker being fed by its father: the young bird crept about on branches and did much pecking, apparently at random. Many studies have been made on pecking responses of chicks; these are summarized by Warden, Jenkins and Warner (1936:250) and Katz (1937); experiments indicate that improvement in accuracy is due partly to maturation and partly to practice.

As to choice of food, the young Song Sparrows did not attempt to pick up large or brightly colored insects. They learned through experience to avoid stink bugs.

In a study of wasp mimicry, hand-raised passerines were found by Mostler (1935) to learn by trial the unpalatability of Hymenoptera; one experience was remembered for 3 to 14 months. If the mimics were given first they were readily eaten; if offered after the Hymenoptera, they were seldom touched. Similar results were obtained by Steiniger (1937); many birds took an insect once, wiped their bills, shook themselves, and avoided the insect afterwards, at least for 2 or 3 months; some birds avoided Syrphidae after trying wasps, although previously they had eaten them.

Although mother Ducks do not call the young to food, baby Wood Ducks raised by domestic hens learn to come to the food-call of their foster-mothers (Heinroth 1910).

2. *Responses to Water*

I obtained no evidence that the Song Sparrows responded to their first sight of water with an instinctive reaction to drink it; they drank when it was "fed" to them on my fingers. At times the full drinking complex was set in motion by the bird pecking into the water for food; at other times the feel of the water on its feet or body served as the stimulus. Very interesting experiments were made by Craig (1912) on Ring Dove's learning to drink; he concluded: "The dove does not instinctively give a drinking response to the sight of water, nor to the touch of water on distal parts of the body. . . . Though doves instinctively imitate pecking, they do not instinctively imitate drinking as such."

Breed (1911) says that chicks of the domestic fowl "usually found the water by fortuitous pecking or by performing the drinking movements in imitation of other chicks." Prairie Chickens from hatching to 9 days of age failed to recognize surface water, but "showed great excitement" over drops of water from a pipette; the author suggets that "dew drops form an early, instinctively sought source of water" (Wing 1935). Weeds dipped in water brought no response from the young Song Sparrows.

As to bathing, Heinroth (1938b) says that when hand-raised birds are first shown water, they often give bathing reactions outside the dish, but that if the surface is moved with a finger, the stimulus is increased and they get into the water. A number of my birds went through bathing movements outside the water, often in response to the first opportunity offered them to bathe. This was true of 2 of the Song Sparrows—R at 13 days and S at 18 and 19 days, with 2 of the Redstarts and Serins, as well as a Magpie at Altenberg. In other cases birds became conditioned to inadequate places and attempted to bathe in them—the Song Sparrows R, F and S to the drinking cup 4 cm. square by 3 cm. deep; and 2 of the Redstarts and both Serins to a narrow trough 3 cm. wide, the birds going through bathing movements partly inside and partly outside.

Performing bathing movements on dry land was reported as occurring in nature with a Hen Harrier 21 days old (Haas 1939), when a stream rose and nearly reached the nest. It occurred with a 3-weeks-old dove (Whitman 1919:145). It is common in hand-raised birds (Hooded Crow of 6 weeks, Strauss 1938a; Golden Eagle of 64 days, Sumner 1934) and has been seen many times by Lorenz and Heinroth. Thus the sight of water often releases bathing movements, but with many birds the orientation to the water has to be acquired.

3. *Orientation in Space*

Animals learn, of course, to orient themselves in their environment, becoming familiar with places for food, shelter and all their many activities.

One of the earliest skills which many young birds have to perfect is that of landing. According to Lorenz, the inborn pattern of a potential landing place is simple—any approximately horizontal boundary line between two colors or shades of colors. The matter of flight and landing involves an interlacement of instinct and learning, the appropriate place to land being the link gained by experience. Lorenz (1935:158) points out that with some species, as Reed Warblers, Dippers and mountain-nesting forms, the ability to estimate distances and reach safe landing places seems to be inborn, but with birds that do not nest in perilous places, this skill is gained through a process of trial and error. A young Raven tends to try to alight too high, like a man learning to fly a plane.

We often read of birds "learning to fly"; Morgan (1896) cited wing-fanning as learning to fly, the typical example of the modifiability of an instinctive action. Experiments on this point were undertaken by Grohmann (1938) who kept some young Pigeons in boxes without opportunity to exercise their wings; when released they could fly as well as their free nest-mates. Experiments designed to hasten the acquirement of flight were as ineffective as those that attempted to delay it. The Moreaus (1940) state that hand-raised Hornbills kept in roomy boxes never "exercised their wings"; they started to fly "quite suddenly". (Hornbills in nature are raised in holes in trees where there is no space for wing exercises.) Young Tree Swallows on leaving their boxes sometimes flew one-half mile at the first attempt (Kuerzi 1941).

Instead of being a matter of learning, wing fanning is a matter of maturation of instinctive action, i.e., the organ is ready before the instinctive coordination.

4. *Choice of Social-Companions*

As Steinbacher (1939) points out, an animal has to deal with man according to its store of instinctive actions. An animal knows parents and other members of the species—as brothers-and-sisters, social-companions and sex-companions. Otherwise the animal knows enemies, and animals to which it is indifferent. An animal cannot have any innate conception of a "keeper". To a young captive animal, he may be only a food-counter). In the rutting season many males man is first his parent-companion and later his social-companion (or strive to dominate their fellows, including their keepers, hence they become dangerous. Or they may try to treat them as females of their own species; this often happens with birds. Their tameness in childhood and fierceness in maturity are both manifestations of the same attitude, i.e., they treat man as a member of their own species.

With my hand-raised Bob-white, Loti, human beings served as parent- and social-companions, but not sex-companions (Nice 1939a). Hatched by a bantam hen, and transferred the next day to a brooder, he had the companionship of brothers and sisters for the first 9 days of his life, but after that saw no Bob-whites until the age of 3½ months. At this time he gave no reaction to young still in juvenal plumage, but to the hostile reception of adults of both sexes, he at once responded in kind. His next contact with his species came the following spring; he greeted the young female with puffing and conversational notes and in a few days the birds were mates.

While a chick, Loti responded to me and to members of my family as parent-companions. During fall and winter he and I shared a laboratory at Clark University; I was his covey-companion and our room was our territory, for he gave the vocal challenge (Stoddard 1931) to every one that entered, but that ordinarily was the extent of his hostility. When, however, Mr. W. A. Matheny would come in *whistling an imitation of the challenge*, Loti would fly from my desk or shoulder to the top of his cage and stand there on tiptoe, every feather erected, wings outstretched and shouting his loudest. He often followed me when I went out into the hall, and if it happened to be time for changing of classes, he would rush in among the crowd of 30 or more students, shouting his challenge, regardless of the size and number of his opponents. Here the noise and movement must have stimulated him, for I do not remember his challenging single individuals in the hall.

Although accepting all people as social companions, Loti's attachment was strongest towards me, with Mr. Matheny as his next favorite, for here there was the bond of common language. It seems probable that instinctive response to the challenge note was one of the chief elements in Loti's immediate recognition of the adults of the species when first introduced to them. His early experience with brothers and sisters may have had an influence in his acceptance of a sex-companion of his own species; Lorenz found this true with Anatidae (see Chapter XVI).

5. *Escape Reactions*

The fundamental nature of the avoidance reaction (*Ausweichreaktion*) in birds is emphasized by Van Essen (1932); this is primary reflex behavior and is the only act which the decerebrated bird carries out by means of its seeing organ. The effect of this fundamental reaction is that the bird meets a new object with a certain caution; a complex of impressions will not be at once accepted, but will be investigated.

In this connection J. J. Hickey suggests in a letter: "Presumably the bird is 'seeking' one or more signals or cues which will determine its reaction to the entire complex. What sets off the escape reaction is a definite stimulus; but a series of cautious reactions are also innate. Cautious behavior is innate when a Song Sparrow carries food to its young; it may possibly be learned as when a Bob-white threads along a hedge row; but it is also present when birds are confronted with a large object like a bird blind which over-night appears near the nest."

Situations to which the Song Sparrows instinctively responded with escape reactions were: threatened capture, movement of the immediate environment, approach of very large moving objects, evidence of fright in companions, sight of birds flying overhead, the specific fear note and sounds resembling it. They did not recognize a cat or a dog as an enemy. (My hand-raised Bobwhite was somewhat afraid of dogs and roosters, but looked upon a cat as an object of curiosity.)

It was interesting to see the unteachableness of the young Song Sparrows in 1939 in relation to abuse from Y from the age of 13 days to over 3 weeks; although severely pecked and their feathers pulled out, they would not learn to avoid danger that normally should not have appeared until they were some 4 weeks old.

With the young Black-headed Gull Kirkman (1937:174-181) found no fear during the first 12 to 24 hours; during the next few days it "might react to emotional excitement on the part of the old birds by uneasy stirring in the nest, or by going to crouch on the ground a short distance outside it"; between the fourth and seventh days it "reacted directly to the cause of alarm by running to cover or water." Baby chickens were noted by Brückner (1933) to fear only loud noises and loss of balance; a rabbit was ignored at first, but feared at 3 weeks.

The most complete set of experiments on the "Response to Stimulus Objects, Enemy or Otherwise" made on any young bird are those of Rand on the Curve-billed Thrasher from the age of 2 to 11 weeks. Painful experience in being seized by predators was ineffective in teaching 19 day old birds (just out of the nest) to avoid these animals. "Even the squeals of distress given by the young when seized do not affect other thrashers of the same age." They did not differentiate between a rabbit and a cat—"a harmless animal and a predatory one". In their response to mammals "there appears to be a direct correlation between the size of the animal and the response. The smallest mammal caused the approach with little sign of excitement and no fleeing; the largest mammal the most fleeing and keeping at a distance, the least approach. Movement also played an important part in the response elicited, especially in the larger mammals. When the cat and the rabbit were slowly moving about, the thrashers watched them, when they retreated, the thrashers followed; when they approached, the thrashers fled" p. 239. The 19-day old birds paid little attention to a Great Horned Owl, while "the 29- to 35-day old birds responded more definitely but less so than the older thrashers."

In a letter to Wallace Craig, Konrad Lorenz wrote, "Many young birds as for instance daws, geese, cranes have no innate 'inlet' for the reactions of fleeing, *except* the warning call and general behavior of their parents. They do not react on seeing a cat, dog, or man, but on seeing their parent frightened and in flight. Just these species grow very tame, if raised from infancy by man, but they lack an outlet for their fleeing reactions. Just these tame birds, who actually are 'afraid of nothing', certainly of no one in particular, are prone to react with wild panic on nothing in particular. They will take some quite irrelevant small stimulus to 'get off' their fleeing reactions, just as one of your doves took a certain corner of the room in which it was confined to bow-and-coo to. (What Freud calls *abreagieren.*)

"Birds with innate stimuli for the fleeing reactions, as for instance magpies, which recognize a carnivore for what it is, even if they have never seen one before, and give all the specific enemy-reactions that wild magpies give, never show these blind ex-vacuo-panics, except perhaps when confined alone." (See Lorenz 1935:211).

Kuhlmann believes there is "an instinctive fear of all stimuli with which food is not associated" (1909:74). Rand concludes that fear is generalized: "Thrashers probably had to learn what not to fear" (1941c:242).

How much are the young conditioned in this field by parental notes and behavior? There are a number of observations on young in the nest (from the third stage on) and out of the nest stopping their cries at the alarm notes of their parents. Examples are given in Chapter XX; see Chapter II where 4M's young was "warned" by its father. Young Jackdaws are especially dependent on parental guidance, following the adults closely after leaving the nest and responding quickly to signs of alarm (Lorenz 1931:107; 1935:205).

It is probably in the fifth period—from flight to independence—that the instinctive fear reactions are modified by parental example. If they do not at this time learn the dangerousness of cats and the harmlessness of rabbits, they would be apt to pick up this knowledge later from the behavior of neighbors. Fear reactions in the adult may constitute the unconditioned stimulus adequate to elicit flight in the young. Simultaneous presentation of the natively inadequate stimulus (cat), and the unconditioned stimulus (flight of parent) may quickly result in a conditioning process as a result of which the cat becomes the conditioned stimulus adequate to elicit flight.

The subject of enemy recognition will be treated further in Chapter XXI.

6. *Song*

Some young birds have to learn the song of their species, while with others it is innate. This subject will be discussed in Chapter XI.

C. THE MATTER OF PLAY

In Chapter VI, "frolicking", "play-fighting" and "play-hunting" are described. Groos considers play as exercise of the instinctive activities: "Natural selection will favor individuals in whom instinct appears only in an imperfect form, manifesting itself in early youth in activity purely for exercise and practice—that is to say, ***in animals which play***" (1898:xx). This is true in regard to play-hunting—attacking perches, seizing sticks, manipulating objects—, which is concerned *with the object of the instinctive actions*. The animal is not so much exercising the activity (whose perfection is a matter of maturation), as it is learning appropriate objects on which to use the activities. Lorenz states (1937c:159): "very important in many of these learning processes is that behavior that we with Groos designate as 'play'. When we observe playful activities in the developing behavior of a young animal, we may always assume that in this chain of activity certain links of a trained or acquired character have been inserted."

We do not consider frolicking and play-fighting as functioning in the perfection of instinctive activities; they would appear to come from a surplus of energy and are manifestations of "instinctive actions without the specific emotion" (Lorenz, personal communication); for example, puppies go through all the motions of real fighting, but not in earnest. They are phenomena of markedly lowered thresholds; Lorenz considers that they go off in vacuo (*auf Leerlauf*) (1935:209). In a letter to me he writes:

> "Most of what you describe as frolicking are emotion-dissociated fleeing movements! The most impressive instance of such frolicking is the pre-bathing play of Anatidae. They do every single stunt that is applied when the eagle is behind them—diving and taking wing at the very moment of emerging and taking a header from the air right under the surface, with a long under-water swim

following, and last, but not least, repeated performance of *Hakenschlagen*—'hooks' or sudden turns. Yet apparently the ducks and geese are *not* afraid, *e.g.*, the whole performance is really dissociated from the emotion which is correlated with all these instinctive actions when they are used in earnest.

"One of the best examples of the playful fleeing-and-defense reactions can be found in smaller stork species. When Black Storks and most of all the small African Abdim (*Abdimia abdimi*) are let out into a larger enclosure (so that the situation is absolutely that of frolicking), they begin a curious dance, evading by 'hooks' and sudden ducking the non-existent attacks of an imaginary eagle, even thrusting at him vertically upward with their bills. The fact that their coordinations of movement are calculated at an enemy attacking *from above* is very apparent."

D. SUMMARY

1. The activities listed in Tables III and IV in Chapters II and III are innate modes of behavior, although some of them cannot function effectively without conditioning. Most of them will be found in all passerines.

2. Learning is largely concerned with the object of the instinctive actions.

3. Learning is involved in the restriction of begging responses to the appropriate situation.

4. The bird has an innate tendency to peck at small differences in the environment; by trial and error it learns what is edible.

5. Drinking may also be learned by trial.

6. While the sight of water, and sometimes the feel, may stimulate bathing movements, the orientation to the water has to be learned.

7. Flying is instinctive and is not learned, but expertness in landing has to be acquired by many birds.

8. The choice of social-companions may be influenced by experience. An animal responds to its companions according to its store of instinctive behaviors.

9. The bird instinctively meets a new situation with caution, seeking signals which will determine its response. Escape reactions are stimulated instinctively by a variety of situations. It may be that fear is rather generalized. The bird below a certain age does not seem to profit by painful experience. Much learning may take place largely through the influence of parents and companions as to what to fear and what not to fear.

10. There are 2 chief sorts of play. Play-hunting is concerned with the object of the instinctive actions, with the acquirement of a link in a chain of instinctive activities. Frolicking and play-fighting are evidences of surplus energy—instinctive actions without the specific emotion.

CHAPTER V

The Course of Development in Passerine Birds

The growth and development of passerine young are compared with those of gallinaceous young in an interesting study by Portmann (1938). He contrasts the slow, even growth of different Galliformes to the rapid, uneven growth of passerines of similar adult weight. (The growth rate of hawks is nearly as rapid as that of the passerines, while that of the duck is somewhat slower, yet still much faster than the Gallinae. The latter have to be able to use their wings as early as possible.) Growth of Gallinae is characterized by "isometry", the different organs growing at much the same rate, while that of passerines is characterized by "allometry", for the intestine and liver quickly reach a maximum (at about 9 days with the Starling) and then decrease in weight. Some young birds that stay in the nest until flight is attained weigh more than their parents at a period some days before leaving the nest; Portmann states that this over-weight is due to the great growth of liver and intestines. (Stevenson [1933] found the stomachs and intestines of several passerines in Ohio larger and longer in nestlings than adults.) Portmann compares altricial young to a larval form; parent and young constitute an entity, the instinctive reactions of both fitting each other and effecting the rapid, successful development of the young.

A. The Age of Fledging and Independence in Passerines

In looking through the literature for data on time of leaving the nest, and the attainment of flight and of independence in passerines I was struck with several facts. First, I was impressed with the ease with which information on weight of adults, length of incubation, part taken by the sexes, and length of the fledging period, could be found for European birds in Witherby's "Handbook of British Birds" (1938-41) and Niethammer's "Handbuch der Deutschen Vogelkunde" (1937-38), and also the general reliability of these data in contrast to the difficulty of finding the same material for North American birds and the unreliability of much of what is given. Secondly, I was painfully surprised to discover how little there seems to be anywhere, except in the Heinroths' classic work, on the age at which flight is attained and the age when the young become independent. Here is a promising field for the bird watcher and bander.

In Table V a summary is given of the age of leaving the nest in 21 passerine families, representative species being chosen. They are divided into five groups according to the age at which this event takes place. Much of the information is taken from the Handbooks already mentioned; the rest was found scattered through the literature.

TABLE V

AGE OF LEAVING THE NEST AND ATTAINMENT OF FLIGHT AND INDEPENDENCE IN REPRESENTATIVE SPECIES FROM 21 PASSERINE FAMILIES

(Age in days; weights in grams)

Family	Weight of adult female	Kind of nest	Length of incubation	Age of leaving nest	Age of attainment of	
					Flight	Independence
Group I						
Corvidae	200-1300	Open	16-21	19-40	Later	
Group II						
Sittidae	33	Hole	13-17	22-24	Same time	36
Cinclidae	53-70	Covered	15-17	18-24	Same time	40 +
Sturnidae	80	Hole	12-14	18-22	Same time	28
Laniidae	35-65	Open	14-16	19-20	Same time	36?
Hirundinidae	14-21	Hole & open	14-16	16-22	Same time	27
Regulidae	5-6	Covered	17	18-20	Same time	
Group III						
Paridae	9-19	Hole	13-16	16-22	Same time	28
Certhiidae	8.5	Hole	15	16-18	Same time	
Ploceidae	23-28	Hole	13-14	16-17	Same time	30
Troglodytidae	9	Hole	13-14	15-17	Same time	27-33
Turdidae I Sialia	30	Hole	13-15	15-18	Same time	28
Muscicapidae	13-20	Hole	12-14	12-17	Same time	26
Motacillidae I Motacilla	17-23	Hole	13-17	14-16	Same time	28
Group IV						
Turdidae II	23-115	Open	13-14	13-16	19, 20	26
Sylviidae	8-30	Open	13-14	9-14	16	24
Motacillidae II Anthus	20-27	Open	13-17	12-14		32
Alaudidae	33-42	Open	13-14	9-11	17	
Icteridae	34-50	Open	11-12	10-11		28
Mimidae	36-70	Open	12-13	10-11	17	31
Zosteropidae		Open	11	11		28
Compsothlypidae	6-20	Open	12	8-11		30
Fringillidae						
Richmondeninae	27-45	Open	12-13	9-10		
Carduelinae	12-20	Open	12-13	12-17	15-17	26
Emberizinae	10-52	Open	11-13	8-10	17	28

The Corvidae are markedly larger than any of the other birds included in the table, their weights ranging from 200 to 1300 grams. Their development is considerably slower than that of the smaller birds. In general they leave the nest before they can fly.

The next group does not leave until their wings are full grown; except for the Shrikes the birds in this group ordinarily nest in protected places. The third group are all hole nesters and their young seldom leave until able to fly. The last two groups nest in the open. The fourth group usually leave before they can fly well. The majority of the fifth group leaves very early, at from 8 to 11 days; they progress by hopping, and hide in the undergrowth. Birds of the subfamily Carduelinae, where the young are fed by regurgitation, sometimes stay in the nest until ready to fly at 16 to 17 days.

There would seem to be two main factors with which the time of leaving the nest can be correlated: safety of the nest and size of the bird. It is evident that birds that nest in holes and protected situations usually stay in the nest until capable of flight. (The Brown Thrasher leaves its open nest at about 12 days (Gabrielson 1912), the Curve-billed Thrasher stays in its nest in the cholla cactus 18 days (Rand 1941c.) Some of these in Group II stay an exceptionally long time, the European Nuthatch, European Dipper and Kinglets; in all these incubation is also prolonged. The long fledging period of Swallows is correlated with the length of primaries and rectrices that must be grown; Swallows must be able to fly when they leave the nest.

Shrikes in general do not seem to leave the nest early, although the Red-backed Shrike does so at 12 to 15 days; here it may be that the pugnacity of the parents ensures their protection (Burns 1921:92).

From nests in exposed situations, and particularly from ground nests which are subject to the dangers of flooding as well as from predators, it is an advantage for the young to leave and scatter as soon as temperature control is well established and the birds can move about on foot and respond to the parents' alarm notes.

As to the matter of size, we find many Wood Warblers (adults weighing 8-20 grams), the Field Sparrow (11-12 grams) and Henslow's Sparrow (12-13 grams) regularly leaving the nest at 7, 8 and 9 days. The Song Sparrow (22 grams) and Cowbird (40-50) leave at 10 days; while the Corvidae (200-3000 grams) leave the nest at 19-40 days when still unable to fly. Incubation lasts 11 days with the Field Sparrow, 12 days with some Wood Warblers, 12-13 with the Song Sparrow, 11-12 with the Cowbird, 16-21 with the Corvidae.

It may be that the rate of growth does not differ widely in all these species with the exception of the 3 families in Group II as mentioned above; however, with the Corvidae the newly-hatched bird is relatively smaller than that of other passerines.

1. *Relative Size of the Newly-hatched Nestling*

As a result of reworking Heinroth's (1922) mass of data on weights of eggs and adults, Huxley (1927) found that fresh eggs of 46 species of passerines that weigh up to 35 grams ranged from 10-12 per cent of the weight of the adult female; eggs of 24 species weighing from 45-135 grams average 8-9 per cent. *The weight of the newly-hatched dry nestlings in all groups investigated by Heinroth*

(*1922:274*) *comes to about two-thirds the weight of the fresh egg.* (Most of the weights given in the literature of first day young are *not* of just hatched birds.) Hence the newly-hatched nestling of the majority of passerines weighs some 6-8 per cent of the weight of its mother.

In the first 10 days the young typically increases its weight 10 to 12 fold; hence reaches 60 to 80 per cent of the adult weight. During the next 10 days the increase drops off sharply, so that at 20 days the young bird has reached some 75 to 90 per cent of the adult weight, occasionally 100 per cent.

With the Corvidae, however, that are larger than the rest of the passerines, the egg is relatively smaller. Omitting for the moment the Raven, let us consider the 4 other species listed by Heinroth, adding to them the Chough (Schifferli and Lang 1940). The females of these species weigh from 175 to 500 grams, while their eggs weigh from 8 to 17 grams, averaging from 3.2 to 5 per cent the weight of the bird that lays them. The newly-hatched nestling then weighs less than 3 to 4 per cent of the weight of the adult. If it grows at the same rate as the smaller birds it will reach some 30 to 45 per cent of the adult weight at 10 days, and will need another 10 days of rapid growth to reach 70 to 80 per cent. (The adult female Chough weighed 293 grams; the fresh eggs averaged 13.15 grams; the female nestling at hatching weighed 10.6 grams or 3.6 per cent the weight of its mother. At 10 days it weighed 82 grams—28 per cent of adult weight; at 20 days 198 grams—67 per cent; at 33 days 284 grams or 97 per cent of the adult weight, and at 4 months 300 grams.) The Raven, weighing 1300 grams with an egg weighing 30-33 grams, needs 30 days to reach 70 per cent of its adult weight (the Heinroths 1924).

Here is the explanation of the long (in comparison to that of its hosts) fledging period of the European Cuckoo, 22-23 days; the adult that weighs 100 grams lays an egg weighing only 3 (Heinroth 1922) to 3.29 (Niethammer 1938 II:132) grams; the tiny nestling, alone as it is in the nest, may reach half the adult weight at 10 days and 80 per cent at 2 weeks (Makatsch 1937:108; Burdet 1926).

B. THE FIVE STAGES OF DEVELOPMENT IN PASSERINES

In Chapter II the five stages of development in the Song Sparrow were listed:

1. The first four days: coordinations mainly concerned with nutrition.
2. Five and 6 days: first appearance of new motor coordinations.
3. Seven, 8 and 9 days: rapid acquisition of motor coordinations.
4. Ten to 16 days: leaving the nest to attainment of flight.
5. Seventeen to 28 days: attainment of independent feeding reactions.

How do these five stages fit other passerines? I believe rather well on the whole. With Corvidae and representatives of Group II each stage probably lasts longer than with the Song Sparrow. With Field Sparrows and many Wood Warblers the first three stages are passed through in 7 days rather than 9.

The chief difference with the majority of passerines seems to be with stages 3 and 4. With the fourth group in Table V stage 3 is longer than with the Song Sparrows and stage 4 is undoubtedly shorter. With Groups II and III stages 3 and 4 are merged, for the nest is not left until the bird is capable of flight. With Group II stages 3 and 4 are merged and prolonged, the birds not leaving until 20-24 days. With some families stage 5 is also prolonged. In the last three groups the mastery of flight seems to be *attained at much the same age, about 17 days,* probably a little earlier with some Wood Warblers, and a little later with some of the Titmice and larger Thrushes and Thrashers. So far as we know a great many of these birds *become independent of parental care at about 4 weeks* (Heinroth 1930b).

Comparing for a moment passerines of groups IV and V with some precocial nestlings, it might be considered that with the latter, stages 1, 2 and 3 are passed in the egg. A Bob-white hatches after 23 or 24 days incubation, at the same time after the start of incubation that a Song Sparrow has been out of the nest for a day. Both species are strong on their feet and both respond to parental notes of alarm. One is covered with feathers, the other with down. Pecking and drinking may come in a day or two for both. Both need parental care, although in different fields; the Song Sparrow must be fed, the Bob-white brooded.

C. Summary

1. The time of leaving the nest is shown in Table V for 21 passerine families.

2. Corvidae take longer to mature than do the smaller passerines.

3. Birds in Group II, Sittidae, *Sturnus vulgaris,* Hirundinidae, Cinclidae and Regulidae, nesting in holes or covered nests, and Shrikes, nesting in the open, do not leave the nest as a rule until well able to fly at the age of 20 to 24 days.

4. Another group of birds, all of which nest in holes—Paridae, Certhiidae, Ploceidae, Troglodytidae, *Sialia sialis,* Muscicapidae, and *Motacilla*—leaves at 16-18 days, well able to fly.

5. A fourth group nests in the open—Sylviidae, many Turdidae, and *Anthus*—; they leave at 12 to 14 days before they are able to fly.

6. A fifth group nests in the open—Alaudidae, Icteridae, Mimidae, Zosteropidae, Compsothlypidae and Fringillidae—; most leave at a very early age, 8 to 11 days, a week before they are strong on the wing.

7. There seem to be 2 main factors with which the time of leaving the nest in altrices can be correlated: *safety of the nest and size of the bird.* Birds that must be able to fly on leaving the nest (Swallows and Swifts) have long fledging periods.

8. With passerines weighing up to 135 grams the weight of the fresh egg averages from 8 to 12 per cent of the weight of the adult female; the newly-hatched nestling averages about two-thirds the weight of the fresh egg, hence the nestling starts at 6 to 8 per cent the weight of its mother. In 10 days it has reached 60 to 80 per cent of the adult weight.

9. With the Corvidae, weighing from 175 to 1300 grams, the egg weighs from 2.5 to 5 per cent the weight of the mother; the nestling reaches 20 to 50 per cent of adult weight in the first 10 days and from 50 to 80 in the next 10 days.

10. The European Cuckoo, weighing at hatching less than 3 per cent of the weight of the parent, may reach half the adult weight at 10 days and 80 per cent at 2 weeks.

11. In general we may expect to find the 5 stages of development represented in passerines with this chief exception: stages 3 and 4 are merged in those birds that do not leave the nest until they can fly.

12. The majority of passerines seem to *attain a certain proficiency in flight at about 17 days,* and to *become independent of parental care at about 28 days.*

13. Precocial birds might be considered as passing stages 1, 2 and 3 in the egg; at hatching a Bob-white is comparable in many respects to a Song Sparrow that has recently left the nest.

CHAPTER VI

The Young Bird After Independence

As with many small passerines, at 4 weeks of age the Song Sparrow becomes independent of its parents and family ties are broken.

In July 1929 I had an opportunity to watch 1M's and 4M's young that were 5 to 6 weeks old, as well as other young Song Sparrows. They frolicked, fought and pursued one another, and chased young House Wrens. They appeared to have a lively curiosity as to their bird neighbors, for they followed a Downy Woodpecker and a Black-billed Cuckoo up into trees.

In the fall on Interpont there is some chasing and many cries of *weech;* some frolicking; much calling of *tsip,* largely among the transients; much warbling from young males and some singing from adult males on their territories. There is a small amount of territorial behavior with the young males, some of which settle on their territories at this time. In October the transients and the majority of the native birds leave for the south.

A. THE POST-JUVENAL MOLT

In my hand-raised Song Sparrows the molt involved only the body feathers. With B, R and Y it started at the age of 7 weeks and lasted 3 weeks, mid-September to the first week in October. With the Michigan birds it started at 6 weeks, D on July 26, F 2 days later. Mr. C. L. Whittle writes me that a hand-raised male in New Hampshire, hatched about July 30, molted from Sept. 15 to Oct. 18; all feathers but the primaries and secondaries were involved. On Interpont I saw and handled many juveniles in molt in September (and in 1931 in October also); some molted their tails, but the majority did not.

The classical work on molts of passerine birds of North America is that of Dwight (1900); an exhaustive study on the molt of over 2000 banded House Finches was made by the Micheners (1940), while careful analyses of post juvenal molt in several species of Sparrows have been made by Sutton (1935, 1936, 1937, 1941).

B. FALL MIGRATION

With the Song Sparrows on Interpont the situation obtained that has been called "individual migration" (Thomson 1926), i.e., some of the breeding birds migrated and some did not, about half the males and from a tenth to a third of the females remaining stationary. This subject has been treated at length in Volume I (Nice 1937); it was found that there were not two strains of Song Sparrows, one migratory and the other not, since offspring did not necessarily follow the status of the parents or grandparents; and that at least 7 birds changed their status, one migrating 2 winters and remaining the third, 4 remaining one winter and migrating the next, returning in the spring, and 2 remaining 2 winters and migrating the third, returning in the spring.

It may be that the migratory impulse is latent in all the Song Sparrows of central Ohio, functioning normally in the majority of the birds, but lying dormant in the others, in some of which it may be stimulated by cold weather in October or inhibited by warm weather. (Some Song Sparrow races are strictly sedentary, others strictly migratory.) "Individual migration" has been reported for a number of other species (Nice 1937:38-39).

Many experiments have been carried out in Germany and Finland on the "migration restlessness" (*Zugunruhe*) of caged birds that are markedly migratory. The Massachusetts Song Sparrows would be expected to be more strongly migratory than those in central Ohio, for so far as known almost all Massachusetts Song Sparrows go south for the winter. I expected migration-restlessness, but there has been little of it. From Oct. 30 to Nov. 5, 1938, the birds moved about a good deal in the cage in the evenings, calling *tsip*. Strangely enough it was not until February that pronounced migration restlessness appeared; B, roosting free in the study, killed himself flying against something during the night of Feb. 1; Y was very restless the following night and also Feb. 19. No migration restlessness was noted with the other birds with the possible exception of the female that was restless at night from Feb. 28 to Mar. 2.

C. PREMATURE APPEARANCE OF BREEDING BEHAVIOR

In many young birds early manifestations of sexual and nesting behavior have been seen; these include attempted copulation, activities connected with nest building, and activities connected with the care of young.

1. *Attempted Copulation*

The first evidence of attempted copulation appeared at 75 days with B, 95 days with Y and 92 days with D. All of these attempts were made with small objects, either rounded or pointed. Strangely enough, in 1940 T showed this behavior at the extraordinarily early age of 23 days.

25 days, 7:00 A. M. T alights on my hand in this light, fluttery manner. Can this be foreshadowing copulation? It looked almost like it on the wire bump on the nest handle.

8:50. He is alighting on top of A. Hovering there. This is *copulatory behavior*. It *started 2 days ago* on my hand.

9:25. As I reach over to feed the Waxwing, T alights on my hand. Does this 3 times.

11:30. T flies to my hand, giving a little cry—*tee-tee-tee*.

11:40. T tried to mount the Waxwing as it sat on my hand; he fell off as Waxwing stood erect.

26 days. T flutters over Waxwing as if trying to copulate.

The next day he started incessantly calling for food, and demonstrating extravagantly when he was fed. He was by far the tamest of any Song Sparrow I ever raised. Early the next morning he was evidently ill; he accepted small crickets, but dropped them. Ten minutes later he was dead. A post-mortem showed inflamation of the intestines. He had been precocious in feather development as well as in sex behavior.

On Oct. 6, 1938, B stood up straight on the pointed ears of a small clay dog, flipping his wings and singing. Eight days later he flew to one of the small posts of the gathering cage that happened to be in the room; he crouched down and fluttered his wings as if copulating. On Oct. 23 he did the same on a hump in the black cloth used for a cage cover, and on both posts of the gathering cage, shaking himself afterwards. I recorded this activity from him 5 times between Nov. 3 and Jan. 4: once on the posts, twice on a round knob on top of a book case, once on a large seed pod, and once on a little box; usually he warbled during the process. Adult male Song Sparrows utter no note during or immediately after copulation.

Nine instances were recorded with Y from Oct. 27 to Feb. 20; the stimulating objects were humps on a sweater and the black cloth, the gathering cage posts and knob on the book case, and a lump of lettuce. The gathering cage had not been in the study throughout the fall and early winter; I returned it for a test on May 2 at which time Y paid no attention to it; on a later test July 3, however, he assumed the copulatory position on the posts, and from May 22 to 27, 1940, there was a return of this behavior, each act being accompanied by warbling. On Jan. 17, 1942, he assumed this position on a lump of lettuce.

On Sept. 14 D warbled rather loudly as he attempted copulation on the ridge-pole of the bamboo cage. I have no other note of this behavior on his part except on Jan. 21 when the stimulating object was the small, rounded knob on the handle of the pencil sharpener.

From the first of February to the first of June, 2 male Bobolinks, hatched in early July and raised by Dr. O. S. Pettingill, Jr., were in my study. From Feb. 23 on both made frequent copulatory attempts, crouching over an object with fluttering wings, but uttering no note. The stimulating objects to L were an end of one of his perches, a rolled up silk stocking and his food dish. K made his attempts on lumps of lettuce and the little clay dog that had stimulated B.

Attempts at copulation by young birds have been reported for a number of species: Sharp-tailed Sparrow with a tussock of grass (Howe 1899); Bicknell's Thrush on a hand, foot, or pencil (when "hardly more than a month old", Wallace 1939:318); Mockingbird on hand and various small objects from 52 days on, Starlings 41 days old with Brown Thrasher a week younger as it begged from him, Bronzed Grackle with hand and other objects, also with a young Cardinal (Laskey 1940 and letter), and 4 species of Swallows with other Swallows: Cliff and Tree Swallows (Brewster 1898, Chapman 1898), Barn Swallow (Hampe 1928), Purple Martins (Howe 1899). Early sex behavior is also reported in Parrots: a male Song Parrot trying to feed the author's finger at 51 days (Hampe 1938a), a female Pale-headed Rosella doing the same at 52 days (Hampe 1938b), a male Elegant Parrot starting to court at 56 days, to feed at 106 days and attempt to copulate at 125 days (Hampe 1940), and male Bourke's Parakeets trying to feed at 46 and 54 days (Hampe 1939).

2. *Nest Building*

The young males of the 1938 brood showed nest molding behavior from the age of one to 3½ months. When R was 35 days old he was scratching in the net that lay on the floor with the cloth drawn rather taut; he lay down in it and suddenly crouched down with widespread wings, repeating this activity three times. My daughter said, "It looks like nest building." The next day he repeated this activity in some lamb's-quarters in a corner of the bamboo cage; he backed a bit, spread out his wings and brought them together again.

I did not see this behavior again until Sept. 15 when Y was 52 days old:

"Y is 'scrape-making' in the black cloth on the table, getting into a corner, pulling with his bill. B comes to fight him; they open bills at each other. Later B pulls Y's tail. Y cuddles down and spreads out his wings as R did in the net. B pulls at the cloth. Then Y flies to the cage 60 cm. distant, gets a piece of pigeon grass and pulls it around the outside of the cage several times. Then back to his nest without it. B also does scrape-making."

Nest molding was a favorite occupation for all 3 birds during their third month, the sites chosen being the cloth with which I covered the cage at night, a mop, a sweater, an apron, a sock and occasionally a small box filled with earth and dead leaves. After the middle of October the birds seldom indulged in this activity, my last records being Nov. 2 for Y and Nov. 13 for B. With the Michigan birds I have only 2 records (S at 35 days, D at 38), but I was absent from Chicago when they were 60 to 78 days old.

This molding was a complete surprise to me as I did not know that the nesting male ever did it. Dr. Lorenz wrote me: "As to the nest-molding Song Sparrows, I think it often occurs that *young* males perform female instinctive actions, much as they show female plumage. I once heard a young Mallard drake give the full female courtship call, the loud *quaquaquaquaquack*, which sounded very curious when performed with a male voice! This bird proved to be a perfectly normal male. Also young cocks have the female note of a low singing when they are half grown; it disappears completely after they get sexually mature."

Twice in July 1929 I noted young Song Sparrows, probably 5 to 6 weeks old, picking up 2 or 3 bits of dead grass, then dropping them. The hand-raised males carried grasses about, but this may have been merely experimenting with objects; they often have torn newspaper and sometimes dropped bits into the bath dish. It is possible that J may have shown nest molding or carrying of material before she came under my observation at the age of 5 months.

There are many records of young birds carrying nesting material: Tree and Cliff Swallows in August (Brewster 1898, Chapman 1898); a male Mockingbird at 8 weeks, a female at 9½ (Laskey letter); and female Mistle Thrushes before they are full grown (Heinroth), while European Barn Swallows have even helped build nests—about a week after leaving the nest (Astley 1934), somewhat older (Chigi 1934). Southern Cormorants while still in the nest help to work in loose material (Kortlandt 1938:35). With the Crowned Hornbill the young repair the nest wall after their mother has broken out of it (Moreau 1936). Ring Doves have been seen sitting on eggs at 21 and 51 days, while a female gave the nest-call at 56 days (Craig 1909:65), and a female Herring Gull did likewise at 50 days (Portielje 1928).

3. *Caring for Young*

Occasionally phases of parental behavior appear in young birds: feeding still younger birds has been reported many times, while brooding, nest sanitation and "injury feigning" seem rather exceptional.

Sometimes young birds feed younger brothers and sisters in nature: Eastern Bluebirds (also removing excreta) (Nice 1931a, Wetherbee 1933b); Mountain Bluebird (Mills 1931); Wheatear (Nicholson 1930); Long-tailed Tits (Morbach 1934) and Barn Swallows (Forbush, 1929:152, White 1941, Williamson 1941). Among non-passerines it has been reported for Gallinules (*Gallinula chloropus*) by Grey (1927) and McIlhenny (1934); in a South American Rail in captivity—*Laterallus leucopyrrhus* (Meise 1934); European Coot (Ruthke 1939); Smooth-billed Ani (Davis 1940a); and Groove-billed Ani, also "protecting young" (Skutch 1935). Young Harlequin Ducks went through an "injury-feigning" display over a younger brood (Tijmstra 1933).

In captivity young birds, hardly able to feed themselves, may help feed still younger individuals of the same or other species. This has been reported for the Bluebird (Miller 1910); Robin (Favell 1935); Chipping Sparrows about 39 days old feeding a younger Red-winged Blackbird (Laskey letter); Barn Swallows (Chigi 1934); Jackdaws (Strauss 1938a); Indigo Bunting (Sanborn 1932b); and White-throats (*Sylvia communis*), Flycatchers, Tree Creeper and Tree Pipits (the Heinroths, 1924 I). One nestling Crowned Hornbill offered food to its nest-mates (the Moreaus 1941). The earliest record for this behavior seems to be that of a hybrid dove 12 days old that fed its nest-mate (Whitman 1919:67).

Mr. H. R. Ivor writes me that he put 15 birds taken from the nest with a hand-raised unmated female Wood Thrush and a 48-day old female Bluebird. "These two took entire charge of the little ones and reared all to maturity. The poor old thrush worked from dawn to dark—when she ate I could not see—and the little Bluebird certainly did her share although she still wanted me to feed her! Then when the young Bluebirds were hatched in the bird-room she helped to take care of them. It was a most comical sight to see her brooding the nestlings with the mother, both sitting on the nest at the same time."

D. "ANTING"

The curious phenomenon where birds sometimes seize ants and rub them on their wings has been reviewed by McAtee (1938), Nice and ter Pelkwyk (1940) and Ivor (1941 and 1943). Records of its occurrence in additional families have been reported by Thomas (1941) and Bourke (1941). It has been recorded in 13 passerine families and at least 38 species. The families are Corvidae, Timaliidae, Cinclidae, Mimidae, Turdidae, Muscicapidae, Bombycillidae, Sturnidae, Meliphagidae, Compsothlypidae, Icteridae, Thraupidae and Fringillidae.

Ivor (1943) has made an intensive study of anting with his hand-raised birds, carefully watching scores of instances from a distance of 16 inches, some of the birds even anting on his hand! By this means he has been able to discover just what the bird does: it brings the wing forward and out from the body, and *rubs the ant on the ventral surfaces of the outer primaries* from the wrist to the tip. At the same time the tail is brought forward and sometimes stepped upon. These exhaustive observations (as well as recent experiences with Y) show that the sketches of Song Sparrow anting (Nice and ter Pelkwyk 1940), although giving a general idea of the strange attitudes assumed, are not correct in detail.

Not all the species in one family anted; for instance in the Turdidae, the Wood Thrush, Hermit Thrush, Veery and Robin anted, but the Bluebird and European Blackbird did not. The following birds in the aviary did not ant: Flicker, Horned Lark, Cowbird, Purple Finch, Greenfinch, Pine Siskin and Brambling. Ivor has no suggestion to make as to the biological function of this strange instinctive activity.

As to the age at which anting first appeared, all my hand-raised Song Sparrows met many ants before they were a month old, but the earliest age at which anting was seen was 36 days with B, and 37 days with A. Mr. Ivor's Veeries, Wood Thrushes and Cardinals were 37-38 days old when first given ants; the other young birds were slightly older. All anted at their first opportunity (Ivor letter).

Y first showed this activity, not with ants, but *with staghorn sumach berries* Nov. 24, 1938 and July 25, 1939 (Nice and ter Pelkwyk

1940); these berries were constantly available. So far as I know he was given his first ant since he was a month old in the spring of 1939; this was a small ant and was eaten. In October 1939 on being offered a large black ant (*Campanotus*), he *started to eat it*, dropped it and began to ant. On May 30, 1940, we gave him a number of *Formica rufa;* he hurried to catch them as they ran, and as soon as he crushed one, started to ant, repeating the process several times and eating some of his victims.

A year later I offered for the first time the Bobolink K a carpenter ant; he took it and dropped it into Y's cage. Y picked it up and at once anted, but did not eat the insect. The next ant was also dropped by K. I then obtained a number of these ants which I stunned. K ate two, then wiped his bill. An ant started to move, K caught it and *anted with it so strenuously that he fell over backwards.* It would seem from these observations on Y and K that anting behavior is first released *through the acid taste* (or smell) of the ant or other object, and that the ant itself is thus learned as the appropriate source of the stimulus.

E. SUMMARY

1. The post-juvenal molt started in 4 hand-raised birds in mid-September at the age of 7 weeks; in others in late July at 6 weeks. When only the body feathers were involved, the molt was complete in 3 weeks; in the one case where the rectrices were also molted, it lasted 5 weeks.
2. On Interpont about half the breeding males and a smaller proportion of the females migrated to the south each fall, the others being permanent residents.
3. The Massachusetts Song Sparrows showed very little "migration restlessness", some indications occurring from Oct. 30 to Nov. 5, and again in February.
4. Attempts at copulation were seen with the Song Sparrows starting at 23, 75, 92 and 95 days. Instances are cited in young birds of other species, the youngest being a Bicknell's Thrush at a little over a month and a Starling at 41 days.
5. B, R and Y indulged in considerable nest-molding between the ages of 35 days and 3½ months.
6. Instances are cited of the carrying of nesting material by young birds of a number of species.
7. Cases of young birds feeding still younger birds are cited, with 2 instances of nest sanitation, one of brooding, and 2 of protective display in juvenile birds.
8. Anting was observed in 3 of the hand-raised Song Sparrows, both with ants and sumach berries; it first appeared at the age of 36-37 days.
9. Anting has been reported in 38 species of 13 families. This instinctive activity consists in the bird's rubbing the ant on the ventral surface of the outer primaries. It would seem that anting behavior is first released through the acid taste (or smell) of the ant or other object, and that the ant itself is thus learned as the appropriate stimulus.

CHAPTER VII

Song Sparrow Society in Fall and Winter

With some species pairs live separated from each other in territories throughout the year, while some are territorial while nesting, yet social during fall and winter. The Song Sparrow falls somewhere between these extremes. During the long breeding season Song Sparrow society is organized on the basis of separation of pairs into territories. In fall and winter the resident birds stay on or near their territories, although not defending them at that season, except that an adult male in fall will drive off a young male which is trying to appropriate the former's territory. Winter resident birds are also sedentary, remaining as a rule within the space of an acre or two; this was true both in central Ohio and Oklahoma. It is chiefly in cold, snowy weather that Song Sparrows come together in loose flocks.

Let us examine the social organization of the Song Sparrow uncomplicated by the exigencies of the breeding season. There are two basic factors in its contacts with other members of the species—social need and dominance.

A. REACTIONS OF SONG SPARROWS TO OTHER BIRDS

There are several ways in which a Song Sparrow may react upon meeting another bird: ignore it; be positively attracted to it; attempt to drive it; retire before it. Its response depends partly upon the time of year as shown in Table VI.

TABLE VI

RESPONSES OF SONG SPARROWS TO OTHER BIRDS

(X) = response present; (XX) = response pronounced; (O) = response absent

Response	Winter		Spring	
	To Song Sparrows	To Other Birds	To Song Sparrows	To Other Birds
Ignore	X (mild weather)	X	O	X
Attracted to	X (cold weather)	X (cold weather)	XX (to mate)	O
Drive	X	X	XX	XX
Retire	X	X	X (when trespassing)	X

In winter all 4 techniques are employed in regard both to other Song Sparrows and other species. In spring, however, a male on his territory ignores no other Song Sparrow, he is attracted only to his mate, he is despotic in all his relations to other Song Sparrows so long as he is on his territory, and only flees when he has been trespassing on another's territory. As to other species, he shows all the responses but that of attraction to them.

Let us consider the behavior of a Song Sparrow in winter. In mild weather no attention is usually paid to other Song Sparrows or to other birds except predators. In cold weather Song Sparrows flock with members of their own species and other Fringillidae that possess a somewhat similar call note and similar feeding habits—Juncos, Tree Sparrows and Cardinals. At feeding shelves certain Song Sparrows are despotic to members of their own species; most of them are despotic to other species their own size and smaller. Some, of course, have to give way before a despot of their own species, while all usually retire before larger species at the feeding shelf and when a hawk is sighted. The subject of the Song Sparrow's relations to other birds will be discussed further in Chapters XII and XXI.

B. Social Integration

A fundamental mode of behavior found throughout the animal kingdom has been variously called social appetite, social drive, social instinct, gregariousness, and social need. In my opinion the last term, suggested by Katz (1937) has much to recommend it.

Social need may be defined as an innate mode of behavior depending on a bond to other individuals that typically increases with the unfamiliarity or unfavorableness of the environment.

An individual derives confidence from the familiarity of the environment; when this environment is altered, support may be gained from another source that gives a sense of familiarity, namely the proximity of other individuals. Allee (1931:357) writes, "Evidently mutual interdependence, or automatic co-operation, is sufficiently widespread among the animal kingdom to warrant the conclusion . . . that it ranks as one of the fundamental qualities of animal protoplasm, and probably of protoplasm in general."

After speaking of accidental groupings of animals that persist because of "social inertia, the tendency of animals to continue repeating the same action in the same place," reinforced by "the social force of toleration for the presence of others in a limited space," Allee (1938:43) says:

"A decided advance is made when animals react positively to each other and so actively collect together, not primarily because the location is favorable or through environmental compulsion, but as the result of the beginnings of a social appetite. In early stages of such reactions, the movement together may come primarily because the collection of isopoda or earthworms or starfishes are substitutes for missing elements in the environment."

He mentions "the grouping of foreigners in a strange city," stating that "basically some of the factors involved are similar. Perhaps there is a closer connection between such aggregations in the wide expanse of a clean aquarium and the schooling tendency found among many fishes of the open sea; perhaps the same phenomenon accounts for the flocking tendency of many birds, as well as mammals on the equally monotonous grassy seas of temperate plains," p. 46.

Some fish "school only under adverse circumstances" (Noble and Clausen

1936:313). The aggregational behavior of bass under adverse conditions "may be considered . . . a manifestation of social behavior of great possible survival value" (Langlois 1936). With sunfish, according to Breder and Nigrelli (1935:46), "Schooling may be considered as a primary impulse with cases of non-schooling as inhibitions of it . . . Adverse conditions, generally, allow aggregating effects to appear. The results to the individual and species may be valuable, neutral, or harmful. For example, temperature, light, CO_2, fright and various toxic substances will cause aggregation." DeKay's snakes (*Storeria deckayi*) aggregate when frightened or "when environmental conditions are unsuitable" (Noble and Clausen 1936:271). Various insects congregate for the night, and this is true also of many birds. Some snakes and insects collect together for hibernation. Red deer herd when the weather turns cold (Darling 1937). Birds, migrating in groups, gain social support in strange environments.

As mentioned above it is only in cold, snowy weather that Song Sparrows flock. When frightened, B and Y took refuge in the same corner, although ordinarily they fought under conditions of close proximity. They never fought in the unfamiliar environment of the dining room.

Heinroth (1912a) mention Brehm's account of the "intelligence" of a pinioned Whooper Swan that, when danger threatened, associated with a Mute Swan: "It is a matter here of the instinct, widely spread in the animal kingdom, that the social drive *(Geselligkeitstrieb)* increases with danger. In the herd the individual feels safer than when alone—and this is also true with man. Young and inexperienced animals behave thus, and I can see no intelligence in such behavior, for there is no profiting from personal experience."

1. *Mechanisms for Group Integration*

In his book on "Les Origines de la Société. Essai sur les Sociétés Animales". Rabaud (1931) states that a group seems to be composed of a variable number of animals each behaving as if living alone: in this he shows himself entirely unacquainted with social animals in nature. With many birds, as Lorenz (1935:347) says, "we find truly organized societies, whose supra-individual function comes about through definite social instinctive actions and chains of instinctive actions of their members." Unlike human societies, these associations are not based on tradition, nor on insight into the benefits of cooperation. "By closer analysis of the instinctive actions that effect the cooperation of the members of such a highly organized bird society, it becomes apparent that seemingly very complicated behavior of the society is brought about through remarkably few and simple reactions of the individuals." A striking difference between insect societies and those of birds, is that, "just as with the higher mammals and man, the majority of social reactions with birds are bound up with personal acquaintanceship of the individuals", p. 348.

A number of mechanisms for group integration are listed by Lorenz (1935, 1937a) under releasing functions of the "social-companion": "inducing of reaction by 'contagion' and so-called imitation"; "releasing of the following reactions"; "of responses to warning"; "social attack reactions"; "responses to the disappearance of the social companion"; "interlocking of instinctive actions pertaining to the pecking-order and to nest-protection".

Tinbergen (1939a) points out that the actor's "behavior may evoke the same behavior" in the reactor "or a different reaction." In these functions mentioned by Lorenz, the first four involve similar behavior in both actor and reactor, but the contrary is true in the last two. The first five will be discussed as pre-eminently characteristic of social integration; the last, being a disruptive as well as cohesive force, will be treated under the subject of "dominance".

a. Suggestion

The "inducing of reaction by 'contagion' or so-called imitation" is a matter of suggestion and not of conscious imitation. (An example of suggestion in human beings is the infectious nature of yawning, a very different matter from, for instance, a person's careful imitation of table manners in a foreign country.)

Crawford (1939:411) calls this *social facilitation,* which "can be regarded as one of the most basic forms of social interaction. In the literature on animal behavior its meaning has been restricted to increments in the frequency and intensity of responses already learned by an individual, shown in the presence of other individuals usually engaged in the same behavior. Imitation, on the other hand, has referred to observational learning in problem situations."

The young Song Sparrows were apt to do many things together—eating, preening, bathing, nest-molding. In the winter whichever bird was caged, although apparently content most of the time, occasionally tried hard to get out on noticing his free brother eating weed seeds in a box below him or tearing up newspaper.

A flock of Herring and Lesser Black-backed Gulls was studied by Richter (1939) at their "headquarters"; it was noted that the activities of preening, sleeping and changing place worked suggestively on all the birds, whereas sex behavior stimulated corresponding activity only in the respective species. Palmer (1941) tells of the social activities of Common Terns, how they bathe together, and fish together, and carry out community activities based on fear and defense.

The usefulness of this tendency to go where another has gone is apparent in the matter of locating sources of food. The suggestibility that tends to make all do the same thing at the same time contributes to flock solidarity in birds with a definite flocking tendency, for all eat at the same time and are ready to fly at the same time. Other evidence of a positive response to members of the species was given in the spring in Ohio when I often noticed that a newly arrived male would attempt to locate his territory in an area already full of Song Sparrows instead of selecting some of the suitable places not yet occupied.

b. Following Reactions

The "following reaction" is perhaps the most characteristic feature of the social need. When an individual is not strongly oriented himself, the natural course is to follow another individual. This would seem to be a special manifestation of "suggestion" or "social facilitation".

With the hand-raised Song Sparrows there was a marked tendency in the fall to follow one another; when one flew to my desk, the others were apt to do likewise, while expeditions into the dining and living room were usually made two or three together. There also seemed in early fall to be some tendency to follow a flying brother without hostile intent. The young Jackdaws raised by Strauss (1938a) wandered around together; "when one of them was investigating something, the other two had to be there too."

With the Song Sparrow, a species that possesses no strong flocking tendency, there are no special structures nor notes to induce following. The case is otherwise with many species that are markedly social during the non-breeding season: the Cedar Waxwing and American Tree Sparrow have characteristic flight notes; the Junco and the Longspurs possess both flight notes and white tail feathers. Apropos of the white bar at the base of the tail in Wilson's Petrel, Roberts (1940a:158) suggests, "Possibly it acts as a 'releaser' eliciting a flying-in-pursuit reaction." Both Heinroth and Lorenz stress the increased social bond during flight.

Flocks of Song Sparrows were not exclusive affairs, as was shown one January day when 50M left the home flock in our garden and worked his way 200 meters south where he joined another flock; 5 days later he was back again. 4M, who by right of age, experience and familiarity with the locality, might have been expected to have been leader of this home flock was apt to bring up the rear. In fact there was no leader. The lack of leadership has been noted in flocks of the domestic fowl (Fischel 1927), the Coast Bush-tit (Miller 1921a), Long-tailed Tit (Paechnitz 1936), and Chickadee (Odum 1942).

Flocks of some species appear to be more or less closed. This was true of the Valley Quail studied by means of colored feathers and colored bands by Emlen (1939). Bob-white may "violently exclude strangers from covey groups" (Errington 1941:91). Jackdaws will not allow any new members to join the flock except in fall (Lorenz 1931). The Anis defend their communal territory from strangers (Davis 1940a), as does the Guira Cuckoo, although less energetically (Davis 1940b); Dr. Lorenz's Greylags were strongly antagonistic to 2 strange Greylags added to their flock in June. At the Kellogg Bird Sanctuary the Blue Geese refused to allow a wild bird of the species to associate with them.

As to Black-capped Chickadees, birds transported to new localities were not driven off from the new flock, but were relegated to a low position in the order of dominance, although some later attained a higher position (Odum 1941a:118). Unbanded Chickadees "that finally joined the old birds at the feeders had to fight their way into a partially closed hierarchy before being accepted by the old-timers" (Wallace 1941). In winter flocks of Chickadees in Wisconsin, Hamerstrom (1942) found that "old-timers appeared to have the advantage in their early encounters with new-comers." A new-comer showed uncertainty in his behavior and this "may have caused the others to pick on him." All the fights were over food. It is likely that "intolerance towards new-comers appears only in the larger flocks". In a flock of Blue Tits, "Residents are dominant to nomads and the social order of the residents is related to territory" (Colquhown 1942:240). Much the same is true of Marsh Tits (Morley 1942). From observations on color-banded Tufted Titmice in Ohio (Nice 1933c) it appeared that these birds remained in small flocks of about 8 birds in rather definite ranges of some 8 hectares (20 acres) during winter. Late in February, however, the flocks broke up and I began to catch my banded birds in traps set for Song Sparrows more than 500 meters from where the Tits had been banded, besides seeing 2 new birds in the range of the local flock.

With Geese there are certainly leaders. In these birds and with Cranes the young birds depend on the leadership of their parents and will not migrate without them (Heinroth 1912a).

An interesting example of "leadership" of a flock is given by Lorenz (1935:352). His pet Jackdaw "Tschock" associated in flight with a flock of Hooded Crows. "In such cases when I called the Jackdaw and he flew hurriedly in my direction, the whole flock of Hooded Crows came after him, to turn aside in fright when almost upon me. This following the example of one who 'knows what he does' gives food for thought. Since these intelligent Corvidae meet with many experiences with increasing years, and gradually become more purposeful and decided in all their movements, I believe that with them the old experienced leader plays an important biological role."

c. Responses to "Warning"

The Song Sparrows respond instantly to evidences of fright in their companions; a sudden flight or the fear note given by one will send the others into hiding immediately. The bird does not "warn" its companions nor even its young; it gives a cry because frightened itself; this behavior and these notes are understood instinctively by all members of the species. Song Sparrows also react to evidences of fright in other species with which they associate.

One December morning I was watching a mixed company of Cardinals, Juncos and Song Sparrows on Interpont when suddenly they gave warning cries and dashed to shelter where they stayed motionless and silent. I did not see the Accipiter which must have been the cause of the terror. In such a case the actions and notes of these species are sufficiently alike to serve as signals for fleeing in the others. The Cedar Waxwing and Song Sparrow A responded to each other's fear notes (Nice 1941a). The Goldfinches became alert at Y's *tik-tik-tik.*

Black-capped Chicadees were "definitely the leaders" in mixed flocks watched by Odum (1942); they "were much the noisiest and by their vocal signals seemed to control the flock. Warblers and vireos react quickly to many of the chickadees' signals particularly the warning 'freeze' call. Many times attacks by accipitrine hawks were observed to fail completely because the warning calls of the alert chickadees instantly 'froze' the entire flock before the hawk could get into striking distance," p. 511.

Although fear notes of closely related species are undoubtedly recognized instinctively, in other cases learning may be involved.

"Perhaps the simplest instance of a learned reaction", writes Tinbergen (1939a:215), "can be observed in places where birds of several species are breeding in close proximity to each other, as for instance in mixed colonies of Terns and Gulls. The Gulls learn to flee at the alarm-call of the Terns. In much the same way, birds of one species can learn to 'understand' the threatening behavior of individuals of the other species. Black-headed Gulls, for instance, learn to avoid threatening Sandwich Terns in colonies in which both species mix."

Learning may also have an influence in the response to alarm cries of members of the same species. "Every Herring Gull reacts to the alarm call of other individuals, but the pattern and the intensity of the reaction depends on which neighbors are calling. The call of neighbor *P* always causes sudden flight, whereas a similar call uttered by neighbor *Q* may result in only a slight increase in attentiveness. The animal 'knows' by experience that *P* warns only when danger is near, and that *Q* often warns because of a distant disturbance" (Tinbergen 1939a:215).

We often read of social birds and mammals "posting sentinels", but we are never told how such "posting" could be effected. Selous (1927), Yeates (1934:76) and others have combatted this idea with many examples where the supposed sentinels themselves left, but gave no warning to the flock. Some individuals are more alert than others and doubtless do more than their share of watching. This is true of the hind that is leader of a group of Red Deer (Darling 1937). In regard to the Sierra Nevada Rosy Finch, Twining (1940:69) writes, "A bird when alone appears to be more wary than when it is one of a flock, although there seem to be certain birds in every flock which are more sensitive to danger than others, or that act as sentinels to warn the flock of the approach of an intruder." It is hard to imagine by what technique flocks could "post sentinels".

d. Responses to Disappearance of the Social-Companion

The Song Sparrow's call note *tsip* is heard most often in the autumn, since the social bond is evidently strong at the time of the fall migration. In the spring and summer one of a pair gives it when it has lost track of the whereabouts of its mate. This "lonely" note is a device for keeping in touch with others of its kind—*Stimmfühlung* as Heinroth (1924) calls it.

With my hand-raised birds in the fall when one went into the next room, he usually called *tsip*, the others sometimes responding to him; perhaps the bird was reassuring himself in the new situation by keeping in contact with the others. In January the room had become familiar, and it was the bird that was left behind —confined in the cage—that was more apt to call than was his brother. After R was killed in October, the others called *tsip* appreciably more than usual for an hour. After B was killed in February, Y uttered many *tchunks*, the note that often expresses disturbance.

In 1940 to 1941 I used to take A into the kitchen once a month to test him with the mounted Barred Owl; Y was usually restless and called *tsip* during these periods. On January 6 he gave 27 *tsips* in 10 minutes; on February 8 he gave *tchunks* at the rate denoting "weak alarm" (see Chapter XXI); in April he and A answered each other with *tsips*.

Atlantic Murres respond to the loss of a neighbor with great uneasiness (Johnson 1938). This reaction is even more pronounced in a Jackdaw colony, where the birds go out to search for the missing member (Lorenz 1931).

e. Social Attack

The mobbing of a predator—owl, cat, snake or hawk (Selous 1931:177)—serves as a social defense, for the enemy cannot successfully hunt with a crowd of scolding birds around. This mobbing probably at times serves to condition young birds as to predators, and here we would seem to have a primitive culture, a passing on of experience by tradition. Twice when an adult Song Sparrow was carried some 400 meters in a darkened gathering cage with a Cowbird, the Song Sparrow gave loud screams; these brought out all the nesting Song Sparrows along the way, their crests up and responding with *tchunks*. In this reaction we have a suggestion of the social attack on a predator shown by Corvidae. Jackdaws attack any predator carrying anything black (Lorenz 1937); Magpies and other Corvidae try to attack the predator from behind (Lorenz 1935:358); Ravens and Hooded Crows attack enemies that have caught one of their fellows (Goethe 1940a). See Chapter XX for further discussion of this subject.

C. SOCIAL DOMINANCE

In the first five mechanisms for social integration the animal is predominantly a member of the flock. Each member is, however, an individual and at times asserts his individuality by the attempt to dominate others. Such behavior may or may not make for flock solidarity. When clearly defined, it depends upon personal recognition between members of the flock.

The dominance "need" or "drive" is an expression of self-assertion. Noble (1939b) calls it an "aversion". Maslow (1935:58) defines the dominant animal as "one whose behavior proceeded without deference to the similar behavior patterns of the subordinate animal." Dominance has also been defined as one individual controlling the actions of another. Allee, Collias and Lutherman (1939:413) say, "Dominant hens are characterized by the lack of any attempt to avoid other members of the flock." Dominance is intimately bound up with the matter of territory (Chapters XII and XIII) and may also play a part in pair formation (Chapter XVI); here we will deal with it in its simplest form, as between individuals in winter.

1. *Social Dominance in the Song Sparrow*

In the fall Song Sparrows frequently chase one another, while in the loose winter flocks there is some driving, particularly at feeding shelves.

The most marked instance of this was the following:

January 22, 1930.—7° C. Four unbanded Song Sparrows are at the feeding station. One is very aggressive, flying from 2½ meters and knocking away a quietly eating Song Sparrow, even though the tyrant does not care himself to eat. 4M came and ate unmolested. Once when the tyrant attacked, I heard the *weech* cry.

At feeding station in Ohio Song Sparrows usually drove English Sparrows and Juncos and sometimes threatened Cardinals (see Chapter XII).

As mentioned in Chapters II and III anti-social behavior began at 17 days with the hand-raised Song Sparrows, the first fight taking place at 19 days. Until the 1938 brood was nearly 2 months old there were occasional bickerings, especially between R and B; chasing was more or less indiscriminate, although on the whole R was top bird, Y middle and B at the bottom. At 2 months, however, B suddenly became despot over Y and 3 days later (Sept. 24) over R. Y had difficulty getting baths as both brothers drove him away as soon as they noticed him in this occupation. (In regard to their captive White-throated Sparrows, Wessel and Leigh (1941) state, "In none of the experiments did the low birds bathe at any time during the experiments.") Many fights were staged between R and Y; ond such occasions B often hurried to the scene giving the *tchunk* note showing disturbance, or the threat note.

After R's death on Oct. 14, B was the benevolent despot over Y, warning him with the threat note when he came too near at meal times. The first week of November Y forged ahead of B in song development and on the 7th he became despot—and a real one. The next morning B was benevolent despot once more, but only for a day; it became necessary to cage one of the birds. From then on till B's death Feb. 2 there were 17 reversals of dominance. These were not effected by fighting; all I can say is that one bird gained confidence and intimidated the other through his loud singing.

In 1939 a similar situation of fluctuating dominance held with the Michigan birds during their second month, although in general D mastered F and S. On my return from a 2½ weeks' absence I found the order fixed in the 80-day old birds—S, D, F. S and F shortly came to their ends. All fall Y dominated D, but in December Y suffered from a protracted case of diarrhoea, and D burst into adult song in the space of 6 days and on Dec. 22 became master. It was not until Jan. 17 that Y again began to sing freely and at the same time became dominant; however there were a number of reversals this winter as well as the previous one. Here Y's illness nullified the advantage of age, and once D had had the mastery, he was able to regain it several times even after Y's vigor was restored. The third winter Y consistently dominated A who never attained adult singing.

These changes of dominance between the male Song Sparrows were closely connected with territorial behavior and will be discussed at greater length in Chapter XII. The day-by-day record of dominance, singing, etc., is given in Appendix II.

2. *Social Dominance in Other Birds and Other Animals*

Social dominance may be of different degrees. The least definite, called by Tompkins (1933:100) "supersedence" is one in which "any approaching bird could successfully usurp the position of any possessing bird". This "fluid relationship" was found in the Golden-crowned Sparrow. Rosy Finches chase each other, first one pursuing, then the other (Twining 1940), and the same was true of European Blackbirds (Morley). Selous (1933:157) describes similar behavior with Linnets displacing each other on thistle heads, "Always the second arrival usurped the first one's place, and this seemed to be accepted by the bird displaced as a part of the inevitable." It would seem as if much of the chasing seen in fall flocks of warblers and other birds were of this indiscriminate nature.

A more definite situation is that called by Allee "peck-dominance"; here there is a give-and-take relationship in which one individual is usually, but not always, dominant, for the subordinate bird wins a number of the contacts. With Tompkins' captive Nuttall's Sparrows, "although dominance was shown, it was constantly changing." Peck-dominance has been found in flocks of Shell Parakeets (Masure and Allee 1934b), domestic pigeons (Masure and Allee 1934a), Ring Doves (Bennett 1939) and Canaries (Shoemaker 1939b).

The third condition—"peck-right"—exists among domestic chickens (Schjelderup-Ebbe, Allee and co-workers) and various species in captivity, as Spotted Towhee (Tompkins 1933), White-throated Sparrows (Wessel and Leigh 1941), and Ruffed Grouse (Allen 1934). Here the dominance is rigid and independent of place. In nature peck-right exists in Jackdaw colonies (Lorenz 1931, 1938). With Black-capped Chickadees, Odum (1942) found peck-right existing at the top and bottom of a flock, but peck-dominance obtaining among the intermediate birds. Other recent studies on dominance in flocks of color-banded Titmice have been made by Hamerstrom (1942), Colquhown (1942) and Morley (1942).

The young Song Sparrows showed supersedence during their first month, peck-dominance during the second, and peck-right from the third month.

Peck-dominance in pigeons was analyzed by Diebschlag (1941) and found to be strongly place-conditioned; the peck-order comes from the endeavor of each bird to defend a certain area from other members of the flock. The bird that soonest becomes familiar with a new place becomes despot. The confidence of the bird is the all-important factor. With Ring Doves Bennett (1939:343) found that, "Usually one or more birds in each [flock] adopted definite locations in the cage and tended to defend these against all intruders." Canaries "subordinate in neutral territory become dominant in their nesting territory" (Shoemaker 1939b).

All these birds tended to have *peck-right in certain places*. The situation with my hand-raised Song Sparrows was peck-right with many reversals of dominance, partly conditioned by the lack of adequate territorial facilities for two birds.

The outstanding example of a highly socialized bird that is known to have a definite peck-order in the wild is the Jackdaw. Here every "bird is jealous of his own position, constantly bickering with those that are his direct subordinates, but distinctly tolerant of those that range far below himself" (Lorenz 1938:210). As in Geese, wives take the rank of their husbands. The "despot" is in some sense the leader, for when "an inexperienced member of the flock loses its orientation, it is at once sought out and led home by some bird which knows the way, very often by the despot of the colony himself, who seems to have some special 'responsibility' in such cases" (1938:212).

Examples of social dominance in other species in the wild have been reported occasionally, i.e., pairs or males are mentioned as dominant over other pairs or males, *despite the factor of territory*: Herring Gulls (Goethe 1937), Mute Swans at Lake Guja (v. Sanden 1935), Erect-crested Penguin (Richdale 1941b), Black-cock (Lack 1939a), Gould's Manakin (Chapman 1935). With Bob-whites, "In one case a cock fought and easily vanquished another that up to the time of mating had been his master" (Stoddard 1831:18). In each group of displaying Sage Grouse there seems to be a "dominant cock", a "sub-cock", and on the fringes a number of still more subordinate cocks (Scott 1942).

Although most of the investigations on peck-order have been made on hens (White Leghorns at the University of Chicago), it is a question as to how social a bird *Gallus domesticus* really is. Strangely enough it is not definitely known whether the Jungle Fowl is polygamous or monogamous (Mayr 1939). The fact that hens depend so much on fighting rather than on intimidating ceremonies points to a low development as a social bird.

Often the despot interferes when two subordinates fight. I first noted this in B; the next fall Y gave the threat note when D and S quarrelled, and in the winter, D, when despot, gave it when he heard Y and J fighting, even though he could not see them. Y gave it when the male Goldfinch chased the female and he ***tchunked*** when he heard Mrs. Ewers' Ring Doves fighting.

This same behavior is seen in Jackdaws (Lorenz), Cranes (Goethe 1940a), and roosters (Schjelderup-Ebbe 1935), while male chameleons (*Anolis*) attack the dominating female (Evans 1938). The leader of a team of sledge dogs "often intervenes in a struggle between two subordinate dogs of the same team" (N. Tinbergen, letter), and adult male howler monkeys and gibbons interfere when young animals are playing too roughly (Carpenter 1934, 1940:135), while with monkeys in a zoo, "any display by a subordinate over a sub-subordinate is done apprehensively" for fear of the dominant (Maslow 1936). The explanation of this behavior of the dominant may be that such an animal responds by aggression to signs of aggression in another animal, even though not directed towards him.

The fact that Y, for long the underling, was a much more tyrannical despot than B, appears to be a rule of wide application in the animal kingdom.

As a girl I noticed that the lowest hen in the peck order would persecute a newcomer more than did the others. Tompkins reports the same with captive Spotted Towhees, while Schjelderup-Ebbe (1935) says in regard to chickens, "A bird which has originally been pecked by all the others becomes strikingly cruel and merciless when it finds opportunity to peck at others; the unpractised despots are the worst of despots." A Blue Tit, dominated by another, sometimes "would immediately turn on one or more tits who were its social inferiors and threaten them, while a tit low in the social hierarchy has been seen to show extreme viciousness when it chanced on a tit that it could dominate" (Colquhown 1942:238). With Marsh Tits, "dominant territory owners" seldom interfere with the subordinate flock birds, unless the former have been recently trapped, then the bird, "too fearful to enter the trap itself, finds a vent for its balked desire by driving off all subordinates to it" (Morley 1942). A male Cardinal in Oklahoma drove off all other visitors to the feeding shelf much more viciously when all the sunflower seeds were put inside the trap (Nice 1927b).

Males of many species are more aggressive than females. Bennett recorded 53.8 pecks an hour in her flock of male Ring Doves, and 20.1

per hour with the females (1939:359). It has been found with hens (Allee, Collias and Luthermann 1939), Ring Doves (Bennett 1940), Canaries (Shoemaker 1939a) and sword-tail fishes (Noble and Borne 1940) that the injection of male hormone in females increases aggressiveness and induces rises in the peck-order. With hens, "Higher social position, once won, was retained." Noble and Borne conclude that "sex hormones cause female sword-tails to rise in their social hierarchies only by bringing a reversal of sex." On the other hand, with wild Valley Quail "the three males treated with testosterone became pugnacious toward other males, but this had no effect on their position in the peck order of the covey" (Emlen and Lorenz 1942).

Interspecific dominance is of common occurrence at feeding shelves.

"Dominance-subordination patterns of behavior may be based on the recognition of other members of the flocks as individuals to which a proper reaction must be made," writes Allee (1942). "This is the method which obtains in many social groups of men, and in all the flocks of birds we have studied. Opposed to this is a type of impersonal behavior pattern such as is found in many of the groups of mice which have been studied in our laboratory. . . . Impersonal group organization depends upon a kind of unoriented, generalized aggressiveness brought in contact with similarly unoriented lack of aggressiveness."

Dominance based on personal recognition is the rule with birds, primates (Maslow 1934, 1936, 1940, Yerkes 1939) and cows, where a straight line hierarchy depending on maturity, strength and effectiveness of horns was found (Woodbury 1941). Interestingly enough, jewel fish (*Hemichromis bimaculatus*) "at an early age also learn to distinguish one another as individuals. A well-marked dominance-subordination hierarchy is formed similar to that of the domestic hen" (Noble and Curtis 1939:15), and the same is true with the sword-tail—*Xiphophorus*—(Noble and Borne 1938, 1940). See also Langlois (1934).

The unoriented type where there may be one despot with no distinctions between subordinates has been reported for a number of animals in captivity: lizards (Evans 1936a), white mice (Uhrich 1938), cats (Winslow 1938), and dogs (James 1939). With squids (*Sepia*) larger individuals dominate smaller (L. Tinbergen 1939). In a group of painted turtles, each individual dominated the next smaller (Evans 1940).

That one animal may be dominant in some relations and the other in others is pointed out by Carpenter in regard to two mountain gorillas, one of which was dominant in feeding and grooming situations, the other in play. "The dominance-submission relation may persist between two animals without fighting as a means of maintaining or instrumenting the relation" (1937:192).

"If we regard dominance as an instinct," wrote Wheeler (1939: 254) "it is certainly one so primitive and fundamental as to characterize all living substance and to be equivalent to self-preservation. Seneca said *'vivere militare est'*, which is paraphrased by Ortega y Gasset when he defines life as the 'the struggle, the effort to be itself.'"

The factor of dominance plays a part in winter flocks, in territory, and between the sexes. The first case is the most fundamental; dominance here depends on individuality, age, strength, aggressiveness, determination. In the second case it depends largely on position, on confidence engendered through familiarity with surroundings. In the third case dominance depends to some extent on privilege.

D. VALUE OF SOCIAL INTEGRATION

Although the Song Sparrow is only slightly gregarious, yet it possesses the fundamental mechanisms for group integration. They are undoubtedly beneficial to it even though much of its economy is based on separation into pairs on territories throughout the breeding season.

Other species have developed these trends much more highly. Since the bond to other individuals increases in adverse conditions, one basic element in the flocking of social species would appear to be protection against such conditions. The presence of others lends confidence.

> In regard to shorebirds, Nichols (1935) writes that they are at first suspicious, but "when they are actually among the decoys, however (well inside the zone of alarm which they hesitate to pass through), and as it were, consider themselves a part of your flock, it is remarkable how loath they are to leave . . . However independent a unit a shore-bird may be when alone, when in a flock its condition changes and it becomes for the time being an integral dependent part of that flock."

The extreme of aggregation would seem to have been reached by a band of some 100 to 150 Bank Swallows found on a cold and stormy night in September huddling together in a mass about 40 x 30 centimeters in size. The birds "formed *one* body, in which individual swallows did not react to outside stimuli—light, touch, shaking, noise" (Keyserlingk 1937).

A flock may be passively protective, as in flocks of small birds where the multiplicity of eyes ensures prompt detection of predators,—the Chickadees mentioned above, Bush-tits (Miller 1921, 1922) that "warn" and "freeze", or in European Coots which suddenly mass together so the Sea-Eagle (Wendland 1937) or Herring Gull (Selous 1931) can find no individual to capture. (The same behavior is reported for the American Coot in reference to the Bald Eagle.)

Or a flock may be aggressively protective, as in many colony nesters that join forces in attacking an enemy approaching nests or young—Terns (Marshall 1942, Vesey-Fitzgerald 1941:525), Black-headed Gulls (Noll 1924), Willets (Vogt 1938), Avocets (Makkink 1936), Red-winged Blackbirds, Yellow-headed Blackbirds (Fautin 1941), and many others.

Flocks have other functions besides those of safety. In some cases, especially with mixed flocks in the tropics, there is food value, for a large variety of insects is driven up as the group progresses. Flocks may be stimulating in the matter of facilitating breeding, as Darling stresses (1938). Starlings in very large flocks go through remarkable aerial evolutions that are never seen with small numbers.

"The cardinal quality of the herd is homogeneity", writes Trotter (1917:29), "the great advantage of the social habit is to enable large numbers to act as one" in hunting. "In protective socialism the sensitiveness of the new unit to alarms is greatly in excess of that of the individual member of the flock. . . . Each member of the flock tending to follow its neighbour and in turn to be followed, each is in turn in some sense capable of leadership, but no lead will be followed that departs widely from normal behaviour. A lead will be followed only from its resemblance to the normal. . . The original in conduct, that is to say resistiveness to the voice of the herd, will be suppressed by natural selection."

A possible hormonal explanation of territorial behavior during the breeding season and gregarious behavior outside it may be suggested. During the nesting season the secretion of male hormone from the gonads induces aggressiveness in the individual, but during fall and winter when the gonads are regressed, the attraction to other individuals is uninhibited. This explanation would hold for those colony breeders that are strongly antagonistic to their neighbors; they nest together partly for ecological reasons and partly for mutual protection. Outside of the breeding season they quarrel very little.

E. SUMMARY

1. There are four chief ways in which a Song Sparow may respond to other

birds of its own and other species: ignore them, be attracted to them, drive them, or retire before them. These responses differ according to the season of the year.

2. Social need is an innate mode of behavior depending on a bond to other individuals that typically increases with the unfamiliarity or unfavorableness of the environment.

3. With many birds we find truly organized societies, depending on definite social instinctive actions and on personal recognition between the members.

4. Six releasing mechanisms for group integration are listed by Lorenz.

5. Many activities induce similar activities in companions through suggestion or social facilitation.

6. The "following" reaction is perhaps the most characteristic feature of the social need. Most bird flocks are not exclusive affairs and have no leader. A few, however, are more or less closed groups.

7. Birds react instantly to "warning" cries or fleeing reactions of members of their own species and often to those of other species.

8. Upon the disappearance of the social-companion, the hand-raised Song Sparrows showed slight uneasiness. This is much more pronounced in highly socialized birds, such as Murres and Jackdaws.

9. Mobbing of predators serves as a social defense. It also must condition young birds to the dangerousness of certain enemies.

10. Social dominance is an expression of self-assertion.

11. With the hand-raised Song Sparrows, chasing was more or less indiscriminate until the age of 2 months, when one bird definitely became master. There were frequent reversals of dominance, not brought about through fighting; one bird gained confidence and intimidated the other by loud singing.

12. Social dominance may be of several degrees: supersedence, when the approaching bird successfully usurps the position of the possessing bird; peck-dominance—a give-and-take relationship, often place-conditioned, in which the subordinate wins a number of the contacts; and peck-right in which the dominance is rigid and independent of place. The development of the first form into the third was shown by the young Song Sparrows.

13. The domestic hen is the classical example of peck-right; since it is unknown whether the Jungle Fowl is polygamous or monogamous, it is a question as to how social a bird *Gallus domesticus* is.

14. The dominant animal may interfere between fights of subordinates.

15. The individual at the bottom of the peck-order is apt to persecute a newcomer with special vigor.

16. Males are usually more aggressive than females and the injection of male hormone into females has induced rises in the social hierarchy in birds, fish and turtles.

17. In winter flocks, dominance depends on age, strength, aggressiveness; in territorial situations upon position, the individual gaining confidence through familiarity with the surroundings; between the sexes partly upon privilege.

18. Although the Song Sparrow is only slightly gregarious, yet it shows the basic mechanisms for social integration.

19. Flocking is basically a safety measure. Flocks may be passively protective in supplying a multitude of eyes for detection of the enemy or a massed group to confuse him. Or they may be aggressively protective when the members join forces to attack the enemy.

CHAPTER VIII

Awakening and Roosting

In Columbus I made some 600 observations on the first morning notes of the Song Sparrows and about one-seventh that number on the last evening notes.

A. AWAKENING WITH THE SONG SPARROW

The suggestion was made by Allard (1930:455) that we cannot "consider the first morning song an indication of the first awakening of the birds." While the bird remains asleep with the bill tucked in the scapulars, it does not seem probable that it could become aware "of weak twilight changes." "There is reason to believe that the birds have abandoned the true sleep position and are waiting alert for the coming of the dawn long before the first morning song is delivered." It seems as if birds must wake at least shortly before they start to sing.

Paechnitz (1936) describes the awakening of a group of Long-tailed Tits: "The outside Tit took his head out from his scapulars, gave a soft *si* and hopped on the nearest twig; the others followed immediately, whispered, stretched themselves and laid their feathers smooth."

1. *Twilight*

Times of beginning to sing in the morning and stopping in the evening are usually given in terms of minutes before sunrise and after sunset. Light, however, depends primarily on the depth of the sun below the horizon, if clouds and mist be left out of account. In low latitudes the interval of time from the moment that the sun is, for instance, 6° below the horizon to sunrise is much less than the corresponding interval in high latitudes where the sun appears to pass the horizon at an acute angle. Also at the time of the spring and fall equinoxes the plane of the sun's path is steeper to the horizon than during summer, so that in the former case there is a shorter time between sunrise and sun-depth than in the latter. So *latitude* and *time of year* make a profound difference.

In studying the early morning singing of birds, we need to know the limits of twilight. Here 3 terms are used by meteorologists and navigators: astronomical twilight begins in the morning and ends at night when the center of the sun is 18° below the horizon, nautical twilight when it is 12° below, and civil twilight when it is 6° below. At astronomical twilight, stars of the 6th magnitude can be seen, at civil twilight, stars and plants of the first magnitude are visible.

Civil twilight used to be the time at which people stopped work in the evening and resumed it in the morning—from "star-setting to star-rising" as expressed in some of the old fairy tales. "If the Sun is much lower, ordinary outdoor civil operations are impracticable without artificial light" (Nautical Almanac, 1941). Civil twilight is important in navigation: "When the brighter fixed stars cease, or begin, to become visible, and the horizon being then clearly defined we have the most favorable condition for star observations," (Brown's Nautical Almanac, 1937).

In Table VII the number of minutes before sunrise at the start of these 3 kinds of twilight are given for 5 latitudes at the equinoxes and solstices; these are taken from the Nautical Almanac and Ephemeris 1941 published in London which furnishes detailed tables for the whole year and for 13 latitudes between 0° and 60°. Kimball (1916) gives tables for civil and astronomical twilight.

TABLE VII

SUNRISE AND TWILIGHT AT THE SOLSTICES AND EQUINOXES AT FIVE LATITUDES

Date		Time of Sunrise 0°	30°N	40°N	50°N	60°N
Dec.	21	5:54	6:52	7:18	7:56	9:02
Mar.	22	6:04	6:02	6:01	5:59	5:58
June	21	5:58	4:59	4:31	3:50	2:35
Sept.	20	5:50	5:47	5:45	5:42	5:38

Number of Minutes before Sunrise at the Start of Civil (C). Nautical (N), and Astronomical (A) Twilight

Date		0°			30°N			40°N			50°N			60°N		
		C	N	A	C	N	A	C	N	A	C	N	A	C	N	A
Dec.	21	22	48	75	27	57	86	30	64	98	39	80	120	58	115	176
Mar.	22	21	45	69	24	54	79	27	59	90	32	70	108	43	93	146
June	21	23	49	76	28	61	97	33	75	124	44	111	all night	106	all night	
Sept.	20	20	44	69	23	51	79	27	59	89	31	70	106	41	92	142

As to the amount of light at sunset and the start of civil twilight, Kimball gives a number of measurements with a photometer exposed on the roof of a building high enough so that the sky was unobstructed in all directions. The measurements for civil twilight in Virginia and Utah in clear weather were: .07, .2, .2, .4, and .6 foot-candles; these give a median of .2. The one reading for sunset was 33 foot-candles.

By means of official times of sunrise and sunset obtained from the United States Weather Bureau at Columbus, and the table of duration of civil twilight at 40° N. lat. given by Kimball, and time checked by an electric clock, I was able to time the start of civil twilight accurately. On week-ends from March 1934 to May 1935 I had the loan of a Weston Illuminated Meter, Model 603, from Prof. Wm. Barrows of the Zoology Department of Ohio State University, and with it I obtained nearly a hundred records morning and evening. It appeared to be fairly accurate, but was not intended to measure intensities of light much below one foot-candle; all values lower than tenths of foot-candles had to be estimated.

Model 603 is calibrated in *foot-candles,* which is a measure of incident illumination. There is no accurate way to translate foot-candles into *candles per square foot,* which is a measure of reflected light. Weston Model 650 Universal Exposure Meter, used by Oberlander (1939) and Wiliams (1941), records in candles per square foot.

The one fall in which I had the photometer showed distinctly higher light values than did the winters and springs, due no doubt to the absence of soot in the air after the summer. Readings were taken out in the open where trees and buildings did not obstruct the light. Fifteen sunrises and sunsets in clear weather from October 6-28, 1934, ranged from 27.5 to 44 foot-candles with a median of 34.5; 14 sunrises and sunsets in clear weather from December to May ranged from 22-32.5 foot-candles with a median of 26. Twelve readings for the start of civil twilight in October, 1934, ranged from .2-.28, averaging .22; 9 during the other months ranged from .2-.25 with an average of .21, the average of the 21 readings in clear weather being .217.

At the start of official civil twilight in Columbus it was rather exceptional for me to be able to read my wrist watch without the aid of a flash light; this was possible twice in October at readings of 0.25 and 0.28 foot-candles, and once in March when a nearly full moon shone near the horizon. Usually it was one to 3 minutes later when there was light enough to see colors and read the watch without aid; the photometer then showed .3 foot-candles. The next minute—at .4 foot-candles—the photometer could also be read without artificial light.

The use of such an unusual term as civil twilight has been questioned. Nevertheless, the depth of the sun below the horizon is of paramount importance in the matter of light intensity. As Allard has shown with his numerous charts, many birds tend to start singing around civil twilight—Wood Pewee, Robin, Kingbird, Song Sparrow, Cardinal, Brown Thrasher and Catbird. After all, for diurnal animals, civil twilight, when there is light enough for human beings to see clearly, is a significant stage, one which in this age of artificial light we tend to ignore.

2. *Time of Arising of the Female Song Sparrow*

It is obvious that we cannot be sure exactly when a wild Song Sparrow awakes. We may consider him fully awake when we hear the first *tsip* or *tchunk* in winter and the first song in spring, summer and fall. As for the female, her appearance is usually hard to detect, but occasionally it is signalized by her *tchunk* or chatter, or by a pounce from her mate.

The records of the rising of the female are few, but consistent—2 for K1, 7 for K200 and 2 for K201. The four on fairly clear mornings came from 4-6 (average 5) minutes after the start of civil twilight, at light values of .3, .38 and .4 foot-candles. The seven on cloudy mornings came from 4-9 (average 7) minutes after the start of civil twilight at light values of .22, .3, .38 and .4 foot-candles. The average of the 7 light values is .34 foot-candles, or about the intensity at which small objects became visible to me. The female Song Sparrows on Interpont arose about 25 minutes before sunrise on clear mornings and about 5 minutes later on cloudy mornings at a light value when they probably could see clearly. *It is at much this same light value that the male rises in January and that he starts to sing during part of the fall.*

3. *The Awakening Song Throughout the Year*

During a considerable portion of the year in Columbus the resident male Song Sparrow gives what I call the "awakening song"; i.e., about one-half hour before sunrise in clear weather and a little later on cloudy mornings—he sings a series of songs, perhaps only 5 or 6 or even fewer early and late in the season, but lasting from 20 minutes to over an hour without a break when in the stimulated or highly stimulated phase (see Table XI). In the spring and early summer he may give single songs exceedingly early, but the "awakening song" typically consists of a *series*. It is not given in late fall and early winter, nor in August and September during the molt; it also disappears after the male has been joined by a mate and does not reappear until nesting has begun—a period that may last a week to over 2 months. During feeding of the young it is of irregular occurrence.

This matter of the suppression of the awakening song at certain periods, and also the habit of night singing, make the Song Sparrow a difficult subject to work with for the first morning song, unless one knows the songs of individual birds and also follows their nesting stages. Wright (1912, 1913) declared the Song Sparrow began singing earlier than the Robin, but F. H. Allen (1913, 1915) pointed out that the very early songs should be classed as night songs, for song should be repeated and continued to show real awakening. In both Allen's and my experience the Robin starts singing very much earlier than does the Song Sparrow. Allard (1930), like Wright, including sporadic night songs, considers the Song Sparrow the earliest of all singers, in late May starting "near the beginnings of astronomical twilight."

There is considerable individuality among the Song Sparrows in their response to the morning light, for there may be a difference of 6 or more minutes in starting time on a single morning. 1M sang early, while 4M was one of the latest to start.

There are 3 main periods in the starting time of the Song Sparrow's awakening song in relation to the beginning of civil twilight, as will be seen in Figue 2 and Tables VIII and IX. In the figure records of the start of the awakening song are given for *clear mornings* from 1929 through 1935. Variations on the same dates are due both to the difference in the starting time of individuals and to temperature variations in different years.

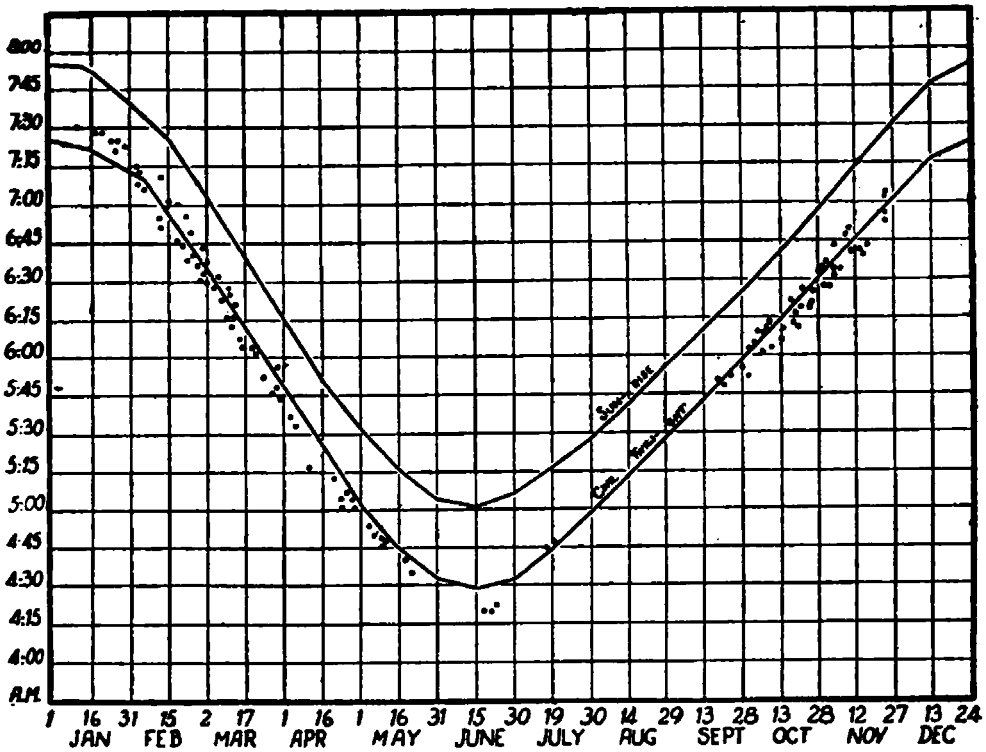


FIGURE 2. *Time of Awakening Song of Sony Sparrows at Columbus, Ohio, on Clear Mornings, 1929 through 1935, Eastern Standard Time which is 32 Minutes Ahead of Sun-time.*

In the "basic period", in January and February, the awakening song occurs about 25 minutes before sunrise and 4 minutes *after* civil twilight on clear mornings. In the "intermediate period", starting from Feb. 3 to Mar. 4, the awakening song comes close to civil twilight. This seems to coincide with the definite taking up of territories by the resident males. In the "established period" which follows from 3 to 14 or more days after the initiation of the intermediate period, the awakening song averages 4 minutes *before* civil twilight. Now the males are in full song, at least until the weather turns bleak again.

The change from the first to the second period is rather abrupt and is closely dependent on the weather. In 1931 and 1933 it came as early as February 3, but in 1934 and 1935 it was delayed till March 4 and 2. When the intermediate period was reached in February, the temperature for the 2 weeks preceding the change showed the following amounts of excess temperature: 68° and 91°C. when it came February 3 (1931 and 1933); 49°C. when it came February 8 (1932);

and 34°C. when it came the 20th (1930). For the 2 years when it was not reached until March, the temperature for the preceding 2 weeks was 44° and 40°C. *below normal.* In each case the change was preceded by a number of *successive* days of excess temperature, from 3 to 11 days in the years when it came early, 2 days when it came late.

In several Januaries there were considerable periods of excess temperature: from the 12th to 25th in 1932 140°C., from the 14th to 27th in 1933 120°C., from the same dates in 1934 70°C., and from the 7th to 20th in 1935 60°C., yet the intermediate period was never reached in January. In February, 1935, the excess temperature from the 2nd to 15th reached 30°C., but because of bleak weather in late January and an average temperature of 8°C. below normal from February 4-7, there had been only 7 days of singing from the Song Sparrows—February 2, 3, 9, 11-14—by the middle of the month. The number of days on which the Song Sparrows have sung in the daytime before the attainment of the intermediate period ranged from 10 to 25 with an average of 19.

It is evident that there is a decreasing temperature threshold for the attainment of the intermediate period in the start of the awakening song. It was never reached in January no matter how warm the weather; after high temperatures in late January and the first of February it came in early February; while after a cold February it appeared after 2 to 3 days of warm weather in early March.

Decreasing temperature thresholds were found for the start of singing, for migration, and the start of laying, as discussed in Vol. I (Nice 1937), Charts VIII and XIV and in Nice 1938b. The threshold of singing was 12.3°C. on January 7 and decreased about two-fifths of a degree each day for five weeks. The formula for the migration of the summer resident males showed that migration started (i.e., birds arrived on Interpont from the south) February 23 at 11.6°C. and the threshold decreased about two-fifths of a degree each day for a month. Thus the curves for the start of singing and for migration start at approximately the same temperatures and have a similar slope, but the dates are a month and a half apart. Singing and territorial activity are well established the fourth week in January at a mean temperature of 6°C., which is also the average temperature at which the main migration of the males took place the middle of March.

The curves for the start of laying come in April and May and are much steeper that those for singing and migrating; that for the first egg started 18.2°C. and decreased .87°C. each day thereafter for 2 weeks; that for the start of general laying started at 22.9°C. and decreased in a similar manner.

The awakening song is also given in the fall. The birds usually showed a basic period at the beginning and end of the season, while during the middle of the season they were in the established song period, starting on an average 4 minutes before civil twilight and 32 minutes before sunrise just as in spring. Singing in the daytime was not as continuous as in spring, but on fine days in October we were sometimes treated to a great deal of song.

From 1929 to 1932 4M appeared to be in this basic period from September 28 to October 7-14 (in 1930 from September 19 to October 8), and again in late

October to early or mid-November, except in 1931, when, in response to the warmest November in 50 years, the Song Sparrows remained in the period of established song till November 24 when a sudden change in the weather brought the awakening song to an abrupt close. In 1933 October was cold and 4M sang before civil twilight only on the 15th and 17th. The next 2 autumns he sang but little, never passing beyond the basic period. The other Song Sparrows sang from 2-15 minutes before civil twilight; most appeared to be in the period of established song until near the end of their singing, when the awakening song came after civil twilight.

Table VIII summarizes the appearance of the awakening song *in clear weather,* showing the basic, intermediate and established song periods in the spring, and the basic and established song periods in the fall. (Some of the January records in this and the next table are based on *tchunks* rather than songs.) Three hundred and sixty records are available for the timing of the awakening song. The range of minutes before sunrise for each period as well as the median are given; and the median number of minutes after or before the start of civil twilight is shown.

TABLE VIII

AWAKENING OF THE MALE SONG SPARROW IN CLEAR WEATHER IN RELATION TO SUNRISE AND CIVIL TWILIGHT*

	Minutes			
	Before Sunrise			After Civil Twilight
Period	Cases	Range	Median	Median
Basic				
Jan.-Feb.	47	17-31	25	4
Intermediate				
Feb.-Mar.	41	23-34	28	0
Established				
Mar.-May	113	29-49	32	—4
June	5	38-43	41	—8-9
Basic				
Sept.-Nov.	75	16-32	25	3
Established				
Oct. (Nov.)	79	22-43	32	—4

*The average length of civil twilight was 28 minutes, except in the first basic period when it was 29, and in June when it was 33.

In relation to sunrise the awakening song in the intermediate period came 3 minutes earlier than in the basic period; while the established period started 4 minutes earlier still, a difference of 7 minutes between the 2 extremes both in spring and fall. The difference in respect to civil twilight reaches 8 minutes in spring, and 7 minutes in fall.

TABLE IX

AWAKENING OF THE MALE SONG SPARROW IN CLOUDY WEATHER IN RELATION TO SUNRISE AND CIVIL TWILIGHT

Period	Minutes Before Sunrise Cases	 Range	 Median	 After Civil Twilight Median
Basic Jan.-Feb.	77	13-16	21	8
Intermediate Feb.-Mar.	22	11-29	22	6
Established Mar.-May	54	15-34	27	1
Basic Sept.-Nov.	64	11-29	22	6
Established Oct.-Nov.	21	16-31	28	0

Table IX shows 238 records of the awakening of the Song Sparrows in cloudy weather. "Cloudy" includes an even greater variety of sky conditions than "clear"; some days were partly cloudy and others very cloudy. The records fall from 3 to 6 minutes later than the corresponding ones in clear weather, the average number of minutes being 4.5.

As to light values in the 3 periods, the 69 measurements obtained averaged .32 foot candles for the basic period, .2 for the intermediate period, and .05 for the established period. In the second period the birds started to sing at 3/5 the light of the basic period, and finally at 1/6 the original light. The light values at the start of singing on clear and cloudy mornings averaged about the same. 4M was a later singer than most of the Song Sparrows; of 27 records for him and 42 for others, the first 2 periods averaged much the same, but in the last period 10 records for 4M averaged .09 foot candles, and 22 records for others averaged .03 foot candles. It is of interest that the light for the basic period—.32 foot candles—is almost the same as the value for the rising of the female.

B. ROOSTING WITH THE SONG SPARROW

Song Sparrows, in common with many other birds, retire for the night earlier in relation to sunset than they start the day in relation to sunrise. They roost in weeds, hedges and small evergreens. A little spruce on our next-door neighbor's grounds was the preferred sleeping place of 187M during the spring of 1934, of 221M during the following winter, and of 204M and his mate during the spring of 1935.

There seems to be little seasonal difference in the time of settling down for the night, observations from December through May and again in October showing a striking consistency. Table X gives the time of the last song and last *tchunk* on 63 clear evenings and 26 cloudy. With surprising regularity the last note of the Song Sparrows came 13-14 minutes after sunset in clear weather; in three-fourths of the cases the last *tchunk* came from 11-15 minutes after and in five-sixths of the cases the last song came from 10-16 minutes after, 11 cases being 13 minutes after sunset.

TABLE X

LAST NOTES OF THE SONG SPARROW IN RELATION TO SUNSET
December through May; October
Last Song

Sky	Cases	Minutes After Sunset		Cases	Foot Candles	
		Range	Median		Range	Median
Clear	35	9-23	13	27	0.8-8.5	3.
Cloudy	11	—1-12	3	5	3.3-7.	5.4

Last Tchunk

Sky	Cases	Minutes After Sunset		Cases	Foot Candles	
		Range	Median		Range	Median
Clear	28	10-22	14	20	0.6-8.2	3.2
Cloudy	15	1-9	5	4	2.7-5.9	3.9

The light intensity at these last notes in clear weather was about 3 foot candles, that is, about 10 times as high as the basic value at which the male arose in January and in fall.

In cloudy weather the last song averaged 10 minutes earlier than in clear, the last *tchunk* 9 minutes earlier. The median light value for the last song was 5.4 foot candles, for the last *tchunk* 3.9. Apparently the Song Sparrow goes to bed even earlier in relation to light on cloudy days than on clear; this is evidenced by the higher light values and also by the greater average difference in time—9 and 10 minutes between clear and cloudy weather, in contrast to 4.5 minutes in the morning. Williams (1941) found that Chestnut-backed Chickadees and Bewick Wrens "tended to come to roost at somewhat higher light intensities in rainy weather."

Song Sparrows may be noted starting for bed some minutes earlier than the figures just given. On clear evenings this might happen with males about sunset or from 6-12 minutes after, while females sought rest earlier—K200, followed by 4M about sunset (at 23.4 and 24.7 foot candles), and K200 alone 2 minutes after (19 foot candles). On cloudy evenings males have started for the little spruce 2 and 4 minutes before sunset (22.5 foot candles) and 3 minutes after, while K200 went into the rose hedge at 10 minutes before sunset (14.8 foot candles) and 6 before (19 foot candles). 4M and his mate might retire early together, but 4M often dashed out several times to drive off trespassers—Field or Song Sparrows or Juncos, finally retiring for good at a low light intensity (on April 3 at .6 foot candles, 22 minutes after sunset).

I can find only one other set of observations on the retiring time of Song Sparrows, namely those of Wright (1913) in the White Mountains at Jefferson Highlands, N. H.; 22 records in June and July of the last song ranged from 14 to 39 minutes after sunset, averaging 23 minutes. Twilight, of course, is longer in this latitude—44°N.—than at Columbus, civil twilight coming about 4 minutes later in the evening. The situation, also, was such as to catch the last light in the evening, an elevation of 1600 feet on the western slope of Boy Mountain. These two factors may well account for the fact that Wright's Song Sparrows ended the day 10 minutes later after sunset than did those in Columbus.

C. AWAKENING AND ROOSTING WITH OTHER SPECIES

Many observations have been made on the time of the first song of birds.

1. *Each Species Has its Own "Waking-Light"*

The "bird clock" is a well known phenomenon—the fact that species tend to begin singing in a more or less definite order. The most comprehensive study of this kind was made by Wright (1912, 1913); some of his conclusions were corrected by F. H. Allen (1913, 1915). In Europe Haecker (1916, 1924), Schwann (1920), Dorno (1924), Trebesius (1930-32), Marples (1939) and others have discussed the first singing in relation to light and other factors; Heyder (1934), Palmgren (1935) and Paatela (1938) studied the situation in the far north, while Meyer (1929) gives a few notes on first song in the Bismarck Archipelago. The most thorough study of the subject either in this country or abroad was published by Allard (1930); based on extended observations on a number of species and correlated with civil and astronomical twilight, this paper is a classic in its field.

Some species are better "time-keepers" than others; Allard found the Robin, Wood Thrush and House Wren best in this regard. Interestingly enough gibbons in Siam on clear mild mornings (65° F.) start calling at 5:00, while on cool, dark foggy mornings (45° F.) they do not begin until 7:00 (Carpenter 1940).

Within the species each individual may have his own "waking-light", as has been shown for European Blackbirds (Trebesius), House Wrens (Allard), various species (Schwann), Chaffinch (Paatela), Song Sparrows, and a Friarbird (*Philemon cockerelli*) in the East Indies (Meyer 1929).

In New England, according to the experiences of Wright, Allen and myself, it seems as if the earliest risers among the birds are the Thrushes, Towhee, Scarlet Tanager, some Swallows and native Sparrows, while the Wood Warblers, Vireos, House Sparrow, Starling and Carduelinae wake later. In Europe the Redstarts, Skylark, Cuckoo and Thrushes are earliest, the House Sparrow, Swift, Starling and Carduelinae coming decidedly later.

As to time of retiring, in general the earliest risers are the latest to bed. As with the Song Sparrows, most birds retire earlier in relation to light than they arise. The Starlings and Bronzed Grackles watched in Columbus in October reached the roost at approximately three times the light values at which they left it (Nice 1935a). The singing in the evening of the 9 latest singers in northern New Hampshire came to a close from 27 to 37 minutes after sunset in contrast to the start at 80 minutes before sunrise—around nautical twilight—, "a shortening of thirty-five to forty minutes" (Wright 1913:533).

Woodpeckers roost early and rise late (Sherman 1910, Wright 1913, Bussmann 1933, Tanner 1941). Jourdain (1936a) reported the close correlation with light of the arrivals and departures of a Green Woodpecker at a winter roosting box.. An interesting study of a wintering flock of Long-tailed Tits showed that on 4 clear afternoons they went to roost 15-17 minutes after sunset, on 3 partly cloudy afternoons from 5 before sunset to 2 after, and on a very cloudy afternoon 11 minutes before (Paechnitz 1936).

2. *Awakening and Roosting in Relation to Time of Year*

As the breeding season progresses, many birds awaken earlier in relation to sunrise than during the rest of the year. This was found for a number of species, including the Golden Oriole, by Dorno (1924). In my experience this has been true with Robins, Mourning Doves, Bronzed Grackles and Starlings in Columbus.

During the first part of March, Robins sang a few minutes before the start of civil twilight, then suddenly changed to the typical very early singing starting long before civil twilight, as much as 73 minutes before sunrise. This change came March 29, 1934, when the latter part of the month had been cold, but the next year with high temperatures the last half of March that stimulated nest building with this species, the change came between March 17 and 22. With Mourning Doves in March the first song was heard from the start of civil twilight to 15 minutes after on clear mornings, while in April and early May it averaged 7 minutes before civil twilight. Bronzed Grackles that roosted alone were first heard on 6 clear mornings in October, 15-21 minutes before sunrise, averaging 17 minutes, at light intensities of 1.2-4.8 foot candles, averaging 2.7. On 5 clear mornings in March and April they were first heard from 17-21 minutes before sunrise, averaging 19 minutes, at light intensities of .78-1.3, averaging 1.01. A male Starling arrived at his hole on 7 mornings (4 clear, 3 cloudy) from March 15-30 at a median light intensity of 4.1 foot candles and an average of 11 minutes before sunrise. On 5 mornings from April 4-12 (1 clear, 2 cloudy, 2 very cloudy) he arrived at a median light of 1.9 foot candles, an average of 12 minutes before sunrise. Here the preponderance of cloudy mornings in April makes the time difference less than it otherwise would have been.

The average time of appearance of the Starling at Allard's home place was earlier from February through May than from September through January (Allard 1940, Fig. 2 and 3). Wynne-Edwards (1929), on the contrary, found that Starlings left a roost in England in December "on the average 8.75 minutes before sunrise, and in the first half of February 6.5 minutes later." The question of social relations is involved here; in Columbus in October the roar from the roost became plainly audible a half mile away a half hour before sunrise, yet no flocks left the roost till 10-14 minutes before sunrise. Grackles in this roost waited till 7-9 minutes before sunrise at light values of 13-16 foot candles, except for the unusually clear morning of October 16 when the first flocks left 13 minutes before sunrise at 8.5 foot candles; compare these figures with the solitary Grackles mentioned above that left their roosts at one-fifth the light values.

In Ireland Burkitt (1935) tells how the dawn chorus of Thrushes starts at 40 minutes before sunrise in February, getting earlier and earlier until it is 84 minutes before at the end of May. Since the difference in the start of civil twilight is less than 15 minutes, we have here a striking tendency to begin singing at lower light values. The evening chorus of Thrushes extends to 45 minutes after sunset in February and March and 76 minutes at the end of May. This earlier start in relation to sunrise from the first of March to mid-June is reported by Falconer (1941) for the Chaffinch, and Clark (1938) for the Blackbird, Song Thrush and European Robin.

All these records of earlier singing apply to male birds.

A female Mockingbird, on the other hand, gave an exceptional record in that she woke later in relation to sunrise as the season advanced, averaging 29 minutes before sunrise in December, 26 in February and 23.4 in March (Emlen 1937).

Heyder's painstaking work on European Blackbird roosts showed great variations in time of arrival during the year: in fall large numbers arrived before sunset, during the winter most arrived after sunset, while in April and May about half arrived before sunset and half after (1933).

3. *The Situation in the Far North*

The question arises as to how birds adjust in regions where there is no night. In north Lappland, lat. 68°, most of the passerines slept from about 6 to 11 P.M., becoming active again before midnight. The relation to waking-light is lost, but the birds are least active during the warmest and dryest part of the day, taking less time for rest in cold, damp weather. This shift of the chief resting time to the hours before midnight may be explained as an adaptation of the sleep rhythm to the most unfavorable circumstances for activity; in lower latitudes the bird reacts with sleep to darkness, in the far north to the warmth and dryness of the afternoon (Palmgren 1935:120).

In Finland at 60° N. lat. in June Paatela (1938) found that passerines slept from 1 to 5 hours, starting at 9 to 11 P.M. and ending at midnight to 2:20 A.M. Birds often slept so soundly that the alarm notes of their mates failed to awaken them.

Snow Buntings in Greenland near the Arctic Circle at the end of March awoke at 3:30 A.M.; they "awoke earlier from day to day during April, until at the beginning of May their activities started at about 1 A.M. Although the nights grew lighter until the end of June, the birds did not rise any earlier from about the middle of May onward; a certain amount of sleep, about 2 to 3 hours, apparently is necessary" (Tinbergen 1939c:11). Much the same was reported by Haviland (1926) for a number of species in northern Siberia.

In Churchill, Manitoba, at about 58° N. lat., "Although during June and July there is almost full daylight from 2:00 A.M. until 10:00 P.M. in the North, Tree Sparrows do not begin feeding until 3:15, and cease shortly before 9:00, making a working day of 17.75 hours" (Baumgartner 1937:77).

4. *Awakening of Night Birds*

Correlation of activity with light has been found with the Nightjar and Screech Owl, but not with the Barn Owl.

A lunar periodicity was reported for the Nightjar by Wynne-Edwards (1930). "About the time of full moon the Nightjar was as much as 20 minutes later than at new moon." With the same species Ashmore (1935) found that the first song in the evening averaged 51 minutes after sunset with moonlight and 35 minutes without it; the first song in the morning averaged 78 minutes before sunrise with moonlight and 40 without it.

With a pair of Screech Owls Allard states that "The mean time of arrival for all clear dawns from March 23 to May 21 inclusive was 15 minutes before sunrise; for all hazy and partly cloudy dawns, 10.1 minutes before sunrise, and for very cloudy and stormy dawns for the same period 2.0 minutes before sunrise . . . The mean time of departure for all clear evenings from March 19 to May 19 was 7.8 minutes after sunset; for all hazy and partly cloudy evenings 8.5 minutes after sunset; for all very cloudy and stormy evenings 7.4 minutes before sunset. It is obvious that very cloudy weather advanced considerably the time of departure, just as it delayed arrival at dawn" (1937:301).

Bussmann (1935), on the other hand, after studying a nest of the Barn Owl with the terragraph found that the parents left at the end of the day, usually between 9 and 10 P.M.; neither leaving nor returning appeared to be influenced by the state of the weather nor the position of the moon.

5. *Awakening and Roosting in Relation to Sex*

The awakening of a male bird is often conspicuous, while that of the female is usually the opposite, hence observations on the start and end of activity of female birds are rare, except during incubation and brooding, and here other factors enter. All the evidence that we have points to earlier rising and later retiring for the male than the female.

With a pair of Black Phoœbes, the female went to roost 10-26 minutes earlier and left 5-15 minutes later in the morning than her mate (Oberlander 1939:145). A male Starling in Columbus from March 22 to April 4 appeared at the nesting hole in the morning on an average 8 minutes before his mate. With a pair of these birds in England that roosted in the same hole the female always went in first at night, and the male always left first in the morning although the intervals were only a few minutes (Morley 1939). With Black-capped Chickadees males roost later than the females (Odum 1942); and the same is true of Blue Tits (Colquhown 1942). With Chestnut-backed Chickadees and Bewick Wrens males roosted 10 and 12 minutes later and rose earlier than females (Williams 1941). With Allard's Screech Owls the female left later in the evening and returned earlier in the morning than did her mate.

Schantz noted that the female Robin nesting on his porch "had difficulty in locating the nest in the darkness of early morning and late evening," so that he often turned on the electric light for her. The male's "ability to see in the darkness was better than mine" (1939:161). I know of no other observations on the relative ability of male and female to see in weak light.

D. Effect of Environmental Factors on Awakening and Roosting

We have seen that time of year, stage of the nesting cycle, and sex may influence the time of rising and retiring. Possible environmental factors that might be of importance are light, temperature, humidity and wind.

1. *Light*

Light appears to be the chief conditioning factor except in the Far North. The moon is of importance just before and after it is full for crepuscular birds and diurnal birds that start singing very early in the morning. Dorno points out that the moon is much brighter in high mountains than on the plains (1924:656). Snow on the ground increased the light at Columbus, nullifying the effect of a cloudy sky.

2. *Temperature*

Very cold weather has an inhibiting effect on song (Alexander 1931), and the same is true of very hot weather. Mild temperatures are stimulating, as shown above with Song Sparrows.

3. *Humidity*

Several writers stress the importance of humidity on song (Schwann 1920, Alexander 1931, Palmgren 1935). The last author found in Lappland that diurnal singers closely followed the curve of relative humidity (1932). Reed (1928) stated that the song of the Western Meadowlark in Southern California "is much less frequent in the arid summer than in the winter. The bird is heard in Riverside most frequently in winter just before or after a rain and sings readily in cloudy, misty weather." Heavy rain inhibits singing.

4. *Wind*

It is a matter of common observation that wind has a disturbing effect on bird activity (Alexander 1931). A Song Thrush sang 34 minutes after sunset on calm, clear days, 25 minutes during strong winds and only 10 minutes during gales (Alford 1925). Colquhown (1939) found that vocal activity of European Blackbirds at a winter roost showed a close negative correlation with wind.

E. SUMMARY

1. Light before sunrise depends primarily on the depth of the sun below the horizon, hence lattitude and time of year make a profound difference in the time before sunrise at which birds start to sing.

2. Astronomical twilight starts in the morning and ends in the evening when the sun is 18° below the horizon; nautical twilight begins at 12°. Civil twilight begins in the morning when the sun is 6° below the horizon; it used to be the time when outdoor work was started. At the latitude of Columbus, Ohio—40°N.—it lasts from 29-31 minutes in winter, 27-29 in spring and fall, 31-33 in June and July.

3. Light intensities as measured by a Weston Photometer, Model 603, averaged 34.5 foot candles for sunrise and sunset in clear weather in October. The average of 21 readings for the start of civil twilight in clear weather was .217 foot candles.

4. The distinction between "foot candles" and "candles per square foot" is pointed out.

5. The female Song Sparrows arose some 5 minutes after the start of civil twilight in clear weather and 7 minutes after in cloudy weather. The average of the light values was .34 foot candles or about the intensity at which small objects became visible to the observer. It is at much this same value at which the male arises in January and part of the fall.

6. The male Song Sparrow's awakening song is given about one-half hour before sunrise; it consists of a series and is given throughout the nesting season except after the male has been joined by a mate and before nesting begins; it also may be given in the fall.

7. There are 3 main periods in the starting time of the awakening song in relation to the beginning of civil twilight: the *basic period* in January and February and early and late in the fall, when it comes about 4 minutes *after* civil twilight on clear mornings; the *intermediate period* in early spring, coinciding with the taking up of territories when it comes *at* civil twilight; and the *established period* later in spring and in mid-fall when the bird is in full song, when it comes some 4 minutes *before* civil twilight. See Chart I and Table VIII.

8. In Table IX 238 records are given of the awakening of male Song Sparrows in cloudy weather; these average 4.5 minutes later than in clear weather. The light values at the start of singing in the 3 periods averaged about the same on clear and cloudy mornings.

9. Sixty-nine measurements obtained with a Model 603 Weston photometer averaged .32 foot candles for the basic period, .2 for the intermediate period, and .05 for the established period. In the second period the birds started to sing at 3/5 the light of the basic period, and in the third period at 1/6.

10. The start of the awakening song depends partly on the time of year, partly on temperature, partly on the stage of the nesting cycle. It is closely correlated with light, the bird singing at lower and lower light values from January to June.

11. Roosting with the Song Sparrow takes place at about 10 times the light values of the rising time of the female, and of the male during the basic period. From December through May and again in October the last notes of the male Song Sparrows came with surprising regularity 13-14 minutes after sunset in clear weather. The female Song Sparrows went to roost somewhat earlier.

12. The most significant papers on awakening and roosting of other species are listed. Each species (and sometimes each individual) has its own "waking-light"; some families are typically early, others typically late. Earliest risers are latest to bed. Birds in general go to roost at higher values than they awake. Starlings and Grackles in October reached the roost at about 3 times the light at which they left it.

13. Singing typically becomes earlier in relation to sunrise as the breeding season progresses.

14. In the Far North the "waking-light" is no longer effective. Passerines sleep from 1 to 5 hours in the late evening or around midnight.

15. The Nightjar and Screech Owl have been found to regulate their activity in accordance with light, but this was not evident with a Barn Owl.

16. With a number of species the male has been observed to arise earlier and retire later than the female.

17. Of the environmental factors influencing the start of singing in the morning and its ending in the evening, the most important is light. Inhibiting factors are extreme cold and heat, heavy rain, strong wind and lack of humidity.

18. It would be of great interest to work on the problem of the correlation of the first and last songs of birds with a photometer especially adapted to measure low light values.

CHAPTER IX

Song of the Adult Male Song Sparrow

One of the most unusual characteristics of the Song Sparrow is its individuality in song. Each male has a number of different songs—6 to 24—that with a few exceptions belong to him alone. Despite this remarkable variety they are almost always recognizable as coming from this species.

A. Character of the Song

The songs of each male are entirely distinct; as a rule they sound pleasant and "cheerful" to human ears, yet a few are disagreeable, while still others are of great beauty. Many individuals have no specially distinctive songs, while some have one or two songs which are unforgettable to an attentive observer. *The same individual may have songs of all degrees of quality: harsh, typical and especially musical.*

The Song Sparrow song typically consists of 3 parts, the first two being much more stable than the last. Songs vary in length from 2 to 3 seconds; they are given at the rate of 5 to 7 a minute when the bird is singing steadily, although on occasion during territory establishment the rate is increased to 10 a minute. A bird sings each of his different songs for a period before changing to another, usually going through his whole repertoire before starting over again.

1. *Form of the Song*

Charts illustrating the form of the Song Sparrow song are given by Saunders (1924, 1929, 1938), Wheeler and Nichols (1924) and Brand (1935, 1938), each with a different technique. Saunders is a specialist on the subject of bird song, recording accurately time, pitch, intensity, quality and phonetics. I am not able to follow Saunders' technique, but adopted a modification of the symbols used by Wheeler and Nichols, also recording the song in syllables as it sounded to me, as shown in Figure 3.

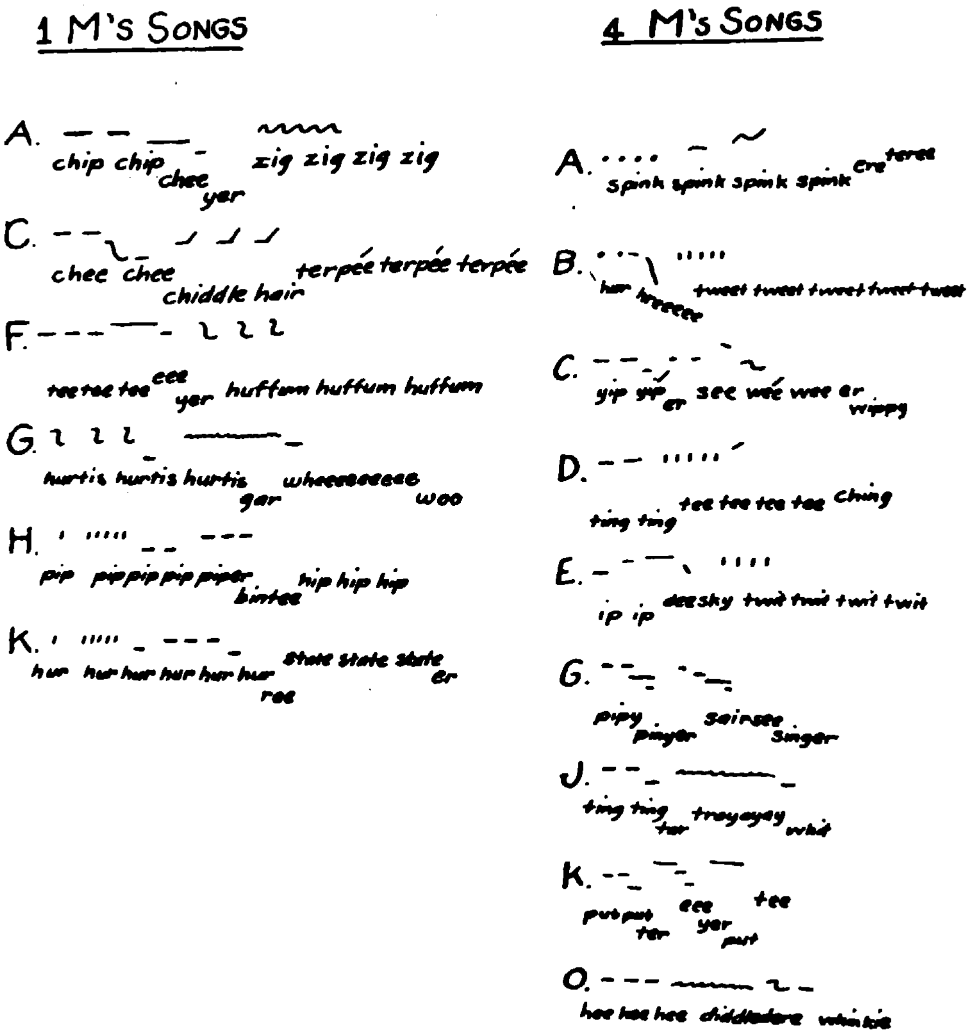


FIGURE 3. *Songs of 1M and 4M.*

I learned by heart all the songs of 3 males that nested in our garden, 1M, 4M and 187M, and also Y and D, coming to recognize each song as surely as songs of different species. I also learned some of the more distinctive songs of many other Song Sparrows.

Brand's intensive studies (1935) on the structure of song by means of photographing them on motion picture film bring out unexpected results. Three Song Sparrow songs, lasting 2.08 to 2.48 seconds were found to contain 35-36 notes, i.e., 15 to 17 per second! From 7 to 11 notes are often all that the human ear can distinguish in a song of ordinary length.

"Many of the notes in the Song Sparrow song and in the songs of many other species are of incredibly short duration; so short that they could not possibly be heard by the human ear except in combination with the preceding or following notes. About three-quarters of them in my Song Sparrow song II being less than 1/50" long, and in my other Song Sparrow song there are many notes that are short. The silent intervals between notes are even shorter and in many instances are less than 1/1200"," (1935:42). The pitch of Song Sparrow song ranges between 1900 and 7700 vibrations with a mean of 4700, which is higher than the highest note on the piano, C7—4096 vibrations (Brand 1938).

2. *Number of Different Songs in a Repertoire*

Of the 5 birds whose repertoires I learned by heart, 4 had 6 songs and one 9. The birds studied by Saunders had the following number of songs: 9, 12, 18, 24 in Connecticut (1924) and 8, 12 and 18 in New York State (1938). Curiously enough all my birds and all but one of his have repertoires that are multiples of three.

When I noticed this 3 years ago, I went through my records of the Song Sparrows on Interpont and found that I had information on several hours' singing of 40 birds. Six seemed to be a common number of songs in this region, for I have records on 11 individuals besides 1M and 187M that apparently possessed this number. For 10 birds I recorded from 7 to 10 songs, and for 4, including 4M, 9 songs. For 8 there are records of 10 to 12 songs, for one 13, and another 17.

Most of my birds have had fairly stereotyped songs with no variations except of the last part. 1M and 4M each had one song which had two regular versions; with 1M it was the middle portion that was shortened; with 4M the last. A few individuals seem to have remained in a more plastic state and may vary both the middle and last part of some of their songs; this was true with birds known to be 2 years old and older.

3. *The Awakening Song*

The periods throughout the nesting cycle at which the awakening song is given and the time of its daily appearance in relation to temperature, time of year and stage of the cycle have been described in the preceding chapter. Here it may be added that the awakening song seems to be of intrinsic importance to the Song Sparrow on his territory; it is given in nearly adult form by the juvenile when the rest of his singing is merely warbling, and with the mature bird it appears to be an index of vigor. 1M, 4M and 187M used each of their different songs with which to start the day.

4. *Flight Songs*

Most of the singing of this species is done from an elevated perch. Singing from the ground occurs during territory establishment quarrels, and is also given sotto voce by juveniles as they eat.

Sometimes a male sings on the wing, usually as he returns home, either as victor after having driven off other Song Sparrows, or after trespassing when chased home by his neighbor. He also does so after a "pounce" or "swoop" over a female. These songs do not differ from the ordinary ones except that they often appear to be given with special emphasis.

The real flight song has no direct relationship with any other bird. It is given during a flight from an elevated perch up into the air, or from one branch of a tree to another, or from one tree to another. It is peculiar in that it always begins with a twitter—*tit-tit-tit-tit*, rather like the note of fear, but louder. The ending is sometimes one of the regular songs and sometimes a kind of a jumble. It is very little longer than the ordinary song.

This type of song is sometimes delivered from the top of a tree with no flight at all; this I call a "pseudo-flight song". Both types of flight song seem to occur most often during the prenuptial period, sometimes during nest-building and egg-laying, and very seldom while there are eggs or young in the nest. The earliest that I have recorded it on Interpont was Feb. 19, the latest July 12. With the hand-raised birds it has been heard only from Y; the first instance of a pseudo-flight song occurred on Jan. 10, 1939; since then he has given it Jan. 13, Feb. 6, April 25, 27 and May 13, and in 1940 Mar. 20 and Apr. 2, 4, 5, 7 and 10—all from a high perch in his cage.

In 1941 Y sang very little until late December, from then on singing a great deal. On Jan. 29, 1942, he started in again with flight and pseudo-flight songs and gave them perhaps every other day through February, and on occasion through June.

The flight song gives the impression of a vestigial performance from the curious, perhaps primitive type of song and the fact of its rarity. Although F. H. Allen (1919) considers that flight songs evolved from "ordinary songs", and Saunders in 1922 agreed with him, later Saunders (1929:123) wrote, "There may be some reason to suppose that flight songs are more or less primitive", an opinion also voiced by Wheeler and Nichols (1924).

B. Relation of Song to Temperature

The stimulating effect of temperatures above normal early in the season and normal temperatures later has been shown in the preceding chapter and discussed at length in Vol. I, Chapter VII (Nice 1937).

C. How Much Does a Song Sparrow Sing?

The Song Sparrow sings the greatest amount at the time of year when he first takes up his territory, the resident usually in early February, depending on the weather, the summer resident as soon as he arrives. A sudden change takes place at the coming of the mate, the male becoming almost completely silent, unless the arrival of a new neighbor excites him to renewed territorial activity. This silence lasts until the beginning of nest-building. At this time and also during egg-laying and especially incubation, the male sings a good deal, but while feeding the young, his singing is again reduced. During each successive brood he sings less and less, unless stimulated to territorial defence by some change in neighborhood relations. As the molt comes on, singing gradually comes to an end, but afterwards with many of the birds there is a period of fall singing, usually lasting only a few days with the summer residents, but extending over 2 months with a few of the residents.

1. *The Amount Sung at Different Stages*

The varying amount of singing throughout the nesting cycle is shown in Table XI where 500 hours of records of 8 males are summarized: 292 hours for 1M, 169 for 4M, and 39 for 6 other birds. Since nesting stages often overlap, the 75 hours under "Young being fed out of the nest" have already been used under "Building", "Laying" and "Incubation".

TABLE XI

SINGING THROUGHOUT THE NESTING CYCLE

Stage	Awakening song	Number hours recorded	Number songs per hour Range	Number songs per hour Typical	Degree of stimulation
I. Proclaiming territory, still unmated	Typical	53	59-310	180-200	Highly stimulated
II. Prenuptial	Suppressed	72	0-76[1]	2-13	Inhibited
III. Preliminary	Suppressed	55	0-55[2]	3-10	Inhibited
IV. Building	Typical	46	1-167	18-40	Uninhibited
V. Laying	Typical	26	8-152	33-70	Uninhibited
VI. Incubation	Typical	95	1-161	40-70	Uninhibited
VII. Young in nest	Irregular	130	0-72[2]	7	Inhibited
VIII. Young out of nest	Irregular	(75)	0-46	8	Inhibited
IX. Late summer	Absent	4	0-14	7	Inhibited
X. Molt	Absent	?	0	0	Inhibited
XI. Early fall	Irregular				Uninhibited
XII. Mid-fall	Typical	19	23-201	140	Stimulated
XIII. Winter	Absent		0	0	Inhibited

[1] Except for the first day, when 1M sang 102 times in an hour, 4M 106 and 118 times.

[2] Except under influence of territory establishment difficulties; under these circumstances there were 85, 103, 184, 194, 278 songs an hour during the preliminary stage, and with young in the nest 6 records ranging from 77-182 songs an hour.

The number of songs per hour listed as "typical" are representative of singing in the morning under ordinary conditions, when the output was neither reduced through bleak weather, nor increased through territorial activities occurring after the arrival of a new male in the neighborhood.

2. *The Different Degrees of Stimulation*

There appear to be 4 rather clearly marked degrees of stimulation in the singing activity of the adult male Song Sparrow: singing may be inhibited, uninhibited, stimulated, and highly stimulated. The number of songs per hour characteristic of each state are approximately as follows: 0 to 20; 30 to 70; 90 to 160; 180 to 300, as shown in Table XII.

TABLE XII

THE FOUR DEGREES OF STIMULATION IN SONG SPARROW SINGING

State	Number of songs per hour	Stage of nesting cycle
Inhibited	0-20	Prenuptial, preliminary, feeding young in and out of nest, molt.
Uninhibited	30-70	Building, laying, incubating, late afternoon.
Stimulated	90-160	Rival males in territory quarrels, proclaiming territory in summer, on cold days in spring.
Highly stimulated	180-300	Proclaiming territory in spring, rival males in territory quarrels.

Singing with a vigorous male Song Sparrow appears to be a normal outlet for excess energy, some individuals singing to a greater or less extent for 9 months of the year (4M and 50M). When singing is absent or markedly reduced, it seems as if it must be definitely inhibited.

Singing may be inhibited by the following conditions: unfavorable weather—too cold, too hot, too windy; physical condition of the bird—molt, resting condition in winter, or fatigue in the afternoon; psychological condition—perhaps anxiety over mate or young, preoccupation with guarding and feeding the brood.

Singing may be uninhibited when all the foregoing conditions are favorable, weather, physical and psychological condition of the bird, but yet there is no special stimulus for zealous singing. Uninhibited singing is heard typically after the mate has begun to build, and while she is laying and incubating. The male has little anxiety since both territory and mate are secured, and he has little to do. Fall singing often comes in this category. This amount of singing, from 30 to 70 songs an hour, may also occur as a compromise between stimulated and inhibited states, as when there are mild territory quarrels during the prenuptial stage or when the male is feeding the young.

Stimulated song—90 to 160 times an hour—is typically uninhibited song plus a special stimulus, sometimes fine weather during the period of laying and incubation; it is especially characteristic of territory establishment activities. It may rarely occur during the prenuptial period if the threat to the territory by the arrival of a new male is sufficiently great. It often occurs during the stage of territory establishment, for a bird cannot always be at the peak of his zeal.

Eight of the 13 hour records of 4M in fall range between 96 and 159 songs; here the stimuli were evidently abounding energy and favorable weather.

Highly stimulated song occurs when excitement is at the highest pitch, i.e., when territory is being proclaimed by an unmated bird, either undisturbed, or especially when stirred up by rivals for his land. (Two of 4M's fall records reached the lower limits of this category, namely 182 and 201 songs per hour.)

3. *The Song Series*

For 288 hours of singing by 3 birds the number of *each song* given is known. Table XIII shows the number of series per hour, the number of songs per series and number of songs per hour for the 4 degrees of stimulation. Twelve of the records are of 10M, 95 of 4M and 181 of 1M. 1M had 6 songs in his repertoire, 4M and 10M 9 songs.

TABLE XIII

SONG SERIES

		Inhibited		Uninhibited		Stimulated		Highly Stimulated	
		Hours	Average songs per hour	Hours	Average songs per hour	Hours	Average songs per hour	Hours	Average songs per hour
Number of	1M	109	3.9	53	6.3	13	8	6	9.2
Series per	4M	33	4.5	16	6.7	23	9.7	23	11.9
Hour	10M	1	3	2	5.5	4	9.5	5	13
Total		143		71		40		34	
Average			4		6.4		9.1		11.5
Number of	1M	109	1.9	53	6.7	13	14	6	25.2
Songs per	4M	33	2.5	16	6.5	23	12.5	23	18.9
Series	10M	1	3	2	8	4	14.1	5	23.3
Total		143		71		40		34	20.5
Average			2		6.7		13.1	6	231
Number of	1M	109	7.3	53	43.2	13	112.2	6	231
Songs per	4M	33	11.4	16	43.3	23	121.3	23	224
Hour	10M	1	9	2	46.5	4	125.6	5	281
Total		143		71		40		34	
Average			8.3		43.3		118.8		234

In general the 3 birds give strikingly similar results. The number of *series per hour* increases less than 3 times from the inhibited state to the highly stimulated state; the number of *songs per series* increases about 10 times, while the number of *songs per hour* increases nearly 40 times. This means that one song holds the field for a certain period, before being replaced by another. According to the table this averages some 15 minutes in the inhibited state, 10 in the uninhibited, 6 in the stimulated, and 5 in the highly stimulated.

A Song Sparrow usually goes through his whole repertoire before repeating any one song; the order in the second set of series is rarely repeated exactly. A bird with 6 songs gives 2/3 of them in an hour in the inhibited state, all in the uninhibited state, all and half again in the stimulated state, and twice over in the highly stimulated state. A bird with 9 songs will present them all in the stimulated state and do the same with a start on a second rendition when highly stimulated. I do not know what pattern is followed by a bird with 24 songs.

Does a bird with 9 songs sing each for a shorter period than a bird with only 6 songs? This might seem to be the case when we compare 1M's and 4M's records especially in the highly stimulated state. However, there may be an age difference here. Forty records for 4M in 1929 to 1930 gave longer series than did 55 in 1935—inhibited, 3.1 songs per series early, 2.2 later; uninhibited, 12 early (only 5 records), 5.6 later; stimulated, 14.1 early, 11.1 later; highly stimulated, 21.5 early, 16.5 later. In other words, although 4M in 1935 gave a high total of songs, yet the series appear to have been about one-fourth shorter than 5 or 6 years previously. (I have 4 records in March 1934 for 187M, a bird hatched in 1933; he gave 20, 18, 20 and 24 series per hour, the total number of songs for the first 3 hours being 193, 234, and 187. These numbers of series run almost twice as high as those for the older birds. The average number of songs per series was 10.7.) It seems evident that very young birds change often; at the height of vigor there is sustained effort, while an old bird may change more often again.

4. *The All-Day Record of 4M*

I had long wanted to investigate the matter of how many songs a Song Sparrow might sing when in full song. Feb. 22, 1932, promising to be fair and mild, I started to take 4M's all day record; he began at 6:42, and sang 234 songs the first hour, and 251 the next, but only 194 the third. A cold wind made it unfeasible to continue. The highest hour records I have obtained were: 1M and 4M, 278; Y 288; 10M 310; 44M 314 and 325. I calculated that a Song Sparrow in full song must give some 1500 songs a day.

On May 7, 1935, 4M's mate disappeared and 4M started singing zealously. He must have been 8 to 9 years old at this time, since I first became acquainted with him as a nesting bird in the spring of 1928. On the 11th I was able to take the whole day record; he sang from 4:45 A.M. to 7:43 P.M., giving 2305 songs in the 15 hours. The hourly records follow: 278, 277, 221, 264, 200, 225, 227, 150, 182, 121, 60, 52, 16, 12, 20. He sang rather steadily for the first 2 hours at an average rate of 4.8 songs a minute; after he had sung for 1 hour 5 minutes he took ½ minute off for a bite of breakfast. During the first 3 hours there were only 13 minutes when he was not singing. He was in the highly stimulated state for the first 7 hours, averaging 242 songs an hour. During the next 3 hours he averaged 151 songs, while in the afternoon his efforts dropped off very much. Since during some evenings he sang considerably more than on this date, I believe this record might well have been surpassed on some other days.

This 2305 is the highest actual count of number of songs given by one bird in a day so far as I can find. A Bob-white gave 1430 *bob-white* calls in one day (Stoddard 1931). The third highest count appears to be that of the Black-throated Green Warbler (the Nices 1932) that sang 1313 times in 16 hours on July 16, although on the 15th he had sung 1680 songs in 7 hours. "A really typical day should have resulted in over three thousand songs." I would like to commend the Dickcissel to some bird student as a favorable subject for such a record.

Table XIV gives the numbers of each of the 9 songs given this day, and the numbers of series of each song, which ranged between 15 and 22 for each song and totalled 159.

5. *The Different Songs of 4M and 1M*

In two instances Saunders (1924) found Song Sparrows showing marked preference for certain of their songs the second year that he studied them. For one he recorded 9 songs in 1920, but only 3 in 1921, and most of the time only one. Another bird had had 12 songs in 1921; in 1922 "it returned and, so far as I know, sang only one song". I never noted any similar cases. 1M sang his 6 songs in 1929 and 1930, and 4M sang his 9 songs in 1935 just as he had done in 1929. Chart II illustrates these songs as I recorded them.

In Table XIV the records of 80 hours of 4M's singing are given in 4 chief divisions: 40 hours from 1929-32; 15 hours on May 11, 1935; totals of these and 25 other hours in 1935; and the grand totals for each song for the 80 hours.

TABLE XIV

4M'S NINE SONGS

(40 hours recorded from 1929-1932, and 40 recorded in 1936)

Song	40 Hours 1929-1932 (11 highly stimulated)		All Day Record 15 Hours May 11, 1935 (8 highly stimulated)			40 Hours[1] 1935	80 Hours
	Total sung	Longest series	Number series	Total songs	Longest series	Total	Total
A	599	53	17	226	25	547	1,146
B	477	40	15	254	32	480	927
C	571	63	15	232	28	527	1,098
D	534	46	18	240	33	554	1,088
E	368	36	17	212	28	450	818
G	392	42	16	220	27	477	869
K	395	57	18	256	33	544	939
J	431	53	22	362	37	605	1,036
O	378	45	21	304	38	604	982
Total	4,115	....	159	2,305	....	4,788	8,903
Average	457.2	48.3	17.7	256.1	31.2	632	989.2

[1] May 11, 1935, and 25 additional hours.

There is little evidence of favoritism for any of the songs except for the fact that E lags behind the others; in the grand total it was used 71 per cent as often as A. As to comparisons between the early years and the last it is evident, as already mentioned, that 4M sang each song a shorter number of times as he grew older. In the first 4 years the longest series in the table reached 63, while the average of the longest series of all the songs was 48. (I have one even longer instance; on Feb. 18, 1930, 4M sang A for 10 minutes at a stretch, giving it 72 times.) On May 11 the longest series was 38 and the average of the highest records for each song 31; in the 4 other records of highly stimulated song in 1935 the longest series was 33. The series in the 12 highly stimulated hours in 1935 averaged one-fourth shorter than they did in 11 similar hours in 1929 to 1932.

4M's daily output of song during spring in 1935 did not appear to be less than it had been earlier. The fact that the 40 hours in 1929-32 give a lower total than those in 1935 is partly due to the fact that in the former period 12 hours in the inhibited state and 5 in the uninhibited are represented, while in the latter 9 in the inhibited and 8 in the uninhibited were used. The 11 highly stimulated hours in the first records averaged 205 songs; 12 in 1935 averaged 233. In the fall, however, there was a distinct decrease in song performance as 4M grew older.

To return to 4M's 9 songs: the first to appear in 6 "springs" (Jan. 8, 8, 8, 14, 21, 24) were usually A, C, G and O, the last being K and B. The first to appear in 6 falls were A, O, K, C, and the last J, E, and B. The first to disappear in the fall were B, E and K, while those lasting longest were A, C and O. As for their use in the awakening song the order of frequency in 345 cases was: K 62 times, A 49, O 46, J 40, E 38, D 36, C 30, G 27 and B 17. This does not correspond to the order of frequency in the 80 hours. It would seem that A, C and O were the chief standbys, and that K, which was the most elaborate song, was late in appearing after the winter's silence, although not so difficult to recall after the molt. Its preponderant use in the awakening song is perhaps further evidence that the bird is then at the peak of his vigor.

Records of the frequency of 1M's 6 songs in 181 hours of singing were: C 1154, A 1090, K 1057, F 971, H 895, G 763, a total of 5930. G was heard two-thirds as often as C. The longest series in the 6 hours of highly stimulated singing ranged from 33 to 58, averaging 46, almost the same as 4M's average (48.3) at about the same age.

D. FALL SINGING

There was always singing in the fall from the Song Sparrows on their territories on Interpont, much in mild weather, little with bleak temperatures. In general the singing of the summer residents was confined to a few days the last of September and first of October, but in 1930, due to an exceptionally early molt, perhaps correlated with severe drought (Nice 1937:61, 134), singing started from the 10th to 18th of September and lasted till the 11th of October. 50M, a resident, sang from Sept. 9 to Oct. 24 in 1930, from Sept. 28 to Nov. 19 in 1931 and from Oct. 2 to Nov. 6 in 1932. 4M sang from Sept. 29 to Nov. 11 in 1929, from Sept. 10 to Nov. 14 in 1930, from Sept. 28 to Nov. 24 in 1931, from at least Sept. 28 (the date of our return to Columbus) to Nov. 6 in 1932, from Sept. 28 to Nov. 7 in 1933, from Sept. 30 to Oct. 5 in 1934 and from Sept. 29 to Oct. 20 in 1935. The regularity with which 4M started singing his awakening song in 6 out of 7 falls is remarkable. His diminishing zeal in fall singing is noticeable, for in 1934 he sang for only 5 days and in 1935 22—although only a little each day—, while before that he had sung over periods of 40, 41, 44, 55 and 65 days.

The character of the late summer and fall singing of adults differs little from that of the height of the breeding season, except that more incomplete songs are given than earlier. 4M varied 3 of his songs slightly in the fall, but with him and all the other banded males there was no "return to primitive irregular singing" as suggested by Wheeler and Nichols (1924) and Saunders (1929); instead of being stimulated to new varieties of song, the bird sings less and less at the end of singing. The "primitive irregular singing" in my experience comes from juvenile birds.

E. SUMMARY

1. Each Song Sparrow has a number of different songs peculiar to himself. These last 2-3 seconds and appear to consist of some 15-17 notes, but in reality contain more than twice as many. The average pitch is higher than the highest note on the piano.

2. Of the 5 birds whose repertories I knew by heart, 4 had 6 songs and one 9. Saunders' birds had from 9 to 24 songs.

3. The Song Sparrow sometimes gives a primitive-sounding, irregular kind of a flight song or "pseudo-flight song".

4. Singing with Song Sparrows shows 4 degrees of stimulation: inhibited, when 0-20 songs may be given an hour; uninhibited, with 30-70; stimulated, with 90-160; and highly stimulated, with 180-300.

5. Table XIII, based on 287 hours of singing by 3 birds, shows the number of series of songs per hour. The number of *series per hour* increases less than 3 times from the inhibited state to the highly stimulated state; the number of *songs per series* increases about 10 times, while the number of *songs per hour* increases nearly 40 times.

6. Young birds change often from one song to another; at the height of vigor there is sustained effort and one song may be sung 60 or even 70 times in succession; an old bird may change songs somewhat more often. 4M's song series were one-fourth shorter in 1935 than they had been 5 and 6 years previously.

7. The highest number of songs in an hour that I obtained from Song Sparrows were 278, 278, 288, 310, 314 and 325.

8. On May 11, 1935, 4M gave 2305 songs during his day of 15 hours. This seems to be the highest published record of the number of songs given by any bird in one day. A Bob-white gave 1430 *bob-whites* in a day, and a Black-throated Green Warbler gave 1680 songs in 7 hours.

9. In 345 records of the awakening song, 4M's most elaborate song was used more than any other.

10. In fall 4M started to give the awakening song in 6 out of 7 years from Sept. 28-30; his periods of song extended for 5, 22, 40, 41, 44, 56 and 65 days, depending both on weather and his own age.

CHAPTER X

Song in Female Birds

Singing in birds is usually thought of as a male prerogative. In some species, however, females regularly sing, while in others they do so sporadically. It is in the latter class that the singing of the female Song Sparrow falls.

A. SONG OF THE FEMALE SONG SPARROW

Ordinarily it is a rare occurrence to hear a female Song Sparrow sing. In 1929 when I was spending several hours each day with 1M and K2, I heard the latter give 10 songs between Mar. 22 and 28. This record may well be representative of an ordinary female, for it was exceptional to record female singing as I went the rounds of Interpont except for four birds—K42, K51, K56 and K135.

In my experience female singing has shown several characteristics whenever recorded: it is confined to the period in early spring before nest building begins (my earliest record being Feb. 12, the latest Apr. 19); it is always given from an elevation—a large weed, a bush or even a tree, in contrast to the female's usual behavior of staying close to the ground; it is short, simple, and entirely unmusical.

The first songs of K2 were rather weak, the later ones louder. Those of the three most energetic singers were decidedly loud. K42 was heard on Apr. 14 and 18, 1931; her songs were harsh, and unpleasant, of 7 or 8 syllables all much alike, given at the rate of 7 songs a minute—the typical rate of the male in highly stimulated song.

On Feb. 26, 1932, K56 was singing almost constantly, whenever she was resting from chasing 120M, a new arrival that morning. At times she chased while her mate sang. She perched on top of elders and sang very loudly, often answering her mate's songs. She was also heard on Mar. 24 and 25.

Curiously enough, in 1934, in K56's former territory on North Interpont a different bird, K135, showed similar behavior.

Mar. 17, she gave a shrill, faint song.

Mar. 30, she was even more zealous than her mate in chasing a new male; her mate would stop and sing, while she pursued. She also sang.

Mar. 31, she sang with her mate.

Apr. 2, "she has a special place on a locust where she sings; her song is shrill and loud; it reminds me a little of a White-throat. There are at least 2 versions; they are not as unmusical as most female Song Sparrow songs. She is chasing an unbanded male as much as does her mate, often taking the initiative in following him."

In 1935 I have only 2 records of her singing—Mar. 2 and 4, but I spent little time on North Interpont that spring.

Saunders (1929:17) suggests that singing females may be "unusual individuals, that possess some trace of masculine characteristics." K42 had a peculiar history of wandering from one mate to another in February, and later was slow in starting to lay, 9 days elapsing between the start of nest building and the laying of the first egg. She was the only female I ever saw giving the puff-sing-wave display—see Appendix II. K56 and K135 were both unusually aggressive in defending their territories on 3 occasions, for although females will often follow their mates as they chase invaders, or will repulse the enemy alone in the temporary absence of their mates, usually the male is far more zealous in this regard than the female. K56 had a normal history so far as nesting went, while K135 gave the earliest records for laying on Interpont for 3 years in succession.

On 4 occasions in the fall of 1931 I heard what must have been juvenile females singing; unfortunately none of the birds was banded.

Sept. 30. A young bird nearly through the fall molt is giving separate, harsh songs of warbling character. Two lasted 2.5 seconds; others were probably longer. They have the faint and unmusical quality of female song.

Sept. 30. A bird in juvenal plumage is giving the harshest kind of female songs—chattery, ridiculous, about 2-2.5 seconds in length.

Oct. 1. A molting bird is giving "female singing"; the effect is somewhat more warbling than yesterday; but it is entirely without music.

Oct. 4. An unbanded molter is giving rather harsh warbling. sotto voce.

The juvenile singing of males is strikingly different, consisting of musical, varied warbling.

Throughout February the hand-raised female J "sang" to a small extent; her songs were faint and characterless, 4-5 notes long.

The only reference I can find in the literature to singing by a female Song Sparrow concerns a remarkable bird in Worcester, Mass. (Wetherbee, 1935). This color-banded female sang a great deal in April, keeping it up at least to June 17. In "April the female's song was heard at all hours of the day. . . . The song was high-pitched, neither weak nor harsh, but a loud, clear series of whistled notes of varying length (usually of seven notes) seemingly all on the same key. It resembled more the song of a White-throated Sparrow than that of any other bird." She "always sang from an elevation of from fifteen to twenty feet". The only other Song Sparrow in the garden was a male "a return-2"; he sang normally and Mrs. Wetherbee believes the birds were mates, but no nesting data were obtained.

A distinction is made by Nicholson (1929:51-52) between "true song" that is a "territorial song" and "invariably uttered at the top of the voice" and the "sub-song" which is "low and inward." He states, "With the possible exception of [European] robins, where the hens keep a separate territory of their own in winter, all records of singing females appear to refer to sub-song, and not the true song." This is not the case with my Song Sparrow females, since their singing, even when faint, was never (except with J) of the nature of whisper songs, and at times it was very loud. Nor does it resemble the warbling song of the juvenile male. It is like the territory song of the adult male with all the music and all the variety omitted. Perhaps it is a matter of self-assertion, as in the male, but in most cases it appears to be a kind of vestigial phenomenon, eliciting no response from any other Song Sparrow.

B. DISCUSSION OF SONG IN FEMALE BIRDS

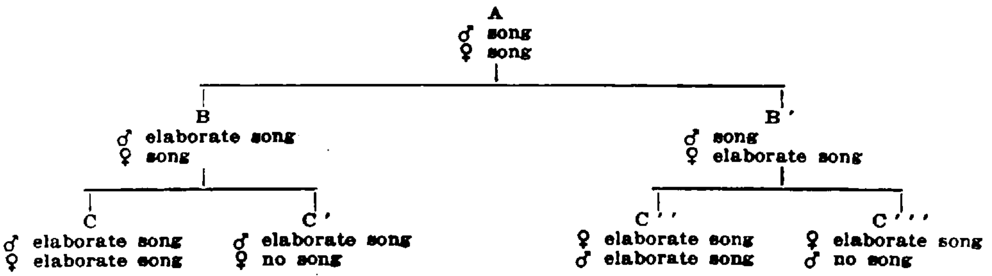
Two aspects of song in female birds are of special interest: its evolution and its function.

1. *The Evolution of Song in Female Birds*

Mr. Pelkwyk and I discussed this subject together and he devised a chart to illustrate the possible evolution of song in male and female birds. A modification of this chart is given in Table XV.

TABLE XV

POSSIBLE EVOLUTION OF SONG IN MALE AND FEMALE BIRDS



We suggest that song was originally present in both sexes, and that there were two lines of evolution, one where the male developed the more elaborate song, the other where the female did so. It will be noted that in the second stage one sex has remained stationary and the other progressed. In the third stage in each case one sex remains stationary while the other either progresses or retrogresses. Convergence appears, for C and C″ are similar.

The different classes shown in the table will be discussed under their captions. Though there are many examples of female song scattered throughout the literature, it is not always easy to decide under which category they should be placed, as in most cases few details are given.

(A). *Male song; female song.* In a vast number of species there is little, if any difference between the vocal utterances of the sexes. This seems to be true of Cormorants, Terns, Gulls, many shorebirds, some Owls and others.

(B). *Male elaborate song; female song.* The special difficulty in allocating cases of female song comes in B and C, i.e. to decide whether a female has merely "song" or "elaborate song". Perhaps we can tentatively put into B those cases in which the female sings only occasionally; her song is of much the same quality as that of the male, and may be given in territorial situations, in solitude, old age, or under the influence of male hormone.

In territorial situations the following females have sung: European Robin (Lack, Burkitt); Mockingbird (Michener 1935); California Shrike (Miller 1931b); California Thrasher (Sargent 1940); Bullock's Oriole (Miller 1931a); White-crowned Sparrow (Blanchard 1936, 1941); Starling (Bullough and Carrick 1940). In the first two and last two species, the females often sing in the fall. Under conditions of solitude the following have sung: Jackdaw (Lorenz 1931), European Blackbird (Ruthke 1938), Cedar Waxwing (Whittle 1928), Violet-eared Waxbill (Sewall 1942), Baltimore Oriole (Scott 1901, Sanborn 1932a), Northern Shrike (Chadbourne 1890), Serin (Lorenz, letter). Canaries have sung when old (Kummerlöwe 1931, Mark 1930) and the same is true with domestic fowl.

(C and C"). *Both sexes elaborate songs.* Here songs are often given in courtship or to keep up the bond between the pair.

Examples are: Cardinal (Shaver and Roberts 1933), Slate-colored Fox Sparrow (Saunders 1910), European Barn Swallow (Hartley 1941), Harris Sparrow (Semple and Sutton 1932), 4 Australian species—White-browed Scrub Wren, Yellow-throated Scrub Wren, Heath Wren and Satin Bowerbird (Gilbert 1927). In the tropics pairs of many species "duet"; this is true of 5 Central American Wrens —*Pheugopedius, Henichorina, Donacobius, Heleodytes bicolor, Thryophilus modestus* (Fuertes 1916, Skutch 1940); several African species, a Barbet *Trachyphonus d'arnandii böhmi, Heterotrogen v. vittatum* and a Bush Shrike (*Laniarius*) and Swamp Warbler (*Bradypterus*) (Moreau 1941a); New Guinea Cuckoo-shrike (Mayr, letter); in India Himalayan Laughing Thrushes Scimitar Babblers and Great Himalayan Barbet (Osmaston 1941). With the California Thrasher the male may sing one bar of the full song and the female the next, using the same or different phrases (Dyer, letter). Many other females sing, often as well as the males: Bullfinch (Witherby et al. 1938), Pine Grosbeak (Ivor, letter), Crossbill (the Heinroths 1932), House Finch (Bergtold 1913), European Dipper (Eggebrecht 1937), Latimer's Vireo, during courtship and building (Spaulding 1937), Philadelphia Vireo (Lewis 1921), Black-capped Vireo (Lloyd 1887), Yellow-throated Long-Claw (Serle 1940), Black and Yellow-throated Spine-tail (Davis 1940c), Elegant Parrot (Hampe 1940). The female Bicknell's Thrush while incubating sometimes responded to her mate's flight song with a "low, whisperingly thin, and hoarse" refrain; when eggs hatched she sang "again and again in full-throated ecstacy" (Wallace 1939:338). One of Mr. Ivor's female Rose-breasted Grosbeaks sings softly when incubating and "also in the trees when she was out after insects and while her mate was on the nest"; his female Catbird sings as well as the male (letter).[1] A female Wren-Tit sang "while her mate and a neighboring male were fighting" (Erickson 1938: 302). With Shamas, "Some of the hens sing almost as well as the cocks" (Amsler 1941).

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[1] H. and J. R. Michener (1943 News from the Bird-Banders, 18:24) report an incubating Black-headed Grosbeak answering her mate with a song similar to his as he came to take his place upon the eggs.

(C). *Male elaborate song; female without song.* Although the female in a great number of species appears to be normally without song, yet in some cases she has been heard to give what might sometimes be called a primitive song. This is true with the Song Sparrow. It is probable that careful observation will disclose that a great many females, ordinarily considered songless, may occasionally sing.

Female Marsh Warblers sing "every now and again, though seldom, if ever, after they have been over here more than about ten days. Their delivery, moreover, is always brief, feeble, faltering and whispered, their mimicry always indifferent when not actually faulty" (Walpole-Bond 1933:65). As to the Willow Warbler, Brock (1910:417) once "heard a female try to sing. This was in May, during pairing-time, and appeared to be the outcome of sexual excitement; the song was very feeble, consisting of a few stammering notes, uttered very similarly to the very earliest efforts of the young males in autumn." A female Chaffinch sang with the "first notes of a typical Chaffinch song, but the ending was missing and some harsh, guttural thrush-like notes were added" (Warburg 1941). A female Bell's Vireo sang twice as she approached the nest from which her incubating mate had just left (Pitelka and Koestner 1942).

To turn to the other and less popular line of evolution. Here it is difficult to get much information, as the habitats of most of these feministic species do not coincide with that of the bulk of bird observers. Again, in cases where the sexes show no dimorphism, it has usually been assumed that the more active bird was the male.

(B'). *Female elaborate song; male song.* In some species both sexes are vocally gifted, but the female more so than the male. This may be true with the Spotted Sandpiper.

(C"). *Both sexes elaborate song.* Discussed above with class C.

(C'"). *Female elaborate song; male no song.* In species where the female takes the initiative in courtship and the male incubates the eggs, the female often gives the "advertising song" rather than the male. This has been shown in detail for the Northern Phalarope (Tinbergen 1935). It is also reported for the Button-Quails and Painted Snipe in India (Meise 1930), Variegated Tinamou (Beebe 1925), Emu (Fleay 1936), and Coucal (Spennemann 1928).

2. *The Function of Song in Female Birds*

When injected with male hormone, female Canaries have sung (Shoemaker 1939a, Leonard 1939), and domestic hens have crowed (Allee et al. 1939, Davis and Domm 1941). Bullough and Carrick (1940) point out the simultaneous appearance in fall in female Starlings of singing and yellow bill color; they suggest that in spring song is inhibited by female hormone. Since all females produce some male hormone, singing females may be birds with an excess supply. Song often serves as an expression of sexual dimorphism; as with color, the difference between the sexes may be great or small, and the male sex is not always the conspicuous one.

Song is innate in both sexes. Where song serves as a means of self-expression, or as an expression of a social bond, and particularly where it serves as a bond between the pair, it may be equally (or fairly equally) developed in both sexes. Where song is largely specialized for territorial uses, and territorial defense is primarily taken over by one sex, then song is most highly developed in this sex, and may almost disappear in the other. In individual cases where territorial responsibilities are thrust upon the normally less active bird, it may respond with excellent song.

C. SUMMARY

1. Female Song Sparrows occasionally sing early in the season before nest-building begins (Feb. 12 to Apr. 19); the song is given from an elevation and is short, simple and unmusical. The most energetic singers were also zealous in chasing male neighbors. A female Song Sparrow that sang a "clear series of whistled notes" from April to mid-June was reported from Massachusetts.

2. This singing does not resemble "sub-song" nor "whisper songs".

3. A table is given showing the possible evolution of song in male and female birds.

4. Song is innate in both sexes; in one line the male developed the more elaborate song, in the other the female.

5. Many females have been reported as singing in territorial situations, in solitude, or old age.

6. In many cases both sexes have elaborate songs; these are often given in courtship or to sustain the bond between the pair, or as an expression of social bond in flocks.

7. Where males have elaborate songs and females apparently have none, it may be that careful observation will disclose sporadic, perhaps "primitive" singing from the female, as was found in the Song Sparrow.

8. Where the female takes the initiative in courtship and the male incubates the eggs, the female often gives the advertising song rather than the male.

9. Male hormone has been shown to induce singing in some female birds. Where song is generalized in its use or concerned with the bond between the sexes, it may be developed in both sexes; where it is specialized for territorial uses, it is often most highly developed in one sex.

CHAPTER XI

Development, Inheritance and Function of Song

The discussion of the evolution and function of song in female birds leads us natually to the problems of the evolution and function of song in birds in general. Before turning to these subjects, let us consider the development of song in Song Sparrows and other birds and also the question of inheritance of song.

A. THE FIVE STAGES IN DEVELOPMENT OF SONG SPARROW SONG

The song of the juvenile Song Sparrow is a formless warble; that of the adult a repertoire of 6 to 12 or more distinct songs, each 2 to 3 seconds long, given typically at intervals of 7 to 9 seconds. The initial and final stages are easily recognizable. Transition stages are rather indefinite, but there are two (II and III) that may be fairly well distinguished.

I. Continuous warbling.

II. Some short songs; much warbling; intervals much shorter than songs.

III. Predominantly short songs, but not yet crystallized into adult form; length of intervals about equal to that of songs; some warbling.

IV. Songs practically adult in form; intervals usually more than twice as long as songs; a period of trying out songs, adding some, dropping others.

V. Songs adult; stereotyped except for endings; restricted to the final repertoire.

The criteria for stages II and III are not clear cut; *nor is there necessarily continuous forward progression through I, II, III and IV.*

1. *Observations on Wild Birds*

In February 1930 I became fascinated with studying the songs of various of the young birds on Interpont and recorded a great deal of data, particularly on 7M. Scattered notes were taken on this subject each fall, winter and spring, and later a fairly full acount was kept of the song development of 186M. In the late winter of 1931 I took a few notes on the song development of 7 juvenile residents.

a. The Progress of Seven Residents Banded in the Nest

Seven males, banded in the nest in May and June 1930, took up territories on Interpont the following fall or winter. On all of these I have some notes on song development, but observations were not made every day. The weather of February averaged 2.2° C. above normal and was unusually even, so no cold waves occurred to interrupt the sequence of song development.

TABLE XVI

SINGING PROGRESS OF SEVEN RESIDENT MALES BANDED IN THE NEST IN 1930

Bird	Date hatched	Stage I Warbling	Stages II and III Some short songs Dates	Age in days	Stage IV and V Adult songs Dates	Age in days
52M	May 5	Oct. 9, Jan. 29	Oct. 21, Jan. 27-31	169-271	Feb. 4	276
54M	May 5	Jan. 17-27	Jan. 24	268	Feb. 3	274
56M	May 14		Feb. 5-12	274	Feb. 16	278
50M	May 17	Sept. 2-16	Feb. 3-12	271		
55M	May 29		Jan. 14, Feb. 5	230-252	Feb. 9	256
57M	June 6		Feb. 3-14	242-253	Feb. 25	264
58M	June 12		Feb. 3-16	236-249	Feb. 27	260

The birds in Table XVI are ranged in order of birth. It will be seen that the older birds reached adult singing earlier in February than the younger birds, the dates with one exception becoming progressively later. 55M was the most precocious of the seven, reaching stages IV and V 7 days before 56M who was 2 weeks older, and probably about the same amount of time before 50M. (Stage IV is not distinguishable from V without considerable study.) The 4 oldest birds were last recorded in transition stages from the ages of 268 to 274 days, and in the final stages from 274 to 278 days. The 3 youngest, on the contrary, were last recorded in transition stages from 249 to 253 days, and in the final stages from 256 to 264 days. 58M was 38 days younger than 52M and 54M and 24 days behind them in song development; 55M was 24 days younger and 5-6 days behind them. The date of attainment of adult song depended partly on age and partly on time of year and temperature.

b. Song Development in Some Other Song Sparrows

The most detailed records were kept on the song development of a male, 7M, known to be young by his warbling songs; in February 1930 he had taken up his territory across the road from our house. Four years later, 186M, known to be young from the pointed ends of his tail feathers and by the character of his singing, settled in our garden; at night he roosted in the vine on our chimney, so his early morning singing was easily followed.

In Table XVII samples are given of the singing of both these birds. (It should be noted that the interval is the time from the *end* of one song to the *beginning* of the next. Measurements were made by stop watch.)

TABLE XVII

AVERAGE LENGTH IN SECONDS OF SONGS AND INTERVALS BETWEEN SONGS OF TWO YOUNG BIRDS

	7M						186M				
	Songs		Intervals					Songs		Intervals	
Stage	Date	No.	Length	No.	Length	Stage	Date	No.	Length	No.	Length
I.	Feb. 6	15	12.6	11	2.9	III.	Nov. 4	13	4	11	3
II.	Feb. 11	59	4.9	43	2.4	III.	Jan. 26	19	3.3	15	3.4
III.	Feb. 12	150	3.3	112	2.3	III.	Feb. 1	45	3	43	3.2
III.	Feb. 13	162	3.9	150	5.5	III.	Feb. 6	27	3.8	24	4
IV.	Feb. 15	18	2.4	15	8.8						

The average length of the songs with 7M decreased markedly and with one exception consistently from the first to the last stage. The intervals were short in the first 2 stages, doubled in the third stage and increased still further in the fourth. In typical adult singing in the highly stimulated phase the song lasts about 2.3 seconds, the intervals 6.2-8.7 seconds.

With 186M the picture is somewhat different—songs 3 to 4 seconds long and intervals much the same. A 2 minute record on another young male—187M—on Feb. 15, 1934, gave an average length of 4 seconds for 17 songs and 3 seconds for 16 intervals.

The most striking events in the 11 days of 7M's song development were as follows:

Feb. 5. Stage I. Almost continuous warbling, canary- and goldfinch-like; songs 4-32 seconds, intervals 1-3.

Feb. 6. Stage III. *4M visits; 7M puffs himself out, waves his wings and sings short songs.* After 4M's departure, 7M reverts to stage I or II; songs 3-28 seconds, intervals 1-6.

Feb. 8. Stage I or II. Spectacular, beautiful, varied song, lasting 3-40 seconds at one time, 10-76 seconds at another; intervals 1-2 seconds.

Feb. 9, 10. Very windy; little singing.

Feb. 11. Stage II. Most songs 2-7.5 seconds long, one of 12 seconds, one of 26; intervals 1-6 seconds. Very different from Feb. 8 when most of his singing was extraordinarily long warbling. His *zip-zip-zip* song is forming; before this I had heard it within the song, but not separated out as the beginning of a short song and repeated again and again.

Feb. 12. Stage III. 7M has 3 fairly well defined songs now, but also indulges in his long, varied, nondescript warblings. He gave 13 *zip-zip-zip* songs in one minute, 14 in the next and 10 in the last. Length of songs and intervals more nearly equal than before.

Feb. 13. A tremendous difference from yesterday, chiefly in the lengthening of the intervals. The timing is now much like that of the adult, the average number of songs per minute for 21 minutes being 7. The song averages a little longer than yesterday; it is considerably longer than that of the typical adult. There were 5 really long songs from 9-18 seconds. He gave 247 songs in an hour.

Feb. 15. Stage IV. His singing is now fully adult, except that there is a great deal of variation in his songs. One is of striking beauty.

In contrast to my experience with 7M where I watched the development of song through 4 stages in 11 days, my notes on 186M show that his development was spread over 5 months.

Sept. 30, Oct. 23-31, stage I; Nov. 1, 3, stage II; Nov. 4-Dec. 1, stage III; Jan. 21, stage II; Jan. 26-Feb. 14, stage III; Feb. 22-Mar. 7, stage IV. After the silence of 7 weeks in mid-winter, the bird *did not begin again with stage III, but reverted to stage II* or "advanced warbling". Although in November, 186M's daytime singing was in stage III, the *awakening song* on Nov. 24 and 25 was *approximately adult;* this has been noted in other juvenile birds in the fall. He was in stage IV at least 2 weeks, after which I have no further record. On Feb. 28 he was "still experimenting"; on Mar. 2, "practising; giving 4M's G for the first time; some songs too long for normal"; Mar. 7, "giving 4M's A for the first time."

Data on stage IV were also obtained for 2 other birds.

187 M settled next our house; he was in stage III Feb. 15 and 21, 1934: on the 22nd his songs were of "the right length but each different; he has 4M's G." On the 28th, "is singing 4M's O". Mar. 7, "Hard to record, he changes so much;" Mar. 10, "6 common songs, all varied considerably," Mar. 13, "Most of his songs are quite definite now." 4M's G had been dropped, but O was one of the permanent repertoire. He seems to have been in stage IV for about 3 weeks.

44M, whose territory was 150 meters south of 4M's territory, was in stage III on Feb. 18, 1930, when one of his songs lasted 8 seconds; the next day he was in stage IV. Since most of his songs were replicas of 4M's except for a few notes added at the end, it was easy for me to keep track of the songs and series sung. On Feb. 19 I kept a half hour's record of his singing, on the 20th and 21st a full hour each day. His most popular songs were 4M's C, E, J and O, but each day he gave a version of A, on the 19th a version of B and G, and on the 20th and 21st K. On the 19th and 20th he had only one song completely his own, but *on the 21st he had added another original one.* Unfortunately he disappeared soon after this so that I was not able to determine his final repertoire.

On the 19th he gave 176 songs in a half hour, on the 20th 325 in an hour and on the 21st 314—the 2 highest records I ever got. The number of series for the half hour on the 19th was 47; for the hours on the 20th and 21st 53 and 29. These should be compared with 187M's 18-24 series per hour Mar. 20-21, 1934, and to the average of 11.5 series per hour of fully adult birds in their prime as shown in Table XIII.

It is clear that there is great diversity in the course of song development in Song Sparrows.

c. Territory Situations and Song in Juvenile Birds

It has already been noted that with 186M and other juveniles the awakening song was given in almost adult fashion while during the rest of the day the bird sang in stage III.

7M's sudden burst into short songs in response to 4M's visit on Feb. 6 was almost startling. An even more remarkable example was afforded in 1931 by 51M, a young resident banded in the fall, that had wintered in our garden but had never sung to my knowledge. On Feb. 3 I found him at 9:30 warbling loudly and continuously: at 10:00 a territory quarrel was in full swing between him and 4M; 51M's warbling had suddenly been transformed into short songs and thus he sang for 2 hours.

Many times I have thought 2 adults were having a territory quarrel, only to have one of them after separation begin to warble. A young resident will sing in adult form high in a tree on his territory, answering his neighbor, but on the ground will warble softly.

Winter resident juveniles warble a good deal in February and March and some of the transients warble on their journey through in spring. A juvenile summer resident, however, ***never warbles after his arrival in late February or in March.*** Such a bird can be distinguished, if observations are made the first day or two after his arrival, by the number of times one song is repeated, for instead of some 20 times, the newly arrived juvenile sings only 4 or 5 examples of one song before he switches to another. 10M was judged to be juvenile from this characteristic during the first few days after his arrival; 2 weeks later his songs had crystallized into somewhat different form from what they had been at first.

2. *Development of Song in the Hand-raised Song Sparrows*

As with the wild Song Sparrows, the hand-raised birds hatched late in the summer—B, R and Y—attained the various stages at younger ages than did D hatched 1½ months earlier. Stage III was attained at 3 months with the Massachusetts birds and 6 months with the Michigan bird; here the greater vigor and social stimulation of the brothers undoubtedly were of importance; moreover, the Massachusetts birds were subjected to much more light in the evenings than was D. B and Y, however, were retarded in their song development when the house was without heat during a severe cold spell in late November, while D experienced no such taste of winter. Stage IV was attained by all the birds at almost the *same date,* i.e. the last of December.

TABLE XVIII

SINGING PROGRESS OF FOUR HAND-RAISED SONG SPARROWS

Age in days

Stage	B		R		Y		D	
	Date	Age	Date	Age	Date	Age	Date	Age
I. First warbled	Aug. 7	14	Aug. 6	13	Aug. 11	17	July 4	20
I. Warbled loudly	Sept. 3	41	....	......	....	......	July 25	41
II. Short songs when fighting	Oct. 3	71	Oct. 6	74	Oct. 9	76	Dec. 17	186
Opened bill when warbling	Oct. 7	75	....	......	Oct. 29	96	Dec. 17	186
III. Loud, short songs	Oct. 13	81	....	......	Nov. 3	101	Dec. 19	188
IV. Adult songs of definite form	Jan. 1	159	....	......	Dec. 31	157	Dec. 23	192
V. Final repertoire	....	......	....	......	....	......	Dec. 23	192

As shown in Table XVIII, the development of the Massachusetts birds was much the same except that in the fall B was ahead of Y. The close connection between song and territory is strikingly shown in the detailed account in Appendix II of the hand-raised birds in their relations of dominance, territory and singing. The amazing development of D's singing in *6 days* from warbling to adult songs was definitely bound up with territorial domination over Y.

B. INHERITANCE OF SONG WITH THE SONG SPARROW

The Song Sparrow with its marked individuality in song is an outstanding subject on which to study inheritance and learning of song, if careful attention is paid to the songs and much banding done on the birds' territories over a period of years.

1. *Do Song Sparrow Sons Sing Like Their Fathers or Grandfathers?*

Among 552 songs of this species recorded by Saunders (1924) there have been but 5 cases of duplicates; this author suggests that "a possible relationship between the two birds might have been the cause of similar songs".

Song Sparrows possess such strikingly different songs that it should be possible to get data on inheritance of songs when father and son are banded. Do Song Sparrows sing like their fathers? If so, is this a matter of inheritance? Or do they learn these particular songs during the first 4 weeks of life? If they do not have their fathers' songs, are they influenced by Song Sparrow singing between the age of independence and maturity?

In my studies on Interpont I recorded something over a thousand songs of the 250 or more males that have taken up territories. Besides knowing the whole repertoires of 1M, 4M and 187M, I learned one or more songs of perhaps 50 birds. My knowledge of 4M's songs and the opportunity to check them constantly for 7 years were fortunate circumstances.

As already mentioned, most Song Sparrow songs consist of 3 parts, the last portion being much less stable than the others. A few songs on Interpont have been exactly alike, while other cases of similarity have concerned the first 2 parts of the song. Among my birds certain songs have been heard from a number of birds, and this is true of all of 4M's 9 songs. Seven have been given by from one to 3 birds besides 4M, A has been heard from 9 and J has been possessed by at least 22 birds. Several songs of other birds I know have been duplicated, and undoubtedly this has happened more often than I suspected. These statements as to similar songs refer not to develop-mental stages, but to the established repertoire of the adult.

Does the possession of like songs mean a relationship between the singers? I have 21 cases of banded sons of banded fathers, two cases of grandfather, son and grandson, and one case of grandfather, daughter and grandson. I have data on the songs of most of these birds and for some of them a great deal.

I found no case of a male having the song of his father or grandfather on either side. For instance, 4M's son had no song like any of his father, while 50M had none like his maternal grandfather, 1M. Two brothers from the same nest had no song in common.

On the other hand, 56M had two of 4M's songs, yet he was 14M's son. Other individuals have had striking songs which I know were not possessed by their fathers.

It is evident that these Song Sparrows did not inherit individual songs from their direct ancestors, nor did they learn them during the first 4 weeks of life.

2. *How Much Do Song Sparrows Imitate Each Other?*

There was a certain amount of what looked like imitation among the Song Sparrows on Interpont. Again and again I have heard young males in stage III repeating exactly the songs of their adult rivals in territory establishment activities. Many of these "imitations" are dropped, while others are adopted into the repertoire, usually in somewhat changed form. Many young birds, however, appear entirely uninfluenced by the singing of their neighbors so far as the form of their songs is concerned.

Each young Song Sparrow has a large fund of potential songs, as is clear from listening to the rambling warblings of juveniles. Some individuals, before their singing becomes set in the adult mold, are capable of singing the songs of various other Song Sparrows hurled at them by territorial rivals. Perhaps what seems to be imitation is rather a calling forth of songs already in the potential repertoire, most of them being later lost through disuse.

One possible explanation for the wide spread occurrence on Interpont of some of 4M's songs might lie in the fact that this notable bird sang such a tremendous amount for 8 or 9 years, and that during most of that time he sang a great deal while the young birds were developing their songs—in fall and winter.

3. *The Case of the Hand-raised Birds*

B and Y were hatched in Massachusetts in late July 1938; after they were 5 and 6 days old they heard no Song Sparrow singing except for 3 or 4 examples in Ohio when they were 25 to 26 days old.

The only bird songs to which they were exposed, besides their own warblings, were occasional phonograph playings of the songs of English birds—Nightingale, Chaffinch, Song Thrush, etc. When their singing became adult at the age of 5 months, it was far from typical Song Sparrow singing; it was loud and whistled and resembled "foreign birds" more than wild Song Sparrows. The songs of the brothers resembled each other in quality and I was never sure which was singing unless I saw him. There was little variety between their songs. *The form, length, timing and even the number of the songs are typical of the species, but not the quality.*

D was hatched in June 1939 in southern Michigan and belonged to the subspecies *euphonia* in contrast to *melodia* of the Massachusetts birds. He heard no Song Sparrow singing from the time he was taken from the nest (6 days) until his arrival in Chicago at the age of 2 weeks; Y was singing at this time, but soon stopped almost completely.

In September I recorded Y as giving single, loud songs on the 15th and 23rd; as "singing a bit at the end of a battle" on the 25th and 26th; and singing more on the 27th. On Oct. 2, "no singing", 4th "a number of times this morning", 6th "sings rather softly", and on the 9th and 17th "no singing".

Y was not in good health in December; D suddenly burst into song, became dominant on the 22nd, and reached adult form the next day (See Appendix II). *He had all of Y's 6 songs. The repertoire of the 2 birds are exact duplicates,* something I have never known of before. Each bird was kept for a while in March by Mrs. Dorothea Ewers who recorded their songs on discs.

The question is when did D hear Y sing enough to have all his songs impressed upon him? From the consistently negative evidence in Columbus as to sons ever adopting any of their father's songs or phrases, I am inclined to think that the learning took place in late September and early October, although opportunities were admittedly meager.

The following year the young male A was markedly subnormal; he barely warbled at all, until March. In June some of his warbling resembled one of Y's songs.

Mr. Ivor wrote me in regard to his hand-raised Song Sparrow, "For a while his song was in imitation of the Cardinal, but later he sang the typical song of his species; he could, of course, hear Song Sparrows outside the aviary."

In summing up this question of learning vs. inheritance there are 3 aspects of Song Sparrow song to be considered: pattern (i.e., form, length, timing); quality; and particular song. Let us consider 3 birds about whose ancestry and environment we know something: 56M, son of 14M, who had no songs of his own father but 2 of 4M's; Y, hatched in Massachusetts in 1938 and exposed to no singing except that of his brother B and a few playings of records of foreign birds; D, hatched in Michigan in 1939 and exposed only to Y's singing and not much of that.

It is evident that the *pattern is innate*. As to quality, with 56M it probably was learned from other Song Sparrows; with Y it might have been learned from the records, and from B, who probably got it from the records; with D it certainly was imitated from Y. In regard to particular songs, 56M neither inherited nor learned any from his father; he may have adopted 2 from 4M while his other 4 may have been original. With Y we cannot tell how much they were original, nor how much they were taken over from B. But with B they must have been more or less original, based on the inherited pattern, with the quality probably suggested by the records.

D's 6 songs were taken bodily from Y. He had no opportunity to hear any other singing and the telescoping of development into a week, due largely to the territorial situation with Y, apparently left no opportunity for improvisation. Stage IV seems to have been suppressed entirely in this case.

C. JUVENILE SONGS OF OTHER SPECIES

Singing appears very early with some young birds; in many cases it is unlike the song of the species.

1. *The Age at Which Young Birds Start to Sing*

The hand-raised Song Sparrows started to warble at 13, 14, 15, 17, 19, 20 and 31 days. The Common Redstarts began at 18 and 19 days, and the Serin at about 24 days. A Blackcap (*Sylvia atricapilla*) sang while still in the nest (Lorenz, personal communication). Bicknell's Thrushes started to sing at 15 and 25 days (Wallace 1939), California Thrashers at 19, 29 and 30 days (Dyer, letter), Curve-billed Thrashers at 20 days (Rand 1941c), American Robin at about 3 weeks (Laskey, letter), female Cardinals at 3 and 4 weeks (Laskey 1937 and letter), male Mockingbirds at 24 and 28 days, a female at 73 days (Laskey, letter), Bourke's Parakeet at 24, 28 and 34 days (Hampe 1939), female Goldfinch at 30 days, male at 46 (Schantz, letter), California Shrike at 39 days (A. H. Miller 1931b), Cedar Waxwing at about 43 days (Nice 1941a), and House Finch at 6 weeks (L. Miller 1921), while with Roller Canaries the "earliest baby song appeared at 60 days and the latest at 148 days" (Metfessel 1935).

Considerable data on the first appearance of song are given by

the Heinroths (1924-33 I, IV): in the nest—Song Thrush and Dipper; 3 weeks—Grasshopper Warbler, Skylark, Starling; 4 weeks—Bank Swallow, Sedge and Marsh Warblers, Jay; 5 weeks—Willow Warbler, Grey Wagtail, Ortolan Bunting; 6 weeks—Crossbill, Nutcracker; 8 weeks—Spotted Flycatcher, Meadow Pipit.

Since the 3 species mentioned above as singing while still in the nest do not ordinarily leave the nest until 13-14 days (Blackcap), 14-16 days (Song Thrush) and 18-24 days (Dipper), we do not know whether or not the Song Sparrow R, starting at 13 days, holds the record for earliest use of song; perhaps it is a tie between him and the Blackcap.

2. *The Character of the Song of Young Birds*

With many birds the first song is an indefinite warble, non-specific in character. This is designated as "ancestral" by Whittle (1925), "tribal" by L. Miller (1929), and "primitive" by Saunders (1929).

Records of such singing have been published for the following species: European Dipper (the Heinroths 1924); Long-billed Marsh Wren (Welter 1935); Goldcrest (the Heinroths 1924); Maryland Yellow-throat (Whittle 1925); Cedar Waxwing (Nice 1941a); House Sparrow (the Heinroths 1924); Cardinal (Laskey 1937, Nice 1927b); House Finch (Miller 1929); Junco (Saunders 1929); Field Sparrow (Saunders 1929; Nice 1931a). I have also observed this type of singing in a number of species in the wild—House Wren, Maryland Yellow-throat, Lincoln Sparrow (Oct. 4, 5), White-throated Sparrow (Sept. 28, 30, Oct. 17), and Field Sparrow (in juvenal plumage June 30)—and in the Common Redstart and Bobolink in captivity.

With the Roller Canary the "baby song is for the most part a nonsense melody of choppy notes covering a wide pitch range" (Metfessel 1935). Three stages are recognized by Lister (1940) in the song development in young Chaffinches: 1, young males in juvenal plumage warble in concert; 2, in mid-August balance and rhythm appear in attempts at the specific song, some good songs being heard at the end of September; 3, in February there is still some warbling and some songs are incomplete.

D. INHERITANCE AND IMITATION WITH OTHER SPECIES

In this country, Scott (1901, 1902, 1904) found that his hand-raised Baltimore Orioles, Bobolinks, Red-winged Blackbirds and others, that did not hear adults of their own species singing, developed songs unlike those of the species. On the other hand, Sanborn (1932a) contends that his hand-raised birds of the above species did sing the species song without the corresponding tutors; however, I have been informed that this author is more familiar with European cage birds than with our native species.

Heinroth (1924), writing from his large experience with hand-raised birds, states that many simple songs are inborn: Bank Swallow, Garden Tree Creeper, Grasshopper Warbler, Chiffchaff, Willow Warbler, and Bullfinch. Mistle Thrush, Song Thrush and Blackbird sing songs much like the adult. With some birds, however, most or all of the song must be learned: Chaffinch, Pied Flycatcher, Nightingale, Golden Oriole, Whitethroat, Meadow Pipit, Yellow Bunting, Goldfinch and Greenfinch; no one could guess their species from the song of these young raised without opportunity of hearing others of their kind. (A young Whitethroat (*Sylvia communis*) and Linnet raised together sang exactly alike, something like a European Robin.) *Yet, when they finally do hear members of their own species sing, they quickly adopt the proper song.*

The first songs of a hand-raised Bronzed Grackle were like those of adults, although no other Grackles were about (Laskey 1937). A female Cardinal sang the species song without tutors (G. M. Sutton, personal communication); and the same was true of my Serin in Altenberg. Mockingbirds seem to sing songs much like that of their species (Michener 1935:138; Laskey, letter), but here the birds heard adults. The first song of California Thrashers is "sweet and low with an occasional articulate phrase, but mostly warbles—a perfectly fascinating little lay, recognizable easily as thrasher music" (Dyer, letter).

E. THE EVOLUTIONARY TREND

"Is the evolution of song progression or retrogression?" asks Saunders (1929:121). He suggests that: "When song first developed the trend was from simple to complex. When the necessity for the territory system arose the trend turned from complex to simple." Nicholson (1929:54) suggests that "song, arising as a spontaneous expression of the emotions, was, in the case of those species which embraced individual territory, captured by what may be called the territorial set of instincts and developed intensively as their expression." Some students, however, believe the territorial state was the primitive one (Lorenz 1938, Diebschlag 1941).

With the Song Sparrow there are three songs that might give us light on ancestral song—the juvenile's unspecific warble, the female's harsh twitter, and the male's jumbled flight song. The course of evolution as suggested by Saunders is recapitulated in many individuals: the juvenile Song Sparrow sings a simple warble which in some birds becomes elaborate and beautiful; he finally settles on a limited selection of his original phrases. I have sometimes thought we have lost a very fine songster in the breaking up of the Song Sparrow's spectacular, varied and beautiful warble.

Rather curiously the American Goldfinch, along with its ecstatic and musical warble, has a harsh, short song, showing all the characteristics of a "territory song" (yet apparently not functioning as such), flourishing along with the warble 2 months before the flocks break up for nesting (Nice 1939c).

With the Song Sparrow, rather than considering evolution of the song as proceeding from the simple to the complex and then to the simple again, it might be better to say that it changes from the indefinite to the definite. This is true of many birds; they start with primitive, unspecific efforts and later develop songs that are diagnostic of the species.

F. A DEFINITION OF SONG

Song is difficult to define, for, as we are considering its function, we cannot confine ourselves to those avian utterances that sound pleasing to human ears. Nicholson's (1929:41) definition is fairly satisfactory with the addition of "sometimes" to the last clause: "Bird song is properly a sustained, more or less uninterrupted repetition of one or more notes conforming recognisably to a constant specific type and [sometimes] used by the male as an expression of independent sovereignty."

This covers a great variety of manifestations, a dozen diverse examples of which are given by Tinbergen (1939c:73). Concentrating upon territory song, this author points out that the most "important character of the song of most song birds" is "its loudness and far-reaching capacity". He calls this "advertising song" and in it includes the love-call of the Grey Heron (Verwey 1930), the sounds accompanying spring flights of Snipe and many other Limicolae, the drumming of Woodpeckers, booming of the Nighthawk, etc. Song, therefore is a widely inclusive term, for it ranges all the way from these loud sounds to whispered warblings.

G. FUNCTION OF SONG IN THE SONG SPARROW

The most spectacular use of song with this species is the proclamation of territory, the announcement "Here is a male with a territory"—a warning to other males, an invitation to a female. Song is one of the most important means of obtaining and keeping territory. Males challenge each other and answer each other with song. The use of song as threat was very evident with the hand-raised birds.

Evidence of self-assertion is given when a trespassing male, driven home by his neighbor, sings as he lands in safety. The same may be true of the song given in connection with "pouncing" on and swooping over the female. While his mate is incubating he gives a "signal song" for her to come off the nest—a sign that all is well and he is ready to guard. He sings near the nest while she is off, a warning that he is ready to drive off intruders. His singing while she incubates may be an expression of satisfaction that all is going well, a method of passing the time when he is alone. While caring for young, there is little energy for singing, except for single songs after feeding the family, and especially after carrying off excreta. The fall singing in fine weather would seem to be an expression of excess energy.

In the White-crowned Sparrow "Song may express . . . .defiance or warning to territorial rivals, the longing for a mate, sexual excitement, concern for territorial boundaries (accompaniment of patrol), eagerness for the female's return to her eggs, and fright or physical shock" (Blanchard 1941:21). This is true also for the Song Sparrow, except perhaps the last two phrases. Only once did a Song Sparrow sing when "frightened" or rather greatly concerned when his 28-day old child screamed as I trapped it. Tinbergen (1939c:73) mentions "the song of a Skylark just after having escaped from a bird of prey; the sudden outburst of song of two fighting birds; the songs of birds visiting light-houses."

Mr. Ernest Dyer described for me 8 different songs of his adult California Thrasher: (1) *Slumber song,* softest of the sub-songs, bird drowsy or napping; (2) *Quarter song,* louder, more varied sub-song, from ground or digging; (3) *Half song,* the "digging song" most often heard, long and varied, audible for 50 feet; (4) *Three-quarter song,* audible perhaps 125 feet, most varied of all the songs and with the most mimicry; (5) *Full song,* audibility 300 yards, extraordinarily rich and varied, sometimes responsive between the pair; (6) *Courting,* short, hysterical snatches of song, as the birds pursue each other, heard for several days as nest nears completion; (7) *Invitation to new mate,* male climbed favorite tree, gave detached phrases of full song, looking over the surrounding country; (8) *Welcome to new mate,* different from all other songs heard. (I never could detect any difference between unmated and mated Song Sparrows singing in the highly stimulated phase.)

H. Some Theories as to the Function of Song in Birds

The song of birds is such a striking phenomenon and much of it is so pleasing to the aesthetic sense of mankind, that this subject has had much attention bestowed upon it.

1. *Early Theories*

The early theories as to the reason for bird song were distinctly anthropomorphic. Dawson (1921) wrote of the "gentle disposition" of the Song Sparrow with his "message of peace and good will", while some fancied this singer was "sending his little prayer of thankfulness straight up to heaven, by the shortest route. Over and over again the sweet and sincere little petition is offered, and who can doubt that it is heeded? Whatever the form of the song, however, its spirit is always the same, and Mr. Burroughs interprets this very faithfully when he says that it expresses 'simple faith and trust'" (Pearson 1917:52).

Not many observers considered that birds sang from piety. Some thought they were expressing happiness. "If bird-song expresses, as we hold, joy in life, rather than merely a passing desire to capture a mate, then is the Mockingbird the most joyful of birds" (Dawson 1921:719).

The most popular theory was that they sang to win and later to "cheer" their mates during the "tedious duty" of incubation. Bound up with this theory is that of Darwin's sexual selection, which F. H. Allen (1919:531) considered the most "reasonable" theory "to account for the beauty of bird song."

2. *Advertising Song*

The territory theory has radically changed our ideas as to the function of song. From Altum (1868), Moffat (1903), Howard (1920), and Nicholson (1929), to Heinroth (1938a) and Tinbergen (1939c), all agree that song is chiefly an invitation to a female and a threat to other males. This, of course, applies, as did the earlier theories, to what Nicholson calls "true song", Saunders "territorial song" and Tinbergen "advertising song". According to this last author (1939c: 80),

"Advertising song is a loud sound, given by a bird of one of the two sexes especially at the beginning of the reproductive period, that serves to attract a sex partner, to warn off a bird of the same sex, or both."

"In its meaning for the defense of territory and invitation to a female," writes Heinroth (1938a:117), "the song corresponds to the cooing of the Ring Dove, the crowing of the cock or the churring of the Nightjar, as well as the call of the Cuckoo and the scream of the elk."

As to the double function of advertising song, Tinbergen says: "With species like the Snow-Bunting, for instance, where inhibition of the advertising

song by the arrival of the female is very marked, attraction certainly is the primary function. With species like the Wren-Tit, which in the pre-mating period shows only a slight increase in song and which sings the whole year round, the warning function is more important. Nevertheless, the occasional occurrence of song in the mated Snow Bunting and the increase of song in a Wren-Tit in spring prove that in neither species has the song only one of the two functions. A correlation of winter song with winter territories can be expected in those species where song has a primarily warning function" (1939c:80).

The sudden stopping of song upon the arrival of a mate has been recorded in many species and will be further discussed in Chapter XIV. I am not convinced that this phenomenon means that attraction is the "primary function" of the Song Sparrow's song; warning is also of prime importance. One great need has been satisfied, but in case a new territorial situation arises, the male may sing as vigorously as though unmated.

In the Brown Towhee "permanently mated males do not sing", so "it would seem that the male song" of this species "has as its chief purpose the attraction and securing of a suitable mate" (Quaintance 1938:101).

In discussing the singing of palaearctic migrants while in Egypt, the Moreaus (1928) write: "Loud and persistent song, such as is associated with territory-holding is almost wholly absent, even at the end of spring. . . . At the same time, there is no evidence of territory-holding, in the combative sense, in Egypt in winter; and it is tempting, and probably justifiable, to accept the absence of 'territorial song' as intimately connected with the absence of territory-holding."

3. *Song as a Signal*

"Song is the expedient used by inconspicuous birds to compensate for the drawbacks of being inconspicuous" (Nicholson 1929:44). Song serves as a signal in many ways: threat to other males, invitation to females, a device for keeping the pair together. In the Song Sparrow and some other birds it also serves as a signal to the female on the nest of the approach of the male.

Some of the uses of song as signals in social control with Pigeons are listed by Craig (1908:99):

"1. Personal control, as that of the male over his mate.

"2. Suggestion; as, the nest-call coo quickly brings the mate, the challenge coo causes the enemy to flee.

"3. Stimulation, as, working up both male and female to the point of pairing, inducing oviposition in the female.

"4. Inhibition; as, inhibiting adultery, inhibiting the use of nesting-sites other than the one chosen; inhibiting copulation out of the normal time.

"5. Co-ordination in space; as, leading male and female to use the same nest.

"6. Co-ordination in time; as, leading male and female to go through the brooding activities synchronously.

"7. To proclaim: (*a*) the bird's species; (*b*) the bird's sex; (*c*) the bird's individual identity; (*d*) the bird's rights.

"8. Tradition; as, when an experienced bird is mated with an inexperienced one, the former takes the lead."

4. *Song as an Emotional Outlet*

Song is much more than territorial and advertising song. "Song is simply an outlet," says Huxley (1916), "and a pleasurable one, for nervous energy; thus, provided certain internal physiological conditions are fulfilled, he [the bird] will continue to sing in all moments of excitement or exaltation, non-sexual as well as sexual." Singing of Starlings, American Blackbirds, Goldfinches, and others seems to be a response to the social stimulation of the flock. As mentioned above, fall singing of Song Sparrows, both young and adults, is attributable to overflowing energy.

Song perhaps is over-developed in some species and will appear in fall and winter in vigorous birds, when there is no special function to be served, nor on the other hand, any inhibitory influence.

Tinbergen thinks it likely "that with some species at least, autumn song is regularly accompanied by testis development. This development nearly always regresses before full maturity is reached; but in exceptionally warm autumns some individuals actually begin a new reproductive cycle", Starlings, for instance (1939c:78). In Starlings the yellow bill color is induced by male sex hormone; in October the bills of both sexes begin to turn yellow and both sexes sing (Bullough and Carrick 1940).

I. THE FUNCTION OF SONG IN BIRDS

Song is a normal outlet of excess energy in many birds. It is a means of self-expression and self-assertion. In some species song has been developed to an extravagant degree—witness the 2305 songs of 4M in one day, the unceasing ditty of the Dickcissel no matter how hot the weather, the endless declaiming of the Red-eyed Vireo, the nightly outpouring of Mockingbirds on the chimney-tops.

Song is one of the biological isolating mechanisms that serve as species recognition marks. In his book on "Genetics and the Origin of Species", Dobzhansky (1941:264) emphasizes this: "The importance of song in the courtship in birds is well known; songs may differ not only in different species but in races of the same species (Promptoff

1930)." Song guarantees the mating of individuals belonging to the same species. The female obviously has an innate ability to recognize the song of males of her own species. This is very important in genera where plumage is almost identical, as in the American Flycatchers of the genus *Empidonax* and in some of the Old World Warblers (*Phylloscopus*), where 2 or 3 species nest in much the same habitat. It is true to a lesser degree of other species with an advertising or courtship song.

Song is one of the most important signals between members of the species. In most "song birds" the male's role is primarily defence of his family; he sings tirelessly to assure himself of a territory and a mate and to defend both. Song has been highly developed here as a weapon, as a symbol of ownership to warn other males and attract females. It may also function in courtship and in sustaining the bond between the mated pair.

J. SUMMARY

1. There are 5 chief stages in the development of the Song Sparrow song: I, continuous warbling; II, advanced warbling, some short songs; III, predominantly short songs; IV, songs practically adult, but repertoire undetermined; V, songs adult, repertoire fixed.

2. With 7 residents, banded in the nest in 1930, the older birds reached adult singing earlier than the younger; the date of attainment of stages IV and V depended partly on age and partly on time of year and temperature.

3. Details are given on the song development of 4 other Song Sparrows in Columbus: 7M progressed through the first 4 stages in 11 days in February; 186M took 5 months—from October through February—to do the same; observations on 187M and 44M gave data on stage IV.

4. While daytime singing was in stage III, the awakening song was practically adult in form. Territorial situations abruptly bring the juvenile male into stage III, after which he may lapse again into stage I or II.

5. The Massachusetts Song Sparrows attained stage II at 71-76 days, stage III at 81-101 days, and stage IV at 157-159 days. D attained II at 186 days, III at 188 days, and IV and V at 192 days, reaching stereotyped adult songs in only 6 days.

6. The Song Sparrow, where each male has a quota of songs peculiar to himself, but where there are occasional duplications in a community, offers an opportunity to test the matter of inheritance or learning of song with banded birds.

7. With this species it is clear that the possession of similar songs is no

proof of close relationship between the singers, as neither brothers, fathers and sons, or grandfathers and grandsons, have had similar songs, while, on the other hand, birds known to be unrelated have shown this phenomenon. Particular songs were neither inherited nor learned during the first 4 weeks of life.

8. A juvenile in late winter will sometimes imitate the songs of a territorial rival, although seldom adopting these songs into his repertoire.

9. With the brothers B and Y, the form, length and timing of their songs were typical of the species, but not the quality, which may have been suggested by phonograph records of English birds. The following year, D, hatched 600 miles from Y's birthplace and belonging to a different subspecies, having heard Y sing a small amount in the fall, and no other singing, burst into song in December with all of Y's songs and nothing else.

10. It is evident that the pattern is innate, but that quality may be imitated. Particular songs may be improvised, or they may be adopted from some other Song Sparrow.

11. Young birds of 16 species are reported as starting to sing from the age of 13 to 24 days, and 15 species from the age of 4 to 8 weeks. With many species the first song is an indefinite warble, a primitive "ancestral" song unlike the specific form of the adult.

12. Many simple songs, however, are inborn. With other birds, most or all of the song must be learned; when hand-raised, these birds do not sing the specific song, but as soon as they hear one of their own species sing, they quickly adopt the proper song.

13. Three of the Song Sparrow's songs might give us light on ancestral song: the juvenile's unspecific warble, the female's harsh twitter, and the male's jumbled flight song. With the Song Sparrow and many other species the trend in song development is from the indefinite to the definite.

14. Song might be defined as a sustained, more or less uninterrupted repetition of one or more notes conforming recognizably to a constant specific type.

15. In the Song Sparrow song serves as a signal to other members of the species and as an expression of the emotions.

16. Advertising song is a threat to other males and an invitation to a female. Song serves as one of the most important of intra-specific signals. It is a normal outlet of excess energy in many birds. It is also one of the biological isolating mechanisms that serve as species recognition marks.

CHAPTER XII

The Male and His Territory

The theory of territory in bird life is briefly this: that pairs are spaced through the pugnacity of males towards others of their own species and sex; that song and display of plumage and other signals are a warning to other males and an invitation to a female; that males fight primarily for territory and not over mates; and finally that the owner of a territory is nearly invincible in his territory.

Territory is of fundamental importance to the Song Sparrow, the basis of its individual and social life for more than half the year. This species may be considered a typically territorial bird, following closely the pattern of the Reed Bunting as described by Howard (1920, 1929).

In Volume I (Nice 1937) three chapters were devoted to the subject of territory: a brief one on "Territory Establishment" and more detailed treatments of "Territory Throughout the Year" and "Territory from Year to Year", illustrated with a table, 3 charts and 14 maps. In this volume I propose to treat the territorial establishment and defence behavior—in practice and theory—much more fully, merely touching upon the more pertinent points of the aspects described in the first volume.

Winter weather in central Ohio varies greatly from year to year and sometimes from week to week, cold and warm waves alternating in a way that brought marked response from the Song Sparrows. Singing, which denoted firm possession of territories, was well established the fourth week in January in 3 of the 7 years at mean temperatures of 6° C. (43° F.). Since migration does not take place until late February, no matter how warm the weather before that time, it will be readily seen that there would be considerable territorial tension in spring on Interpont, when former summer residents return to find their territories in possession of young residents.

A. Requirements of Territories

The Song Sparrow must have cover for nesting, roosting and protection from enemies, he must have outlooks for singing posts, and he must have a certain amount of space, for the pair carry on practically all of their activities within the territory. A large variety of habitats will suit his needs. The territory may have many trees, one tree, or none at all; it may have shrubs and it may have weeds. A few territories on bluffs consisted merely of weeds and tin cans. Others were in willow woods with little undergrowth; here the debris from floods served as shelter for nesting. Few of the territories on or near Interpont had water on them, so the birds had to leave them for purposes of drinking and bathing.

The minimum size of a territory was some 2000 square meters (½ acre); an average size in a region well filled with Song Sparrows was some 2700 square meters (⅔ of an acre), while a few might include 6000 square meters (1½ acres). During the later years when the population was comparatively small, Song Sparrows might range over a larger region than when Interpont was filled to capacity.

Territories, as pointed out by Howard and Tinbergen, may look very different when the bird leaves them in fall from what they do on his return in spring, especially in those cases where they are covered with snow. Tinbergen (1939c:12) writes: "As far as our experience goes, no Snow Bunting ever settles on the fjord ice, which in some places, where shallow bays penetrate rather far inland, is really difficult to tell from land. Yet their knowledge of one character only, *e.g.* a more or less hilly or irregular contour as opposed to a quite flat surface (ice) would, in most cases, suffice to enable the birds to stake out their territories on land. In other species that are much restricted to a special kind of habitat there seems to be little doubt that their knowledge of it is inherited. The fact that birds hatched in incubators and released after having reached sexual maturity, chose the species' normal kind of habitat leads to this conclusion."

Grinnell (1928) in discussing habitat choice writes, "The Song Sparrow taking part in post-breeding dissemination . . . does not blindly content itself with an attempt to find subsistence on grassy upland, or in a forest, or in dry chaparral, but keeps going, and seeks out locally its own 'natural' type of habitat, the stream-side thicket—the ecologic niche of its species."

Habitat selection, according to Miller (1942) "might appropriately be called perception of adequate environment." It depends on an "automatic, instinctive reaction . . . to a few key aspects of the environment." With Olive-sided Flycatchers apparently the key aspect is height of trees. "This instinct is just as much a part of the vital equipment of the species as a structural adaptation." "Song Sparrows have broken up into about 28 races on the North American continent, whereas Lincoln Sparrows [belonging to the same genus] have divided into but 3. The Lincoln Sparrow, apparently through habitat selection, adheres to a more sharply circumscribed environment than do the Song Sparrows, whose selecting instincts have permitted pioneering of somewhat diverse situations, thus opening up to the species new geographic areas and new possibilities of adaptational adjustment. Establishment of numerous geographically and ecologically isolated colonies of Lincoln Sparrows has been thwarted by the rigid adherence to a certain type of fresh-water marsh," p. 33.

Habitat selection involves learning as well as instinct. "Perhaps the hill-dwelling song sparrows of San Francisco do not associate with those on the salt flats, figuratively and literally on the other side of the railway tracks, because of their upbringing," p. 34.

In his paper on "Habitat Selection in Birds", Lack (1933:259) says, "Most distribution could be explained only by postulating the existence of specific habitat selection—that each species selects its ancestral habitat, instinctively recognizing it by the conspicuous, not necessarily the essential, features." Hickey (1942:196) emphasizes the great role played by *ecological magnets*—a tall cliff in the case of the Peregrine Falcon:

> "Rowan (1921) has cited the perfect illustration of this ecological magnet in his description of a patch of old heather which was used for nineteen successive years as a nesting site by Merlins (*Falco aesalon*). Although there were a score of other patches on the moor that these Merlins could have used, the birds always chose this particular one in spite of the fact that *every year the nesting pair was shot and not a single egg hatched*." In a community with perhaps an over-population of Yellow Warblers, Kendeigh (1941a) found that when singing posts were lacking, confusion ensued with much chasing, perhaps due to "the inability of the birds clearly to define the limits of their territories by singing."

Territories are sometimes settled on in the fall by juvenile Song Sparrows, both resident and summer resident. Other species that do this are European Robins (Burkitt, Lack), California Shrikes (Miller), Mockingbirds (Michener, Laskey), and European Wren (Kluijver et al., 1940). The Nuttall White-crowned Sparrow often claims as his territory in January the place where he settled after the post-juvenal molt (Blanchard 1941).

B. BEHAVIOR OF THE MALE ON HIS TERRITORY

When a male Song Sparrow definitely takes up his territory in late winter or spring he stays consistently on it, except for brief excursions for water or trespassing on neighbors' territories; he gives the awakening song and he sings a vast amount from vantage points. He drives all other Song Sparrows from his territory and he also drives most other birds. Like many other species, at first he claims a much larger territory than he really needs.

1. *Defense of Territory*

The owner of a territory must intimidate those individuals that might attempt to take his land. He needs to advertise his ownership far and wide, and he needs to defend it from those rivals undeterred by his proclamation. He must have a means of distance threat and of close range threat.

His method of advertising is his loud song, delivered from high points on his territory; from here his song carries far and he is in a position to watch for trespassers. (4M's songs were plainly heard by me at a distance of 200 meters.) The threatening function of the advertising song was very evident with the hand-raised birds (Appendix II).

Trespassers—migrating Song Sparrows and birds of other species much the same size or smaller—are dealt with by a rapid, determined flight directly at the trespassers, the latter usually leaving the vicinity before the owner reaches them.

Intruders, on the other hand, are responded to differently. Territory owners on meeting neighboring territory owners on the boundaries, erect their feathers, thus increasing their apparent body size. Cott calls such postures "expansion displays" (1940:213). Kramer (1937: 754) in his paper on lizards notes that enlargement is an element of all "impressive behavior" (*Imponiergehaben*). With the Song Sparrow the enlargement is usually more vertical than lateral, making the bird appear taller and larger in the shoulder regions. I called this "ballooning". It might also be called a "threat-posture". In such boundary encounters males often go through "sham feeding", a substitute activity shown by the Snow Bunting, domestic cock, Skylarks, Blue Tits, Coal Tits, Garganey Teal (Tinbergen 1939a:225), Prairie Horned Lark (Pickwell 1931), European Avocet (Makkink 1936) and Howling Monkeys (Carpenter 1934:37).

When a returning male finds his territory usurped, he goes into a specialized threat-display, which I have called the "challenge" or the "puff-sing-wave" (psw). He *puffs himself out* into the shape of a ball, more laterally than vertically; he *holds one or both wings upright* and *vibrates them;* and he *sings softly* and continuously incomplete songs. He flies slowly, maintaining the puffed out position. Here there are three intimidating elements—expansion, song and movement.

This activity was first shown by R at the age of 74 days (without the puffing), by Y at 94 days, by B at 160 days and D at 178 days. On Interpont I saw it shown by 52M at the age of 158 days when another Song Sparrow alighted above him. With Y it appeared two months before the attainment of adult singing, with D 6 days before, while with B the two coincided. It is released in a male in territorial mood by the following situations: another Song Sparrow, not his mate, alights above him, or suddenly flies near him, or when an interloper has taken his territory. It releases nothing in young birds, but it may have a decidedly intimidating effect on a somewhat older one, e.g., B after the revolution of Nov. 7; D on Dec. 17 when he started to challenge Y, and Y reciprocated so much more violently that D sat there, his crest up and his feathers compressed. However, on the 22nd, D intimidated Y by puffing, waving and singing *loudly* instead of softly. (See Appendix II for detailed records.)

This demonstration is the *threat of a bird at a temporary disadvantage,* of one that intends to dominate. This is shown in captivity by the behavior of Y before he gained the mastery and afterwards when he was caged, or his opponent was caged. It is shown in nature when a summer resident comes back to find a resident has appropriated his territory (1M and 4M, 5M and 8M), when a young resident is "visited" by an old resident neighbor (7M and 4M), and often when an owner finds a mounted Song Sparrow on his territory. *It is a substitute activity, a formalized threat, a signal that the demonstrator is powerful and intends to attack.*

(Before I had a chance to study the challenge with the hand-raised birds I partly misinterpreted its meaning (Nice 1938c), largely, I believe, because I had often seen it given *at* the domineering 4M and never *by* him. Apparently 4M was never at a disadvantage!)

In May 1935 I tested a number of males by placing a mounted Song Sparrow in the middle of their territories.

4M disregarded the mount for 10 minutes, then flew down, a little puffed, pecked at its rump and flew away.

221M hopped about it, *all puffed out;* flew to a branch above and *sang softly;* his mate approached, he descended to the mount, faced it, *all puffed out* and started to fight it, attacking it breast to breast twice, then pecked it 3 times on the head. The female gave the threat note. I removed the mount.

220M hopped around, evidently confused; there was no puffing nor singing. Finally he pecked its bill, pecked several times. He went into the trap on which the mount was standing and ate bread. He came out and fought, bumping breasts and clutching with his feet. I removed the mount.

204M came at once, *all puffed out, holding his left wing very straight and vibrating it, and singing continuously sotto voce.* Then he attacked the mount, again and again. He no longer vibrated his wing, but he did sing. He attacked it so violently around the head, hitting it as males do in fighting, that I took it away.

Two days later I tried it again with 204M, this time changing its attitude so that its head was lowered. 204M hurried there, *puffed out and vibrating his left wing vigorously, and singing softly.* He was so greatly puffed out that he sat on the top of the trap without his feet showing at all. He dashed for the mount head on, buffeting it; then attacked it on the head with his feet.

A mirror was first shown to Y in March 1939; he fought his reflection from then through June; no further attention was paid it until May 1940 when he again attacked it, but since then he has ignored his image. On Apr. 7, 1939, he was presented with an enlarging mirror; he examined it first with one eye and then the other and attacked. Four days later, however, when again shown it, he raised his crest, and *tchunked,* but did not fight.

As is told in Appendix II both D and Y, when underlings, intimidated the female J for a while, thereby building up their confidence, before they turned to the larger task of intimidating the male rival. They treated J as an underling male, and she never gave them any indication that she was not such an individual.

On Jan. 9, 1939, Y first showed a further substitute activity immediately following the challenge, namely picking up stalks. This was commonly seen thereafter, especially when Y was caged; he tugged at strings, or picked up leaves and carried them about, or violently manipulated weeds; he seemed to be venting his frustrated emotions. Once when A suddenly approached, he merely pulled at strings without preliminary display. Neither B nor D behaved in this way. It reminds one of the tearing up of plants by Herring Gulls threatening each other (Goethe 1937a:28).

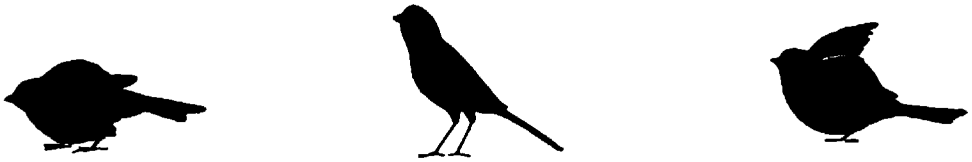

FIGURE 4. *Intimidation with the Song Sparrow. From left to right: 1, threat posture, puffing; 2, subordinate bird with raised crest; 3, challenge, puff-sing-wave.*

A full territory establishment encounter goes somewhat as follows: The present or former owner gives the challenge (puff-sing-wave display), while the usurper follows him silently with shoulders hunched in the threat-posture. Both may fly slowly with puffed-out feathers. After a while the usurper starts to chase the owner, but the latter returns again and again. A rough and tumble fight on the ground ensues, after which the birds separate, each to sing loudly, answering each other. Encounters may go on for many hours, the roles gradually changing, until the former owner becomes the pursuer and the usurper is finally routed.

2. *A Summary of Song Sparrow Methods of Intimidation*

Ten methods possessed by the Song Sparrow for intimidation and attack are shown in Table XIX.

TABLE XIX

METHODS OF INTIMIDATION USED BY SONG SPARROWS

Method	Posture	Sound	Between Sexes ♂♂	♂♀	♀♀	♀♂	Actor and Circumstances
Advertising Song..	Erect	Loud song	XX	X			Male on territory
Threat-note	None	Zhee	X	(X)[1]	X	X	Dominant male to subordinate; female to mate, to neighbor male and female when threatened by them.
Antagonism	Open bill	None	X			X	Young birds towards dominant; female to mate.
Menace	Lowered crest, crouched body, extended neck, bill pointed at victim	None	X	X			Dominant male towards young birds (Y to D, F, S); male to neighbor female (4M to K2, 1M to K3).
Pursuit	Rapid flight	None	X			X	Pair on territory.
Striking		None	X	X	X	X	In fights.
Fighting	Spring in air, bump breasts, clench feet, peck	None	XX		X	X	Male over territory; females over territory boundaries, females when pounced on by males.
Threat-posture "Balloon"	Enlargement vertically. Sham feeding	None	X	X	X	X	Males meeting on boundaries, females meeting on boundaries, female meeting neighbor male.
Challenge "puffsing-wave"	Feathers puffed, wings vibrated, slow flight in puffed position	Soft songs	X	(X)[1]		(X)[2]	Male, that intends to dominate at temporary disadvantage. Male finding territory usurped by intruder, even by a mount.
Pounce	Darts down, hits female and flies off with a song	Song		X			Male on territory pounces on his mate and other females.

[1] Y sometimes gave the threat-note and challenge to J, but he treated her no differently from the subnormal male A; she showed no feminine behavior.

[2] Only one instance—the belligerent female K42.

Sound is used in connection with four of these methods: song in three and a special threat-note in the fourth. In "menace" the initiatory movement of attack is shown. The threat-posture and challenge are formalized displays, depending for their intimidating effect on apparent enlargement, and in the challenge on sudden, peculiar movement of the wings, and on song.

Six of these techniques—from the threat-note through fighting—are used by young birds. All 10 are employed by adult males, and 6 normally by females. Nine have been seen used by males against males, 5 by males against females, 4 by females against females and 6 by females against males. The complete repertoire of intimidation techniques is characteristic of territorial situations, but only 3 mechanisms—the threat-note, pursuit, and striking—have been seen during the rest of the year. Pursuit is the only technique ordinarily used against other species. The threat-note has been given against Cowbirds, Juncos and Cardinals, as well as a young rabbit. Several times I have seen Song Sparrows use the threat-posture against Cowbirds and also strike them. With the hand-raised birds, J opened her bill (antagonism) at the Goldfinches, while Y often "menaced" the Bobolinks and once showed elements of the challenge to a threatening Bobolink above him, and twice did so towards the Goldfinches, each time waving a wing and once puffing.

C. FAITHFULNESS TO TERRITORY

The male Song Sparrow is markedly faithful to his territory, as a rule returning to or remaining on the same spot year after year, unless driven out by cultural changes (Nice 1937:73-74). The female is less able to return to her former home, for often upon her arrival she finds her place pre-empted. However, in 37 per cent of 54 cases on Interpont she returned to her former territory, in 30 per cent to an adjacent territory, while in 33 per cent she settled from 100 to 700 meters distant.

The Song Sparrow is much more strongly attached to his or her territory than is the House Wren, where only 31 per cent of 278 males had the same box 2 years in succession and 26 per cent of 279 records involving females; the rest of the instances of male and female location ranging from "less than 1000 to 6000-7000 feet", except for 3 females that nested from 2¼ to 6 miles distant from their former nesting boxes (Kendeigh 1941b:17). Many more nest boxes were available "than were needed."

The homing ability of the Song Sparrow is good, so far as it has been tested. I regularly released at the house birds captured on their territories from 400 meters to 1.6 kilometers (1 mile) distant; every male returned to his territory and every female but one; she had joined her mate only 2 days before her capture and instead of returning the 400 meters she stopped on the way home and stayed with an unmated male.

Manwell and Herman (1935) relate how Song Sparrows regularly returned when carried 1½ miles from the place of capture; Manwell (1936) tells of further experiments that proved the birds returned when carried 2, 9, 15 and 35 miles in different directions. All these tests were made in spring.

D. RELATIONS OF SONG SPARROWS TO OTHER PASSERINES

The attitude of the Song Sparrow in the nesting season is a despotic one towards most other passerines that enter the territory, although these are driven off much less vigorously than members of its own species. Both male and female usually drive off species ranging in size from the Ruby-crowned Kinglet to the Red-eyed Towhee. Song Sparrows average some 22 grams in weight; they dominated all but 2 species weighing up to 42 grams (Towhee), and even 50 if the male Cowbird is included. With the Catbird, weighing some 35 grams, and nesting commonly on Interpont, I never recorded any encounters. Male Cardinals (42 grams) usually drove the Song Sparrows. Once 1M flew at a Brown Thrasher (70 grams), but the latter drove him off. Robins and Starlings (both some 80 grams) were ignored.

All the species driven (except House Sparrows) that were larger than the Song Sparrows were transients and so had little motive for resistance. Field Sparrows, Maryland Yellow-throats, Indigo Buntings and House Wrens avoided the attack, and went about their business. House Sparrows and Goldfinches often ignored the menace, and the Song Sparrows usually did not press the matter. With 22 different Song Sparrows, 8 of which were females, I have records of House Sparrows being driven off 14 times and tolerated 5 times; of Goldfinches being driven 7 times, tolerated 5 times; Juncos being driven 20 times and ignored 7 times. With this last species the explanation probably is that the aggressive impulse of the Song Sparrow tired after continued exercise on this harmless visitor.

A total of 19 species driven by male and female Song Sparrow is given in Vol. I (Nice 1937:68-69); to these should be added Bewick Wren and Purple Finch. These intruders were driven from the main body of the territory, whether they alighted in trees or on the ground. The earliest record I have of a female Song Sparrow driving is on Mar. 6, 1930, when K7 chased a House Sparrow. On Mar. 29, 1929, I first noted K2 doing likewise after a fortnight's residence. After the nest is started, intruders are driven from its vicinity and also from the body of the territory, and in 1929 even from its border 15 meters distant, but the feeding station maintained in this location brought in of a complicating factor. This intolerance of other species never in my experience worked any special hardship on the birds that suffered from it; the summer residents mentioned above nested freely among the Song Sparrows.

Various species are reported as intolerant on their territories towards other species besides their own. Hummingbirds are outstanding examples. A pair of European Nuthatches drove off Blue Tits, possible nest-site competitors, but not other species that alighted in the nesting tree (Venables 1938). Tree Swallows ignored Barn, Bank and Rough-winged Swallows, but attacked a female Purple Martin (Kuerzi 1941:14). The Prothonotary Warbler drives off other species

(Walkinshaw 1941:17). The male Galapagos Mockingbird chases off every bird that approaches the nest (Venables 1940). The territories of 2 Bishop-Birds in East Africa—*Euplectes h. hordacea* and *E. capensis,* often overlap; there was complete tolerance between the *established* birds, but strange males of either species were chased by the territory owners (Lack 1935:823). Davis (1941c:161) analyzed the situations under which a male Eastern Kingbird drove out intruders of other species: "the bird must be moving into, about, or from the nest tree"; belligerency wanes soon after sunset, something not true of the Song Sparrow. A pair of Loggerhead Shrikes (*Lanius ludovicianus*) in North Dakota "defended" their nest "from other species that came near about once in 20 minutes"; Arkansas and Eastern Kingbirds were driven off 34 times in 16 hours and 6 other species 12 times (A. Johnson 1940). The Black Oyster-catcher (Webster 1941) and European Warblers (Heilfurth 1935) are also intolerant of intruders of other species on their territories.

In discussing the reported attacks of territorial males upon other species, Tinbergen (1939c:63) says "in nearly all cases it is impossible to see whether the author speaks of sexual fighting or of fighting against predators. . . . Occasional attacks on strange birds may often be caused by incomplete discrimination. The attacking animal reacts to sign stimuli (Russell 1934) as a consequence of his innate or conditioned capacities ('releasing mechanism', von Uexküll and Lorenz). When the threshold of the fighting reaction is extremely lowered, some animals will react to inadequate sign stimuli, which have only some similarity with the optimal stimulus."

With the Song Sparrow and the species mentioned above the threshold of the fighting reaction is certainly low. The birds show an aversion towards others about their own size. Does this come from failure of the perceptual inlet to be sufficiently exact? It certainly is not "sexual fighting" nor "fighting against predators". Might it arise from an hypertrophy of the territorial impulse?

E. SUMMARY

1. Territory requirements are not rigid for the Song Sparrow; so long as he has cover and singing posts, a large variety of habitats will be accepted. Birds appear to instinctively recognize their specific habitats: they may be responding to conspicuous features (Lack), key aspects (Miller), or ecological magnets (Hickey).

2. For defense of the territory the owner's method of distance-threat is the advertising song.

3. Trespassers—migrating Song Sparrows and most other passerines—are pursued.

4. Boundaries are defended from neighboring Song Sparrows by the threat-posture, or "ballooning". This is shown by both sexes.

5. When a returning male finds his territory usurped, he goes into the "challenge" or "puff-sing-wave display". This is the threat of a male at a temporary disadvantage.

6. A mounted Song Sparrow was placed on the territories of 4 Song Sparrows; 4M paid little attention to it; 220M fought it; while 221M and 204M gave the puff-sing-wave display and then attacked it vigorously.

7. Y showed the puff-sing-wave display more often than the other hand-raised males; he added a further substitute activity, violent manipulation of materials at hand.

8. A full territory establishment encounter consists in the challenge by the rightful owner and the threat-posture by the usurper; chasing by the usurper; a fight on the ground; separation and loud singing by both birds.

9. Table XIX shows 10 methods of the Song Sparrow for intimidation.

10. Both male and female Song Sparrow show a high degree of faithfulness to their nesting territories, in remaining on them or returning to them. Homing ability is well developed, nesting birds having returned from distances up to 35 miles.

11. Male and female Song Sparrows on Interpont were recorded as driving from their territories 21 other species, ranging in weight from 6 to 42 or even 50 grams, the Song Sparrow's own weight averaging 22 grams. Nevertheless, several of these species nested freely among the Song Sparrows.

CHAPTER XIII

The Function of Territory

The subject of territory has been treated to a greater or lesser extent in the last 6 chapters and will play a rôle in many of the remaining ones. Elsewhere I have treated the subject of "The Role of Territory in Bird Life" at some length, giving an historical sketch, a description of various types of territory, brief mention of its occurrence in other vertebrates, and a discussion of the bases and functions of territory, with a bibliography of some 400 titles (1941c). Here these subjects will be touched upon very briefly and from a somewhat different angle.

The essence of territory is given in this rhythmical sentence by Howard (1935:2) in regard to a Waterhen, "The pond with the surrounding ground is his, in the sense that he lets no other male upon it or strays himself beyond it."

"The strict definition of territorialism [is] at present difficult or even impossible", writes Davis (1941b), who contends that "the behavior shown by any species is a stage in the evolution of that species", and "The concept of territorialism should be grouped with such concepts as 'species' or 'community', ideas which have no objective existence and therefore should not be strictly defined."

Several attempts at definitions have been made, notably by Mayr (1935) and Tinbergen (1936a, 1939c). Personally I prefer the simplest —that of Noble (1939b)—: "a territory is any defended area".

A. HISTORICAL SKETCH

Although territory was casually mentioned as early as 1622 in regard to the Nightingale in an Italian book on The Aviary (Olina), and noted very occasionally by other writers in the 17th and 18th centuries, it was not until 1868 that the theory was formally promulgated by Bernard Altum. This German ornithologist stated all the essentials of the territory theory, including the modern view of song as a threat to other males and invitation to a female. He also thoroughly believed in the food value of territory. Altum was far ahead of his times and his theories were not known outside of Germany.

It remained for Eliot Howard to rediscover the principle, to study it painstakingly in the Old World Warblers (1907-14) and Buntings (1920) and to analyze its foundation and functions (1929, 1935, 1940). Howard's revolutionary influence on students of bird behavior is well expressed by Hickey (1941): "His most signal contribution was his success in convincing the scientific world that birds generally recognize certain territories as their own or as others' . . . and that they act and breed accordingly. This thesis . . . forced the re-writing of every song bird life history that had previously been published. It gave new meaning to song and color in bird life, and provided bird watchers with a refreshing stimulus which they will feel for at least half a century to come."

The extraordinary impetus given to territorial studies by Howard's "Territory in Bird Life", published in 1920, is shown by the chronological arrangement of the 387 titles through 1940 in the bibliography of my review on territory published in 1941, where an attempt was made to give a fairly comprehensive list of titles on this subject in birds, with a few references on other forms. "There are 3 titles from the 17th century, 2 from the 18th, and 6 from the 19th, 11 in the first decade of the 20th century, 15 in the second, 48 in the third, and 302 in the fourth."

B. TYPES OF TERRITORY

A territory, in the last analysis, is any defended area. There are many types of territories, some of which will be listed here:

A. Mating, nesting and feeding ground. Examples, Song Sparrow, Snow Bunting (Tinbergen 1939c), Prairie Horned Lark (Pickwell 1931).

B. Mating and nesting, but not feeding ground. Examples, Bishop-Birds (Lack 1935, the Moreaus 1938), Scarlet Finch (Haas 1939), Yellow-headed Blackbird (Fautin 1941).

C. Mating station only. Examples, Prairie Chickens, Blackcock (Lack 1939a), Gould's Manakin (Chapman 1935).

D. Nesting station restricted to narrow surroundings of nest. Examples Gulls (Goethe 1937a), Murres (Johnson 1941), Night Heron (Lorenz 1938), House Sparrow (Daanje 1941), Tree Swallow (Kuerzi 1941).

E. Feeding territories. These may be defended winter territories located elsewhere than the summer territory. (Many birds are attached to winter areas without showing any disposition to defend them.) Defended winter territories have been recorded for American Robin (Price 1933), Black-bellied Plover (Michael 1935) and White Wagtail (Greaves 1941). Or feeding territories may be defended at other times of year, as patches of flowers or syrup vessels by Hummingbirds, berry bushes by Townsend Solitaires (Lockerbie 1939), fishing station by Night Heron (Lorenz 1938). Perhaps feeding shelves should be included also (Mockingbird, the Micheners 1935).

F. Roosting territories. Examples, British Tree Creeper (Rankin 1940), Bewick Wren (Williams 1942b).

These types are not rigid, as some birds may belong to one type in one locality and to another in another; especially is this true of types A, B and D. Some birds cannot well be fitted into any of the types, for instance, the Eastern Kingbird (Davis 1941c) and Black-capped Chickadee (Odum 1941b) both mate before selecting territory; the Kingbird feeds outside the territory, the Chickadee inside; the former makes itself conspicuous, the latter does not. In his interesting paper on territoriality in North American Hummingbirds, Pitelka (1942) suggests "an additional category" of types of territory, viz. "mating and feeding," which should include most male Hummingbirds. With these birds pugnacity is displayed toward both sexes and all species of Hummingbirds and "the conspicuous factor in male territoriality seems to be food supply."

With such a broad concept of territory, non-territorial birds would appear to be rare. The Cowbird does not defend its nesting area (Friedmann 1929, Nice 1937:154), nor do some Parakeets (Davis 1940c), nor Macgregor's Bird of Paradise (Rand 1940), nor some Cuckoos (Baker 1942).

Territory is strongly developed in many fish (ter Pelkwyck and Tinbergen 1937, Noble 1938, Noble and Curtis 1939) and lizards (Noble 1934, Evans 1936a). It also occurs in some mammals (Gordon 1936, Tinbergen 1939a, Darling 1937, Carpenter 1937, 1940, Heape 1931).

C. THE PROBLEMS OF TERRITORIAL AND SEXUAL FIGHTING

The matter of sexual fighting was emphasized by Tinbergen (1936a) in a protest against the over-emphasis on "fighting for territories, not mates." Sexual fighting is defined as "all fighting occurring shortly before and during the formation of sexual bonds" (1939c:59). Fights "to settle a social hierarchy, fights against predators and against direct food competitors" are excluded. Sexual fighting "serves to secure one or more objects or situations which are necessary for reproduction" (1936a:8). Tinbergen calls all territorial fighting "sexual fighting", saying that, even before the arrival of a mate, "a territory is, to the male, a 'potential female'" (1936a:7). "Sexual fighting therefore serves to defend mate, territory, or other things that are indispensable for reproduction, against sexual competitors" (1939c:67).

Other authors make a distinction. With the Willet, the "female appears to be defended by the male before he defends territory", writes Vogt (1938:40). "At a later date the territory is vigorously defended, by the male, both against other males and the mounted bird." After "strange males were not permitted within territorial bounds, clear sexual defense vanished," p. 25.

With the Ani, Davis (1940a:205) found: "Sex is not a factor: the whole colony defends the territory against a strange bird no matter of which sex it may be." The "behavior is related only to a piece of land." "The defense of a piece of land, it is reasonable to assume, developed from the defense of the nest." "The defense of territory in *Crotophaga* . . . is merely an extension of the defense of the nest site."

With the Chickadee, pairs fight upon meeting each other during the "prenesting" period. "In several cases the fighting was clearly a defense of mates and not territory since the birds involved later established territory elsewhere" (Odum 1941b:326). The Sierra Nevada Rosy Finch "has no fixed territory" (Twining 1938). The mated male is busy driving other males away from his mate, most pursuits consisting of "short twisting flights in which the intruder is routed without bodily contact," but at other times strenuous fighting takes place. "Rosy finches feed peaceably in flocks on the feeding grounds except when a mated pair is present, whereupon other males are driven away. A building female is seldom unaccompanied, and is always defended from all other males by her mate." When she starts incubation, he feeds her on the nest and "evidently becomes entirely unconcerned over the presence of other males."

Turning to the Eastern Kingbird, Davis (1941c) found that the birds pair and then select a nest site and defend its vicinity, both sexes driving off other members of the species, the male also driving off other species that enter the nesting tree. Davis believes that "When a male Kingbird is fighting with another Kingbird within his own territory he is simultaneously defending territory and sex-partner. The female defends the sex-partner only," that is, drives off other Kingbirds some of which might be "females which might attract the male away." This distinction is not convincing to me, particularly as the sex of the trespassing Kingbird was apparently not recognizable by the pair. I would rather agree with another statement in this paper: "The evidence obtained indicates to the author that the excessive fighting of the *male* is merely exaggerated territorialism," p. 165.

With the Song Sparrow it is possible to separate to some extent territorial from sexual fighting. With the male much of the fighting I believe can be considered clear defense of the territory, and not defense of a female—actual or potential. We have seen that the challenge, which is the one display confined in nature to territorial situations, is a matter of social hierarchy, of settling questions of personal prestige. Territory means that a bird is dominant in that area. To my mind, a great deal of the "fighting occurring shortly before and during the formation of sexual bonds" is fighting "to settle a social hierarchy".

The threat-posture, on the other hand, is used ordinarily by male against male and female against female, but also rarely by male against female and less rarely by female against male; also by both against Cowbirds. This is a more generalized technique of intimidation than the challenge; it seems to be used against intruders in general.

Some of the fighting by the male certainly has a sexual motive—when a female has just arrived and the male keeps between her and a neighbor male, and when a male has pounced on a neighbor female and is attacked by her mate (See Appendix III).

As to the female, she shows the threat-posture primarily to neighbor females. Examples of sexual jealousy are given in Chapter XV and Appendix III. Although with the female sexual fighting is of most importance, yet she also shows territorial fighting in pursuing neighbor males, either alone or in company with her mate, and in driving off other species.

To conclude, both incentives function in the fighting of the Song Sparrows; the territorial is predominant in both sexes in much of the defense against males and in the pursuit of other species, but some of the fighting is certainly sexual.

D. The Female and Territory

In some species it is the female that proclaims and defends territory; the Northern Phalarope is the outstanding example of such behavior, as told by Tinbergen (1935). In other species females hold territory for themselves during fall and winter, as the European Robin (Burkitt, Lack), California Shrike (Miller 1931b), Mockingbird (the Micheners 1935), and some Woodpeckers (the Heinroths 1924-33). It is chiefly at this season that female Mockingbirds and European Robins sing. Two female Nuttall (White-crowned) Sparrows mated to the same male defended their portions of the territory against each other (Blanchard 1941).

Many females appear to ignore the boundaries of their mates' territories, crossing them at will, occasionally nesting outside them, showing no disposition to defend the territory and fighting only against trespassing females. With the Song Sparrow it seemed to me that the female learned the boundaries in the first week or so after her arrival when the pair stays close together. I have seen the male drive his mate home when she chanced to be frightened from the territory. Some female Song Sparrows help their mates drive off neighbor males and sometimes they drive them alone. (See Chapter XV.) Resident female European Blackbirds chased off both females and males except their own mates (Morley 1937).

E. THE BASES AND FUNCTIONS OF TERRITORY

The chief theories as to the functions of territory are: (1) to conserve the food for the young (Altum 1868, Howard 1920); (2) to prevent undue increase of the species (Moffat 1903); (3) to prevent interference in family life (Nice 1933d, Mayr 1935); (4) to bring the pair together (Lack 1935, Noble 1939b).

The food value of territory has aroused a great deal of discussion (the Lacks 1933). Often it plays no role, but as Tinbergen (1939c) points out, "it is necessary to recognize that there are many species of Passerines to which the territory is necessary to provide a *certain amount* of food."

Moffat's theory that the chief function of territory is the prevention of the undue increase of the species seems a little far-fetched. As to the possible limiting effect of territory on the number of birds nesting in a certain area, in many cases territory does limit the population, certainly in the Song Sparrow, but sometimes when food is superabundant, territorial lines break down.

From my detailed study of individual Song Sparrows, I came to the conclusion that one of the chief functions of territory is to prevent interference in family affairs, to allow the orderly sequence of the nesting cycle to proceed without interference. The difficulties which faced 1M and K2, 4M and K3 when territorial lines were broken down through K2's nesting in 4M's territory are told elsewhere (Chapter XV and Nice 1939a).

As to the last suggestion, Noble says, "Sexual territory . . . functions primarily to test sexual readiness of the opposite sex and to make possible the formation of sexual bonds" (1939b). This is true of many territories, especially of typical examples of types A, B and C and sometimes of D. Yet in some species pairing is effected before territory is selected.

In the Song Sparrow, territory provides an ample food supply for young and adults, it does limit the number of pairs on an area, it is essential for the protection of family life, and it assuredly brings the pair together.

Mayr (1935) makes a suggestion as to the evolution of territory. "The wide occurrence of sexual jealousy among birds leads me to the belief that this is one of the fundamental motives in the behavior of birds. Territory has become in some species a means to assist the pairing and to facilitate the task of the male of guarding the female. In time, territory obtained in some species an added significance as a feeding station. The solution of the argument concerning the significance of territory is probably the following: *Territory was originally developed only in connection with the mating, but it has acquired in certain passerine species a secondary significance as the food providing area.*"

To turn to the fundamental basis of territorialism, Katz (1937: 95) writes, "from the animal's point of view the spot in which it has always lived undergoes an internal structuring, analogous to the structuring of the functional or 'life' space of man. Such an internally structured 'life' space we shall call 'personal space'. The structure of this personal space cannot be understood simply in terms of the animal's sensory-motor equipment, but only in connection with its affectively toned vital needs", p. 97.

Animals act from some point of reference; they need a certain amount of familiarity with the environment for security. This support may come from acquaintance with special environment, or from the presence of other animals that may function as social-companions and not enemies. With some animals the former conditions are more important, with others the latter. (In monotonous environments, such as plains and oceans, flocking is common, as pointed out by Allee; see Chapter VII.)

Familiarity with a place gives confidence to an animal and enables it to dominate newcomers. This matter of place-conditioned dominance depends partly upon the conservatism of the animal mind. Habit is powerful and too much novelty is abhorrent. For some, the place is unimportant per se, while dominance originally gained in familiar environments carries over into new environments (domestic fowl, Jackdaws). In still others, the *place* is of paramount importance; the animal remains there and remains dominant.

In the first case the natives may not be defending a place, but they act surely; they know what they are about. Schjelderup-Ebbe in discussing the "home-cage effect" says, "The psychological reason for this is most probably to be found in the support which the native birds of the place find in their accustomed surroundings; everything has been explored, everything induces confidence" (1935:967). From their experimental study of "Intercovey Social Relationships in the Valley Quail", Howard and Emlen (1942:169) suggest that the dominance of aliens by established residents is in large degree related to a favorable psychological attitude gained through familiarity with the physical features of the covey's range.

In territorial situations, the bond to the place is strong. Experiments with pigeons have shown that new environments brought new dominance relations, the bird that first became familiar with a place becoming despot there, whereas a return to the old environment evoked the former relations (Diebschlag 1941). With a territorial bird the support from its own piece of land is so strong that it is undefeatable on its territory. Here the confidence induced from familiarity with an area is reinforced by the male's protective instinct towards his young, even before their arrival.

The function of territory is protection—protection of the male against the despotism of stronger neighbors, protection of the family from interference from neighbors, protection of the food supply in some cases. It also may function in bringing the pair together.

"With animals, as with men," writes Craig (1921), "the cause of a quarrel is very commonly a coveted territory". Territorialism is a deep-lying characteristic of a large proportion of vertebrates. The instinctive display, the colors and structures, that function in the proclamation and defense of territory, point to the long road of evolution away from brute force and towards law and order.

F. SUMMARY

1. A territory is any defended area.

2. Territory is known to have been mentioned as early as 1622; the theory was formally promulgated in 1868 by Bernard Altum in Germany, but it was Eliot Howard who brought it to the general attention of the scientific world.

3. Seven types of territories are listed, four of which are nesting territories, the others winter, roosting and feeding territories.

4. Territory is strongly developed not only in the birds but in many fish and lizards and in some mammals.

5. Tinbergen considers that territorial fighting is "sexual fighting". Some other observers distinguish the two kinds of fighting.

6. With the Song Sparrow, the territorial incentive is predominant in both sexes in much of the defense against males and other species, but some of the fighting is certainly sexual.

7. Occasionally females hold territory for themselves; sometimes they help defend the male's boundaries; sometimes they ignore the boundaries.

8. The chief functions claimed for territory have been: food value, limitation of the numbers of a species in an area, protection against interference in the nesting cycle, assistance to pair-formation. All of these are true in some cases, but not in all. They are certainly true for the Song Sparrow.

9. With a territorial bird the support from its own piece of land is so strong that it is undefeatable on its territory.

10. The function of territory is protection—protection of the male against the despotism of stronger neighbors and protection of the family from interference.

CHAPTER XIV

The Male and His Mate

The establishment of territory by the male is the first step in the nesting cycle; the coming of the female is the second.

A. The Course of the Nesting Cycle

The nesting cycle of the Song Sparrow falls into 8 principal stages, as already noted in Table XI in Chapter IX. Howard (1929) divided the nesting cycle of the Reed Bunting and some other passerines into 4 phases, while Tinbergen distinguished 9 for the Snow Bunting (1939c). In Table XX the stages of the Song Sparrow cycle are compared with these 2 other schemes.

Table XX

STAGES IN THE REPRODUCTIVE CYCLE OF VARIOUS PASSERINES

Song Sparrow		Snow Bunting (Tinbergen)		Reed Bunting (Howard)
		1. Males in flocks		
1. Male proclaims territory	=	2. Males on territories	=	1st phase
		3. Females present		
2. Female arrives; prenuptial	=	4. Female on territory; pre-oestrum	=	2nd phase
3. Preliminary activities 4. Building	=	5. Coition occurs	=	3rd phase
5. Laying	=	6. Laying		
6. Incubation	=	7. Incubation	=	4th phase
7. Care of young in nest	=	8. Nestlings		
8. Care of young out of nest	=	9. Young have left		

The cycles of the Song Sparrow and Snow Bunting correspond well, except that the latter starts to build the nest more promptly than does the former and 2 stages can be distinguished for the Song Sparrow where only one is evident with the Snow Bunting. With the European Robin, Lack names 3 stages corresponding to the first 3 in the Song Sparrow—"pre-pairing," "pre-nuptial," and "post-nuptial" (1939b:184).

Blanchard (1941) divides the "cycle of the Nuttall Sparrow into four phases: the base level of fall and winter behavior, the rising tide of territorial and sexual instincts, reproduction, and the subsidence of territorial and sexual instincts." Her "rising tide" corresponds to the first 3 stages in the Song Sparrow, "reproduction" to the last 5.

The activities of male and female Song Sparrow throughout the nesting cycle are summarized in Table XXI.

TABLE XXI

ACTIVITIES OF MALE AND FEMALE SONG SPARROW THROUGHOUT THE NESTING CYCLE

X means activity, XX pronounced activity

Stage	I Proclaims territory	II Prenuptial	III Preliminary	IV Building	V Laying	VI Incubation	VII Young in nest	VIII Young out of nest
MALE								
Song[1]	H. st.	Inh.	Inh.	Uninh.	Uninh.	Uninh.	Inh.	?
Guarding	X	XX	X	X	X	X	X	X
Pouncing		X	X	XX				X
Coition			X	XX	XX			X
Building play			XX					
Feeding young							XX	XX
FEMALE								
Trill		X	X	XX	XX	X	X	X
Chatter		X	X	XX	X		X	X
Coition			X	XX	XX			X
Building play			XX					
Feeding young							XX	X
Other activities				Builds	Lays	Incubates	Broods	Starts new nest

[1] H. st. = highly stimulated; inh. = inhibited; uninh. = uninhibited.

The division of labor between the male and female is clear and at the same time their cooperation. The last 5 or 6 stages are repeated for each brood. Stage VIII may overlap stages III, IV, V and VI.

The two pre-nesting stages after the female's arrival will be discussed in this chapter—prenuptial and the preliminary stages.

B. PRENUPTIAL STAGE

The female Song Sparrow announces her sex by various notes, used only by females and typically in connection with a mate and nest, chiefly a trill and a chatter. Upon the arrival of a mate the male stops singing almost entirely; his courtship display consists in "pouncing" on his mate, while his general attitude is that of guardian.

Howard (1929:8) says of the Reed Bunting after the arrival of a mate, "Formerly he fought with determination, now with fury." Fighting of the male Snow Bunting becomes more frequent. The European Robin may obtain a mate between mid-December and mid-May; *"whatever the date* aggressiveness markedly increases and song fairly markedly declines," (Lack 1939b:201). With the Song Sparrow there are more occasions for fighting after a male has a mate than before, due to the fact that many fights are started by a male pouncing on his neighbor's mate. Also as with the Snow Bunting there is some trespassing by unmated males, who attempt at first to get the females to come to their territories.

The prenuptial period in which coition does not take place has been noted for a number of species. Howard designated this a "prior sexual condition", Lack "pre-nuptial", and Tinbergen "pre-oestrum". The terms oestrus, oestrum, etc., denote definite stages in mammals, but are not in a strict sense applicable to birds.

The prenuptial period may last two months or more with resident female Song Sparrows, or for only a few days at the beginning of the nesting season; later, in second and third broods and in the replacement of mates it seems to be suppressed.

Examples of behavior upon the first arrival of mates are given in Appendix III.

1. *The Cessation of Song*

The change from almost constant singing all morning long to 2 to 10 songs an hour or possibly none at all is startling. The awakening song is suppressed. Only if a new male tries to take up territory in close proximity will highly stimulated song reappear temporarily. 1M on Mar. 15, 1930, sang 278 songs in an hour when engaged in territorial controversies with the new arrival, 10M; this happens to be one of the highest records I have.

Contrary to the situation with the Snow Bunting, the inhibition of song does not commence the moment that a mate comes; during the first few hours after her arrival the male may sing from 54 to 147 times an hour. The inhibition lasts until the female starts building her nest, at which time the awakening song typically appears, although day-time singing may not reach its height until incubation is under way.

This cessation of song upon the arrival of the mate has been reported in many European birds: Reed Warbler (Howard 1907-14), Reed Bunting and others (Howard 1920), Chaffinch, Yellow Bunting, Lesser Redpoll, Robin, Chiffchaff, Willow, Sedge and Grasshopper Warblers, and Whitethroat (Burkitt 1921), Northern Phalarope (Tinbergen 1935) and Snow Bunting (Tinbergen 1939c). "The partial or complete suspension of the song after pairing has taken place is the most interesting, as it is the most noticeable feature" of the relationship between song and the presence of the female. "In fact, in greater or less degree, a change is noticeable in the song of many resident and migratory species under similar circumstances, a deterioration so marked that we learn by experience to regard it as a certain indication of the arrival of a mate" (Howard 1920:131-133). Burkitt states that "Mating generally puts a brake or stopper on song" (1922) and that "any strong continual singes is mateless" (1921).

Strangely enough we do not have many observations on this point on birds in America. A sudden decrease in the volume and amount of song is characteristic of Mockingbirds (Laskey 1933, 1935, the Micheners 1935). I noted in Ohio that Indigo Buntings sang appreciably less after the coming of their mates. With the resident Nuttall [White-crowned] Sparrow the male sings in January till he has "regained possession of all or part of the territory he patrolled the year before. With this achievement, if the male is already mated, song and frequent pursuits fall into abeyance, perhaps because there is no further need of them" (Blanchard 1941:18). Song appears again with the start of incubation in March or April. The period of abeyance of song ranged from 45 to 58 days. With the migratory Puget Sound [White-crowned] Sparrow 8 days were spent in singing and territory establishment, then 2 weeks of silence ensued before incubation begins.

As to the correlation of behavior to the gonad cycle, Blanchard writes: "The beginning of increased and forceful singing and of chasing and of fighting (in the Nuttall Sparrow) correlates with the time of increase in numbers of functional interstitial cells (histologic stages 3 and 4 of the testis . . .). The cessation of loud singing, when segregation has been achieved, occurs roughly at, or a short time after, the arrival of the testis at stage 5 (when the interstitial cells no longer appear to be increasing in numbers and the tubules are filled with primary spermatocytes in synapsis). The ensuing interval of rare singing normally corresponds with the greatest and most rapid increase in the size of testes, from less than 20 to over 100 mm.^{3}, though this correlation is not requisite, since unmated males may sing throughout this period," p. 21.

"In *pugetensis*, on the other hand, the attainment of stages 4 and 5 is accompanied by none of these phenomena but by the departure and flight of perhaps a thousand miles to the breeding grounds. By the time of final settlement on breeding territory the testes of *pugetensis* are eight times the size of those of *nuttalli*," p. 78.

In various non-passerines, males stop calling and displaying as soon as joined by mates, as, for instance, the Grey Heron (Verwey 1930), Black-crowned Night Heron (Allen and Mangels 1940) and Brandt Cormorant (Williams 1942a).

What is the explanation of the stopping of singing? Tinbergen suggests that it shows clearly that attraction of a mate is the primary function of advertising song in such species (1939c:80). If this is so, why do Snow Buntings, Song Sparrows and others sing so much after nesting has begun? With neither of the races of the White-crowned Sparrow studied by Blanchard does the stopping of song occur immediately upon the arrival of a mate; perhaps there is so much territory settlement to be attended to that the situation is analogous to that when 1M, although mated, sang so vigorously in defiance of 10M. If terrritory is also settled, both objects have been achieved, and the male might be considered as entitled to a rest. Why then does he resume singing later? Partly perhaps on account of loneliness. I have the impression that song is definitely *inhibited* during the prenuptial and preliminary periods. The male spends much time with his mate, he mounts bushes as if to guard her while she searches for food, and he gives the fear note *tik tik tik* at the sudden appearance of a person. Occasionally the female deserts at this stage. I have wondered whether anxiety over his mate may have something to do with the inhibition of song.

2. *Pouncing*

The male Song Sparrow's "courtship" display is as follows: he suddenly flies down to his mate, collides with her, and immediately flies away with a loud song. At times he hits her severely, while at other times he merely "swoops" down nearly touching her, but giving the loud song as he leaves. The female stands still and usually gives one of 2 notes—the trill, typical of copulation, or the threat note *zhee;* early in the season the former is the usual response, later the second note is heard more often.

In 1929 K2 responded to her mate 1M's pounces as follows: Mar. 22 to Apr. 14 (preliminary and nest-building stages) 17 times with the trill, once with *zhee*, and twice with silence; from May 16-22 (preliminary and nest-building) 4 times with *zhee;* June 18-21 (preliminary) once *zhee*, followed by a chatter, 8 times *zhee*.

In 1935 K200 responded to her mate 4M's pounces as follows: Mar. 7 to Apr. 11 (prenuptial) 9 times with the trill, twice with a chatter, twice with *zhee*, twice with *zhee* followed by a trill, and once by fighting; from Apr. 12-29 (preliminary and nest-building) once with the trill and 11 times with *zhee*.

Pouncing on the mate is confined typically to the early stages of the nesting cycle—the prenuptial, preliminary and building periods, and is very rarely seen during egg laying, incubation or while the young are in the nest. It may reappear, however, the day that the young leave the nest, if another brood is to be started immediately. If one day a pair was known to have eggs and the next day the male is seen pouncing, it is an almost sure sign that the nest has been broken up. The earliest records I have for pouncing are Feb. 11, 1931, Feb. 12, 1932, Feb. 17, 1933, Feb. 22, 1930, Mar. 4, 1935, and Mar. 29, 1934. The latest is July 14, 1930.

Pouncing appears to be analogous to the sexual chase in Old World Warblers, Reed Buntings and others (Howard 1929) and the Snow Bunting. With the European Robin there seems to be nothing of the kind (Lack). The male Nuttall Sparrow from early March on "punctuates long periods of indifference by 'attacks' upon the female. Suddenly, with no warning that I can detect, his indifference changes to aggression. He chases the female and jabs her with his beak" (Banchard 1941:24). There were 7 records of such attacks, occurring from 18 days before copulation to 2 after. The male Canary at times attacks his mate severely (Shoemaker 1939b).

Howard believes that the sexual chase shows that the male is ready to copulate; this cannot be true of the pouncing of the Song Sparrow early in the season. Pouncing has no immediate connection with copulation.

As will be described in the next chapter the male does not confine his pounces to his own mate. Pouncing on the mate occurs during the long period while song is inhibited and also during building. It may be a technique of the male for impressing himself upon his mate during the time of silence, of making his presence keenly felt!

3. *The Female's Notes*

Some female Song Sparrows are vocally expressive, while others are quiet. I never noticed any correlation with age, except that K2 was noisy while building her first nest in 1929 and just the opposite during this process for her 3 later nests this year and her 3 nests in

1930. Although the chief notes are those I call the trill and the chatter, some females have a great variety of other notes which they use early in the season.

a. The Trill

This is the note usually given after copulation; it appears to be *always used in connection with the mate.* It is a nasal, shrill note, difficult to transcribe with letters. I have called it *ee-ee-ee,* but sometimes wondered whether *ä-ä-ä* would not have been better. It is given on approach of the mate on foot, or when he is flying over or swooping over her; after a pounce early in the season; sometimes when the female comes into a tree below the male, or he alights above her; often in answer to a song when she is in the open or on the nest; and finally when he is having a fight with neighbors. The earliest records I have for this note are Feb. 15, 1933, Feb. 28, 1931, Mar. 7, 1935, Mar. 15, 1929, and Mar. 30, 1934.

b. The Chatter

This note is usually given in connection with the nest or copulation, and is almost always given during or just after a *flight.* It is often used as an invitation to copulation, and it is typical of nest building. It has been heard during all stages of the nesting cycle except incubation. While the young are in the nest it is given in subdued form. My earliest records for it are Feb. 15, 1932, Feb. 20, 1933, Mar. 7, 1935, and Mar. 10, 1930.

c. The Song

The song of the female Song Sparrow has been discussed in Chapter X. Here I will merely mention that it has been noted on Interpont from Feb. 12 to Apr. 19, 6 times in February, 14 times in March and 19 in April, always during the prenuptial and preliminary stages. I have recorded it from 11 of the 200 breeding individuals, with two of them 2 years in succession. The hand-raised female gave a brief, whispered song throughout February.

4. *Behavior of Y and D Towards J and A*

Neutral sex behavior was observed in two of the hand-raised birds. The female J behaved in much the same sexless manner as the subnormal male A. Apparently Y and D treated J as an underling male.

J hatched about Aug. 4, 1939, and was in my study from late November until her death by accident in mid-March. For some time she was kept in the cage with the pair of young Goldfinches; in general the two species ignored each other, unless startled by sudden movements of the other bird. On Jan. 6, J pecked towards a Goldfinch, on the 9th she opened her bill at them. On this day she was put into the large cage by herself. One or the other of the male Song Sparrows was loose in the room constantly. *J never showed any distinctively female behavior.*

The first time she was heard giving any note was on Jan. 9 when she uttered a low *chip chip chip*. It was not until Feb. 1 that she gave the call note *tsip*. On Feb. 5 she first gave the threat-note *shee* at Y. Throughout February she gave brief whispered warbles.

Both Y and D tried to dominate her by flying at her. Often she fought back, at times giving the threat note, but often she was much disturbed by their repeated "attacks", as evinced by her raised crest. Y even went through the puff-sing-wave display at her 8 times from Feb. 2 to Mar. 2. (See Appendix II.) A post-mortem examination showed that she was very fat, weighing 24.5 grams; possibly this condition had something to do with the non-appearance of sex behavior in the environment of the warm room and lights on often in the evening. It is true that she was a late-hatched bird.

The following year I had a control experiment in the atypical male A, small (yet with wing measurements of a male) and slightly crippled in his feet. Although kept until 11 months old, he never sang except occasionally in a weak, whispered warble. Y's behavior towards him and his towards Y did not differ from that seen the year before with J. Only once did I hear A giving the threat note to Y (from well within the safety of his own cage), but he did sometimes *tchunk*.

C. Preliminary Stage

This stage is marked by the start of copulation. Symbolic nest-building, performed by both sexes, reaches its crest at this time, although it appears to a slight extent in the prenuptial stage. Singing is still inhibited in the male, but may be performed—such as it is—by the female.

Howard, Tinbergen and Lack make one stage including the beginning of coition and nest-building—"Second Phase," "Fifth Period" and "Post-nuptial Period" respectively. With the Snow Bunting and Reed Bunting both activities begin simultaneously (Tinbergen 1939c: 29), while with the European Robin coition does not occur until *after* the commencement of nest building (Lack 1939b:190). With the Song Sparrow, however, coition may begin at least 10 days before the start of nest building. Moreover, with the Song Sparrow an important change takes place with the male when his mate begins to build, for then he starts to sing once more.

1. *Coition*

The female postures by spreading her wings and quivering them, and raising her head and tail; the male mounts, balancing himself with his wings; the act is consummated in about a second, after which he usually flies a short distance away. The female generally gives the trill directly afterwards, but the male never gives any note or song, in contrast to the pounce which is always followed by a song. He often returns immediately and the process may be repeated 2 or 3 or even 4 times in quick succession. Sometimes the female chatters while posturing. Copulation usually occurred when the pair first came together, especially after one or the other had just alighted from a flight. It did not happen after the birds had been feeding near each other for a minute or two. It always took place on or near the ground

In 1929 copulation was noted with 1M and K2 from Mar. 27, although it might have occurred as early as the 21st; the first egg was laid 14 days later. In 1932 the first copulation was seen Apr. 5, and the first Song Sparrow egg on Interpont found 18 days later; here the same pair was not involved. In 1935 it was first seen with 4M and K200 on Apr. 20, their first egg being laid 13 days later. Blanchard has records of copulation 15 days before the laying of the first egg with the Nuttall Sparrow (1941:26).

From Mar. 21 to Apr. 10, 1929, I have notes on 28 successful copulations, and also 13 instances when K2 postured with no response from 1M and 4 cases where unsuccessful attempts were made. Some samples are given in Appendix IV.

2. *Symbolic Building*

Although the male normally never assists in building the nest, yet early in the cycle he may pick up and carry nesting material. It may well be that he sometimes molds his pieces into the beginnings of a nest. Nest molding was seen with the hand-raised males when 2 to 3 months old (Chapter VI). Manipulation of nesting material by the male appears occasionally during the prenuptial stage, but is most pronounced during the preliminary stage. This activity may cause confusion to the observer hoping to find a nest, for a bird with stuff in its bill may not be building. Both male and female indulge in this symbolic nesting, often the male more than his mate. It usually seems to be a joint affair; while one bird carried material, its mate was apt to accompany it. 1M had favorite spots at the opposite ends of the territory, one being in a tunnel under rocks. K2 built her third nest—in May—in one of the places she had often carried stuff to in March. 4M and K200 carried on their symbolic nesting separately. Often the birds picked up pieces of bark or grass and flew with them at random, soon dropping them.

Symbolic nesting plays an important part in courtship in many species—Grebes, Cormorants, Lapwings, and others. With Mockingbirds, when a female arrives the male picks up twigs and carries them into shrubs or vines (Laskey 1933). In Jewel Fish "both sexes practice head standing which . . . might be called 'symbolic' nest building" (Noble 1938:136).

Lorenz (1932:55) mentions the strong impulse shown by his tame Ravens and Jackdaws to *fly* with nesting material much further than necessary under the circumstances. He cites the behavior of the Canary, that ordinarily never "thinks" of flying, but that tries hard to do so when it has nesting material in its bill. The Song Sparrows usually flew with their loads.

D. SUMMARY

1. The nesting cycle of the Song Sparrow is divided into 8 stages as shown in Table XX.

2. The different activities of male and female in each stage are shown in Table XXI.

3. Records of behavior upon the first arrival of females are given in Appendix III.

4. The second stage—prenuptial—is characterized by the cessation of singing by the male. It may last two months with resident pairs.

5. Cessation of song upon the arrival of a mate has been noted in many birds, especially with European species.

6. The male Song Sparrow's "courtship display" consists in "pouncing", i.e. he flies down, hits the female and leaves with a loud song. This occurs during the early stages of the nesting cycle, but ceases with the start of egg laying.

7. The female Song Sparrow has 2 chief notes: a trill given after copulation and on other occasions in connection with her mate; and a chatter given in connection with the mate or the nest, often uttered in flight, and sometimes given before copulation.

8. Y and D behaved towards J as if she were an underling male.

9. The third stage—preliminary—is marked by the start of copulation and by symbolic building, in which both sexes pick up and carry nesting material. Symbolic building is characteristic of courtship in many species.

10. Copulation takes place upon invitation of the female; it usually occurs just after the birds come together or alight after a flight; the male never gives any note, but the female often trills. See Appendix IV.

CHAPTER XV

Relations of the Pair to Each Other and Their Neighbors

Relationships between members of the pair and between them and their Song Sparrow neighbors are instrumented by personal acquaintanceship. This was clear to me after I had tried to catch individuals by putting birds of the same sex in traps on their territories; as a rule in March and early April birds were excited when *neighbors* of the same sex were used and often entered the trap to fight the intruder. There was evidence that 2 females, the center of whose territories were 200 meters apart, knew each other, but in general I do not believe that acquaintanceship extended for a distance greater than 150 meters, i.e., the nearest neighbors and those one territory further off. Trapped birds from territories further than this aroused little interest in the male and even less in the female. In this non-sexually dimorphic species, sex is distinguished by behavior, and birds make no mistake as to the sex of the Song Sparrows living near them.

There is a definite bond between members of a pair, but it is not as strong as in some birds. There is antagonism towards neighbors of the same species, yet there exists a lively mutual interest, and it must be remembered that neighbors are potential mates, in case of the death of one of a pair, an event that happened all too often on Interpont (Nice 1937: Chapter XVII).

A. The Bond Between the Pair

As mentioned in the previous chapter, the male is solicitous over his new mate, acting as sentinel to watch for danger, both from predators and rivals. The pair keeps together much of the time, first one, then the other taking the lead. When they lose track of each other they call *tsip*. (When the male Snow Bunting loses sight of his mate he gives the call note, and if he gets no answer, he starts to sing (Tinbergen 1939c:25).)

What does a Song Sparrow do when its mate is caught in a trap? It was rather exceptional for a bird to show concern. There was no tendency for a bird to follow its mate into the trap, nor, on the other hand, did the mate's experience appear to condition the bird against the trap. I have 2 cases in which the female *tchunked*, and one case where she *tchipped* when the male was in the trap. As for the males, the most common behavior was to sing from an elevated perch. In 6 cases they showed concern.

When K2 was caught in March 1930, her mate 5M and neighbor 10M both *tchunked*. When K34 was caught, her mate started to *tchunk*, then sang. I found K204 in the trap and 204M singing; he uttered *tik-tik-tik* as I removed her. When K7 was caught, her mate 4M and neighbor 1M *tchunked;* 3 minutes later 4M entered the pull-string trap himself. When 4M's mates in 1932 and 1935 were trapped, he *tik-tik-tiked at my approach.* On June 3, 1935, his second mate, K201 and her 3 weeks old young were in the trap; 4M was excited and gave an unusual note very near me as I put them in the gathering cage—*puh-puh-puh.* As I carried them into the house to weigh them, 4M began to sing. When I returned with the captives in a small cage, he stopped singing and began to *tik-tik-tik.* He did not pounce on K201, as males often do when their mates return from such an enforced absence, but came near, apparently excited in guardian role over his step-child. Later in the day on the 2 occasions that I visited the garden and when my daughter did so, 4M gave the *tik-tik-tik* note with vigor. In this case his concern was both for his new mate and for the young bird.

There seem to be few observations as to the behavior of birds when their mates are caught in traps. Tufted Titmice at Columbus were greatly excited in winter over the capture of one of the flock in a trap. When a male Robin was caught, his mate seemed disturbed. One or more Wren-tits "may circle the trap while another is being banded" (Erickson 1938:301). If one of a pair of Marsh Tits "is caught in a trap the other usually shows disturbance and distress, but when the trapped bird is transferred to the hand, and is transformed from a fluttering, struggling and perhaps ejaculating object into a silent, still one, the mate ceases to be so concerned" (Morley 1942).

1. *How Permanent Is the Bond?*

Although the majority of Song Sparrow pairs remained together throughout one season, there were 11 known cases on Interpont where females deserted their mates, and one where a male did so. Five females changed mates early in the prenuptial period; 2 did so just at the start of nesting (one was mated to a bird with a broken leg); and 4 followed their young into the territories of unmated neighbors and remained to nest there. Of the first 5, one bird was trapped the day of her arrival; she joined a new mate 200 meters distant; another female stayed with the adult summer resident owner of the territory after he had driven her first mate, a young resident, into an adjoining territory.

K42 joined 9M Feb. 22, 1931; on the 25th she was having a territory quarrel with 11M; on the 27th she started wandering, giving loud threat-notes to both 11M and 9M who had followed her for a distance; on Mar. 2 she was with 66M, 250 meters distant (see Map 3 in Vol. 1, Nice 1937); from the 5th to 20th with 11M, finally returning on the 22nd to 9M with whom she nested. She sang vigorously Apr. 14 and 18, and was very dilatory about starting to lay and in her incubating.

K58 was 65M's mate in 1931; in 1932 she arrived Mar. 3 and joined 101M, 65M's successor. On Mar. 16, I found she was with 9M, 100 meters to the east. I walked over 101M's territory and soon routed him out; he flew to his northern border and was chased by the owner of the next territory; he then went over to 9M's land, and he and K58 hurried home, chased by 9M. By the 19th, however, K58 had moved to 9M's territory for the season. The next spring she arrived on Mar. 14, and joined 4M who had taken over 9M's land (9M being dead); 2 days later, however, she had joined 143M just to the west and remained with him. Both years she had joined the male holding the territory of her former mate, but before long had joined a neighbor.

Tinbergen tells of a female Snow Bunting that went back and forth many times between 2 males on the day of her arrival (1939c:23), while female Mockingbirds may stay a few hours or days and then leave (Laskey 1933). The male Mockingbird "guards" his new mate, "giving soft warning notes at the approach of some one"; if he comes too close, she pecks him.

The male Song Sparrow that deserted his mate and young was disturbed by my placing a trap over the nest; his territory had been taken up late in the season; he procured a third territory for himself 200 meters to the west, obtained a mate, and the following year returned to this spot.

Two pairs that were driven out by destruction of cover on Mar. 1, 1933 separated; one male disappeared, while his mate settled some 150 meters southwest. The other male settled some 150 meters to the south and his mate (K135) 400 meters to the north. I suspect that females probably at times desert after their nests have been broken up, possibly after a narrow escape from a predator. However, I never located such a bird on or near Interpont. With Nuttall White-crowned Sparrows Blanchard found faithfulness the rule; twice polygamy and extended territories complicated the picture, while "the shock of losing nestlings may have been responsible for two of the three desertions of one mate by the other" (1941:36). Howard writes (1929) that he never found a bird deserting after she had once joined a mate, but Howard did not band his birds.

As to faithfulness throughout one season, some years ago I gathered together the material I could find on this subject with banded birds (1930b), and found that in the majority of cases the mates stayed together, but that with some species that temporarily leave the territory after the young are fledged, change of mates often occurs, as in Catbirds, Bluebirds and House Wrens. Since then I have found one case of Robins changing mates, but two cases of their raising 3 broods together (Schantz 1939, Nice 1941b); most of the evidence still points to no change during one season. With House Wrens Kendeigh reports remating taking place in 41 per cent of possible cases (1941b). In Hungary Warga (1939) found that with banded individuals pairs of Great Tits and Common Redstarts remained together for the 2 broods in one nesting season.

Some times Song Sparrows remate for a second year; there were 8 such instances on Interpont out of 30 cases where mates were present 2 years in succession, or 27 per cent. Since males retain or return to their territories and females attempt to do the same, it seems strange that remating did not occur more often; the explanation would seem to lie in the many chances a male had to get a mate before the arrival of his last year's mate, particularly when the proportion of resident females was high. In the House Wren there was remating in subsequent years in 40 per cent of the possible cases; here the relatively short span of time between the arrival of different females that had nested before would give a bird more chance to obtain her former mate than was possible with the Song Sparrows. The same pairs of Royal Albatrosses nested together—3 pairs since 1938, one since 1937 and one since 1935 (Richdale 1942).

Even if both birds of a pair were resident and wintered near together, I could see no evidence of a bond between the two during fall and early winter. With many birds there appears to be a real personal attachment between the mates. This seems to be the case with the Nuttall (White-crowned) Sparrow (Blanchard 1936, 1941). Warga (1938) found evidence of permanent mating with banded Great Tits in Hungary. Colquhown (1942) writes of color-ringed Blue Tits in England: "In winter, it is difficult to tell whether a bird is paired or not: the most certain way is to watch the roost. Paired Blue Tits . . . very often roost close to each other, while they indulge in a 'good-night' display which probably has considerable social significance in maintaining the relationship." In northern New Jersey Tufted Titmice go more or less in pairs throughout the winter (Mayr, letter). The faithfulness to mates of Greylag and other Geese in captivity is well known (Heinroth 1912a); Tavistock found the same was true with some of his Parrots that had their liberty on his estate.

B. Relations of the Pair to Their Neighbors

The relations of both male and female Song Sparrows to neighbors of their own species during the nesting season are hostile. The female by association with her mate seems to learn the boundaries of the territory, and she takes part in its defense. In general males fight males and females, females, as Tinbergen found with the sexually dimorphic Snow Bunting, but there are many exceptions with the Song Sparrows.

1. *The Male and Other Males*

Quarrels along the boundaries are the rule in a thickly settled Song Sparrow community. 1929 I saw many of these nearly every day from March into July between 4M and 1M, particularly at the feeding station which I maintained on the border between the two territories. 4M at this time was a markedly belligerent bird, dominating all his neighbors; in later years he became more peaceable. In his threat-posture, he expanded his feathers chiefly in the shoulder regions—what I called "ballooning", while 1M puffed himself out more laterally.

Mar. 17. Both males are puffed out and somewhat hunched up. They face each other only a few inches apart, then proceed to hop and walk and scratch, picking up food, each staying on his side of the boundary.

Mar. 30. 1M and 4M threaten, back and forth; one retreats, the other follows; the first one stops, and turns about; the other retreats. Both are somewhat puffed up. K2 goes for 4M, her tail spread; they stand facing each other, then both retire. 4M utters a few *shees*—the threat note.

Apr. 6. 4M ballons at 1M, who puffs at 4M; the females stay in their respective backgrounds. 4M goes near his mate who pecks at him. K2 ballons at K3 who retires. The males come within 3 inches of each other, 4M balloned, 1M somewhat puffed and with spread tail. Suddenly a real fight is staged, the males hopping up and down, the females clenching.

Both pairs—1M and K2, 4M and K3—often deliberately trespassed on each other's territories.

Mar. 24. 1M and K2 are searching in 4M's rose hedge; he chases them home with much *sheeing*. 1M stops on the trough with his tail spread, K2 utters *shee shee*.

Mar. 27. 4M and K3 are in 1M's territory; he pursues them to their land, where they turn and pursue him.

Apr. 6. 4M comes into 1M's land, his tail twiching nervously; he comes into the south cherry, rapidly climbs the bank and goes along it till he reaches the south end where K2 is at work on her first nest; she attacks him, starting him towards his territory. 1M comes dashing from the north end and finishes driving him home, being in turn chased by 4M and his mate.

Apr. 28. 1M suddenly flies directly west over the rose hedge and swings back home with 4M and K3 in hot pursuit. He sings as he lands in safety, puffed out and tail spread. K2 joins him with a *shee shee*. The males have a vigorous fight, while their mates give the threat-note.

This matter of trespassing makes one think of what Rinkel (1940) wrote of the Lapwings, "Especially the 'ground fights' of the ♂ ♂ and their 'aerial combats' ('border clashes') make the impression of plays only, which the birds seem to need; this also points to the love of 'social' breeding".

2. *The Male and Females Not His Mate*

The Song Sparrow male pounces on neighboring females when the mates of the latter are at the other end of their territories; these attacks are usually much more severe than those on his own mate, and they elicit a violently antagonistic reaction in the female, who fights back, at the same time uttering loud threat-notes. Usually her mate comes rushing to the rescue and fights the interloper, while the mate of the latter hurries near and trills and postures.

Howard says in regard to the Yellow Bunting: "Putting aside all theory, there is a fact which shows beyond a doubt that in the second phase he is in a state of organic preparedness, I refer to stolen matings. These are by no means uncommon where territories adjoin and different females are in different stages of development; and despite the efforts of the owner to prevent it, a male will sometimes succeed—as far as one can tell—in reaching a sexual union" (1929:42).

The pouncing of the Song Sparrow on neighboring females differs from these observations in several respects: it is not a matter of the female being in Howard's third phase (from the start of coition through egg laying), for most of the attacks recorded were made on incubating females, and they happened while the male's own mate was in all possible stages. These pouncings did not result in "stolen matings", for copulation never occurs in this connection, and, moreover, the male was almost always fought.

With the Ovenbird stolen matings do occasionally occur (Hann 1937, 1940), also with Grey Herons (Verwey 1930), Herring Gulls (Goethe 1937a), and Rooks (Yeates 1934).

4M pounced on 1M's mate, K2, rather frequently in 1929 and in later years on the mates of other neighbors.

Apr. 5. A fierce fight between 4M and K2; he knocked her down on the east bank in 1M's territory; 1M comes rapidly and attacks 4M, while K3 hurries near chattering and scolding. K2 was silent, but 4M sang.

An interesting example of delayed reaction took place on May 12: K2 started for her nest with a caterpillar, 4M pounced on her, then flew to a burdock and sang. K2 went ahead to her nest, preceded by 1M; after he had fed, he came puffed out near 4M. K3 hurried up with the threat-note.

A curious instance of pouncing on an unprotected female occurred in 1930. As already mentioned, 29M had deserted his mate, K29, and young on May 20; the next morning I noticed 5M quietly watching K29 as she went to the nest; when she flew, he pounced on her and sang, while she gave the threat-note. He then turned home, being attacked on the way by 10M. His territory was separated from hers by another territory 60 meters wide. It shows that Song Sparrows may be aware of neighborhood happenings 2 territories distant.

The male's habit of pouncing on unprotected females opens the way for bigamy when an incubating female loses her mate. There were 4 cases of bigamy that came to my notice on Interpont; in 2 of them I knew the female had had a nest with eggs when her mate was killed. (If a male comes to his end during the prenuptial period, his mate leaves her territory and joins a bachelor.)

3. *The Female and Other Females*

As a rule female fights with female.

Mar. 16, 1930. K2 comes to the top of the dike to threaten K13; K2 is puffed out enormously.

Mar. 19. I hear loud threat-notes between these 2 females.

Apr. 5, 1931. K11 (4M's third mate in 1930) has returned and joined a neighbor, 20M; 4M's present mate, K41, seems determined that she shall not come on to 4M's territory. She accompanies the new arrival in the weeds, guarding 4M's territory from K11, and when the latter and 20M fly west well into their territory, K41 flies to a maple and gives a raucous chant.

In 2 of the instances of bigamy I did not see the females meet, but in each of the others I saw one meeting of the 2 females and neither time was there hostility. Blanchard describes the territorial differences of the 2 mates of one male Nuttall White-crowned Sparrow: "each female created for herself a subdivision of the main territory which she defended *against the other female* by loud singing and fighting, and in which she finally chose her nest-site" (1936:149).

4. *The Female and Males Not Her Mate*

The female is the victim of her neighbor's pouncings, but she, in turn, defends herself. Sometimes males drive females when both are on the ground.

Mar. 20, 1930. (K2 had arrived Mar. 15 and joined 5M, in his territory just west of 4M. A young male, 10M, was trying to wedge in a territory between 5M and 1M.) K2 is near 10M; they have a "boundary feint" much like 2 males, i.e. both assume the threat-posture. 5M comes flying down; 10M leaves.

Mar. 21. K2 and 10M have another boundary feint; he drives her further and further west, as much as 5 meters; then she turns, but he drives her again. 5M appears, and 10M hurries away.

Mar. 10, 1935. K200 (4M's mate) is feeding in the southwest corner of the territory; 4M flies home and sings. 220M joins her. She hunches her shoulders, puffs and utters the threat-note *zhee zhee,* but 220M comes nearer and nearer. She flies home with loud *zhees.* 4M rushes at 220M and drives him off. K200 chatters again and again.

Sometimes a female accompanies her mate in chasing male neighbors. This happened at times with 1M and K2, 4M and K3, and many others. 4M's first mate in 1930 was an outstanding example. See Chapter X for the exploits of K56 and K135.

Sometimes the female drives off a trespassing male alone.

Earlier in this chapter (1. *The male and other males*) an instance is given of K2's driving 4M when he trespassed far over into her territory.

Mar. 12, 1932. 100M comes into 101M's territory, but the latter is singing and does not notice the intruder. 101M's mate says *tchunk tchunk* and drives 100M off.

Feb. 25, 1931. K42 is making most extraordinary noises, a kind of grumbly song; she is all puffed out and *flipping a wing* at 11M below her. Her mate, 9M, sings at a distance; suddenly he attacks 11M and drives him home.

This is the only time I ever saw a female give the puff-sing-wave display. K42, as mentioned earlier in this chapter and also in Chapter X was an eccentric individual, who wandered from one mate to another, sang loudly and was an indifferent nester.

There were 2 instances of special interest involving relationships between females and neighbor males; in one she courted him; in the other, due to territorial tangles, she intimidated him.

In early April 1932 3 pairs were present on the first dike—from east to west, 130M and K125, 68M and K100, 109M and K60, who had been 68M's mate in 1931. In late April K100 deserted 68M for an unmated male, 66M, 100 meters distant. On May 18-19 K125's nest was destroyed; on May 21 K60's young left the nest, while 68M was still unmated. On May 30 I found that both 130M and 109M had disappeared; that K125 had a nest far up in 130M's land in which the set must have been complete on the 28th; that K125 was "courting" 68M, but that he was more interested in K60, who repulsed him.

8:00. The 2 females are having great threatening ceremonies in K60's territory, again and again, like 2 males. K125 is exceedingly vocal, twittering, chattering and giving *cluk cluk cluk* notes. K60, very much puffed, drives off K125, after which they fed within a few inches of each other. K60 is always keeping K125 to the east. K125 flies chattering into K60's land and is driven off by her. K125 then flies to a weed, trills and postures; 68M comes to her, but apparently they do not copulate. She goes again into K60's land and K60 chases her away. 68M sings, K125 chatters and joins him, but I can't see what happens.

8:23. K125 is very vocal. All 3 are together in K60's land. K60, very much puffed out, drives off K125. K125 postures and trills, but 68M goes toward K60. I could not see what happened. K60 gives the threat-note at 68M and drives K125. The latter flies up on the bank and postures in extreme form, but 68M sits silent and inactive nearby. She flies into the ditch, is very vocal; he follows, sits on a post and sings. She makes queer noises, then approaches him and trills, but he does nothing.

8:34. Again she chatters and postures in vain.

In the hour between 8:00 and 9:00 K125 postured 8 times, while 68M responded once or possibly twice. K60 was being followed by 2 young; she showed little interest in 68M. Seldom had I seen a female as puffed out as K60, and never before had I seen one as amorous as K125. Her nest was 200 meters from the scene of the encounters.

On May 31, one of K60's young ran to beg from 68M, but he looked at it threateningly. I did not see K60 after June 3. K125's young hatched June 7 and 8; in the half hour I watched on June 9, 68M did not feed the young. Since we left Columbus for the summer soon after, I do not know anything more about the happenings in 1932. The next spring K125 arrived 5 days after 68M was mated; she joined 4M and proved to be a quiet, undemonstrative individual. It was curious that a female with a completed set of eggs should have been so sexually excited; her need to attach a male as protector, and the opposition she met in this endeavor stimulated her to a high pitch of effort.

Perhaps we can separate sexual from territorial defense in the behavior of these 2 females on May 30: K125's motives were sexual, K60's territorial and maternal. K125 intruded into K60's territory because 68M was there; much as she wanted 68M she was in no position to drive K60 in the latter's own territory. Her puffing was probably an effort to keep herself in 68M's territory. She may have been jealous of K60 since 68M openly preferred his last year's mate to her. K60, on the other hand, was antagonistic to both visitors; she was not yet ready for a new mate and her one motive seems to have been to clear her land of intruders. Probably her defensive instincts toward the young were heightened by the fact that all the responsibility for protecting them lay on her alone.

A very interesting course of events took place in 1929, when K2 built her fourth nest in the rose hedge which was just over the border on 4M's territory; 4M would not allow 1M to come near his (1M's) nest, and K2 had to take over the protective functions of the male. One of K2's young from the third nest had settled in 4M's hedge and later moved further into 4M's land; K2, as always in such situations, took care of this fledgling, while 1M fed those that remained in the home territory.

June 19. 4M's mate K3, is building her fourth nest in the north rose bush. 4M chased K2 home from the hedge.

June 20. 6:00 A.M. K2 is trying to get material at the hedge. K3 comes, hunched up, follows her and she gradually retreats.

6:18. K2, on top of a post in the hedge, *tchunking* at a cat. She is not driven off. (All the posts are in the hedge.)

June 21. 5:33 A.M. K2 tugging at twigs in the hedge; 1M joins her and they give the nest-call.

6:20. 4M is watching; dashes at 1M. Watches till 6:26, then leaves.

6:30. 1M pounces on K2 at the feeding station, actually hitting her; she *zhee zhees*. The next moment 4M dashes in and attacks 1M. The 2 males threaten each other back and forth.

June 22. 6:13. K2 goes to rose hedge; 1M follows.

6:19. 4M watching, drives off 1M.

6:43. K2 on top of a post; *4M flies at her, she crouches, zhees, and leaves.*

7:20. K2 carries stuff to the hedge; 1M watches from a post.

7:28. 1M to a post, 4M drives him east.

June 23. 5:25 A.M. K2 gets material and takes it to the nest; 1M joins her. 4M drives 1M twice.

5:50. K2 on post *tchunking,* 4M flies towards her; she *zhees* and *remains.* Again he flies at her; she counters *zhee zhee; he* retreats. She flies further over into his land and preens herself. As long as her nest was there, that was her land, and she no longer gave precedence to 4M. But 1M retreated before 4M, unless well within his original territory.

6:47. K2 is building and 1M is watching, but 4M arrives. 1M retreats, then returns. They fight in the sweet clover. 4M flies to a post and sings; *he stops in the middle of a song as he notices K2 gathering material below him;* she continues to work and he starts to sing again.

June 24, K2 has one egg; K3 3 eggs.

June 25. 4M went into the trap and I pulled the string. *1M flew to the top of the trap and started to fight 4M.* The side door fell open and 4M escaped.

6:49. *1M pounces on 4M's mate, K3,* fights her, she fights back; she *zhee, zhee,* he sings. This is the first time I have ever seen 1M pounce on K3.

7:24. Apparently 4M accepts K2's presence; she is preening on a post.

In the 3 hours I watched, 4M chased neither 1M nor K2.

June 26. 7:23 A.M. Trap 4M, give him a new colored band. He flies west.

7:29. K3 is coming towards the trap; 1M *is crouched and menacing on top of the trap;* she turns away, but he flies at her, circling above her; she *zhees;* he sings. At 7:45 he sits on one of the posts.

8:57. At last K3 came off the nest after 40 minutes on the nest; her usual period on was about 18 minutes. But 4M is staying at the other end of his territory with his young. 1M pounced on her. She drove 2 young House Wrens from her rose bush.

June 27. 4M still spent most of his time at the far end of his land, leaving K3 to drive off young Robins and House Sparrows from the vicinity of the nest. 1M swooped over her once and pounced on her twice.

June 28. I was able to watch only 2 hours in the late afternoon and evening; 4M was caring for his young, but 1M was nowhere to be seen.

June 29. 1M returned, but was *very much afraid of 4M.* 4M must have caught him pouncing on K3 and punished him severely. 4M still showed no disposition to defend his territory.

July 1. 10:43. K3 is coming to the feeding station; *K2 comes and threatens 4M. She drives K3 from the seeds.* 4M circles around K2 who eats ahead, paying no attention. Territory lines have broken down.

July 2. 4M does not let 1M come near his own nest.

7:13 A.M. *K3 is coming to feeding station; 1M hurries away.* He is afraid of K3 as well as 4M!

7:14. K2 postures, 1M mounts and they copulate. She has been incubating 6 days.

7:17. 1M and 4M come near hedge, K2 flies down, *zhee zhee zhee* at 4M. *She drives 4M,* while 1M stays behind. She goes to her nest, the males have a mild territory establishment encounter, 1M singing softly 6 inches from 4M.

This happens again at 7:49. Later K2 gave the threat-note so loudly at 4M, her tail spread, that he left the vicinity. Both males still feed their young and each father drove off a child of the other family for the first time.

July 3. 9.23. K2 comes off her nest, goes to the feeding station; gives threat-notes at the sight of 4M standing puffed up nearby. *She repeats the threat-notes and goes for him; he retreats.*

July 4. 7:35. K2 to the feeding station; 4M starts to come, but left.

9:11. 4M darts down and drives off one of 1M's young; 1M hurries to the rescue and K2 also. The males have a mild territory encounter.

July 5. 9:02. One of 4M's eggs hatching.

July 6. K2 drove 4M again. 4M approached 2 of 1M's young; 1M hastened to the rescue and the males fought. At 8:20 4M was right below K2's nest and 1M did not dare drive him away. This morning there were 4 territory establishment encounters between the 2 males, 1M doing all the singing. At 9:23 there was a fierce fight on the ground, and the territory troubles were largely settled. *At 10:00 1M was actually singing loudly right over his nest.*

July 7. 1M's eggs hatched.

9:31. *4M pounced on K2;* she gives the threat-note—*shee shee.*

In this series of events the primary difficulty came from K2's building her nest outside her mate's territory. This is something I never encountered in later years, unless the female mated with the neighboring male, who in each case was unmated at the time she followed her young into his territory. 4M normally dominated 1M, but 1M dominated him for a minute or two on June 25 when 4M was caught in the trap; after this 4M showed little interest in defending his mate and territory for the next week. 1M, confident from his momentary ascendancy over 4M and from the fact of 4M's long absences, began to bully K3, something he had never done before to my knowledge. (With Jackdaws and Geese the wife takes the rank of the husband; before this I believe 1M had been too dominated by 4M to venture to pounce on 4M's mate.) 4M must have caught 1M pouncing on K3 and attacked him so severely that he was greatly subdued, very much afraid of 4M and even avoided K3.

In the meantime, K2 became more and more belligerent towards 4M; by dint of her persistance and her loud threat-notes, she had him cowed. The territory formula had broken down; all relationships were personal—K2 by exaggerated aggressiveness dominating 4M and K3, 4M and K3 dominating 1M, and 4M not allowing 1M to approach his own nest. The day before 1M's young hatched, many territorial ceremonies were gone through, concluding with a strenuous battle; 1M won the land around his nest. *The next day 4M pounced again on K2.*

In 1930 1M upon his return spent all his efforts to get the rose hedge into his territory and quickly succeeded. K2, curiously enough, showed herself almost timid in her encounters with the young 10M. Apparently it was not through a dominating character, as possessed by K200 and Schantz's female (1937) see Chapter XVII—that K2 intimidated the belligerent 4M. It was the sheer necessity of defending her nest and herself with no help from her mate.

C. SUMMARY

1. Relationships of Song Sparrows to each other are instrumented through personal acquaintanceship.

2. There is a definite bond between the pair; the birds are attached to each other during the nesting season, so long as they are closely associated.

3. Song Sparrows sometimes show concern when their mates are trapped, but often seem indifferent.

4. On Interpont Song Sparrow pairs normally remain together throughout one season, but there were 11 known cases of females deserting their mates and one of a male doing so.

5. Remating in subsequent years occurred in 8 instances—27 per cent of the 30 possible cases. The high mortality of the nesting birds, especially in the later years, and the long season over which pair-formation took place—from early February to April—are thought to be responsible for these low figures. With some species there is a high degree of constancy between mates.

6. Male Song Sparrows are hostile to their male neighbors; they defend their boundaries with threat-postures, sham feeding and fights. At times they deliberately trespassed on each others' territories, either on foot alone or in company with their mates, or on wing alone.

7. The male pounces on his neighbors' mates when they are temporarily unprotected. The female normally responds by fighting. This habit of the male is the occasion for many fights. It also opens the way for bigamy when an incubating female loses her mate.

8. Females are hostile towards neighboring females, using the threat-posture, threat-note and fighting.

9. Females are normally antagonistic to neighboring males, fighting when pounced upon and often driving them off when they trespass.

10. An account is given of the demonstrativeness towards an unmated male of an incubating female that had lost her mate; the question of sexual and territorial fighting with this female and her rival is discussed.

11. When K2 built her fourth nest in the rose hedge in 4M's territory, 4M did not allow 1M to come near his own (1M's) nest. K2 had to take over the defensive role of the male and intimidated 4M. When finally, just before the young hatched, 1M through territorial ceremonies and fighting was able to get control of the rose hedge, 4M started to pounce on K2 again.

CHAPTER XVI

The Problem of Pair Formation

The problem of pair formation is primarily that of recognition—specific and sexual. "Courtship may be defined as an elaborate sexual response involving recognition, selection, and pursuit", writes Abbott (1941). "Courtship is, in fact, an almost exclusively *visual* process; courting animals (not insects exclusively) depend almost entirely upon the visual impressions they receive." This is doubtless true of many fish, and partially true of birds, but with birds voice also plays an important role. In lower mammals and in many insects the olfactory organs are important, while in some insects auditory cues play the primary role.

Special techniques for recognition are important to prevent interspecific crosses in animals as highly interfertile as birds prove themselves to be. Dobzhansky in his book on "Genetics and the Origin of Species" (1941) when discussing "isolating mechanisms" mentions sexual or psychological isolation—copulation does not occur because of the lack of mutual attraction between the individuals of different species. This lack of attraction may in turn be due to differences in scents, courtship behavior, sexual recognition signs, and the like," p. 257.

As pointed out by Cushing (1941b), with some birds the recognition of mates must be an inherited matter—witness Cowbirds and parasitic Cuckoos. With others, however, the mating preference is acquired apparently at a very early age—Pigeons, Ducks, Raven, Shell Parakeet, etc. Social birds, when hand-raised, are very apt to transfer their reactions to man. Some of Lorenz's Jackdaws treated him as their wife, others as their husband. A male Eagle Owl courted Dr. Heinroth, his sister courted Frau Heinroth. A male Corn-Crake and female European Partridge both courted Frau Heinroth, while a male Pheasant courted Dr. Heinroth, and the South American Bittern (*Tigrisoma*) at the Amsterdam Zoological Garden would, with its ceremoney of nest relief, invite Portielje (1922) to step into its nest and incubate!

"In Jackdaws I have repeatedly found," wrote Lorenz (letter), "that when I got a brood of young, all at the same date, the eldest ones of that brood would show a normal sexual reaction when reaching maturity, while the youngest ones, who, when isolated from the parents were at the utmost 4 or 5 days younger, would become humanized and refuse to give any sexual reaction to their kind. Anatidae, on the contrary, show normal behavior, when hand-raised in company of their own kind."

Craig tells us (1908:90), "we must believe that young doves have no inherited tendency to mate with birds of a particular kind; they learn to associate with a particular kind during the period when they are being fed, when the characteristics of their nursing-parents are vividly impressed upon their young minds."

A. Lorenz's Views of Pair Formation

In his paper on the "Kumpan" (1935:319-337) Lorenz describes 3 types of pair formation. In all of them the male displays. In the lizard type a male in breeding condition displays in turn, while weak males and females flee (for example, Muscovy Duck). In the labyrinth-fish type (which includes the majority of birds, some sexually dimorphic, others not), the female gives a submissive type of display and is dominated by the male. In the cichlid type, both display, the sexes are not ambivalent, and there is no dominance (examples, Herons and Cormorants). Later (1940) he goes into greater detail in regard to the 2 last types, especially that of the labyrinth fish. He gives instances where a male Ruddy Sheldrake (*Casarca ferruginea*) had been for some years the "female partner" of a New Zealand Sheldrake (*C. variegata*), and later was the husband of an Egyptian Goose (*Alopochen aegyptica*); where an old female Jackdaw was the "husband" for 2 years of a young female, and after that the wife of an old male; where a young female Raven first acted as the male of a pair with her sister, then became the mate of an older male Raven.

With the cichlid type there "is little sexual dimorphism in size or plumage. It is only the instinctive actions that are different in both sexes, that work, so to speak, like sex-recognition marks that bring the pair together" (1940:279).

Lorenz had based his "lizard type" on Noble and Bradley's (1933) report; Kramer (1937) working on lizards (*Lacerta*) under more natural conditions found that the female is not entirely passive; she nods her head in response to the male's courtship and if receptive quivers her tail. Evans (1938), on the basis of field studies on chameleons in Cuba, criticizes Noble and Bradley for "drawing their conclusions from observations based upon lizard responses in crowded habitats." He found that the female responded to the dewlap display of the male by "an unmistakable nodding". "Courtship on the part of the male involves quite as elaborate an exhibition of dewlap color display as in the intimidating or territorial displays of two rival males or two rival females. This would tend to indicate that the color display of the male's dewlap has evolved, perhaps, as much because of its sexual selective value as because of its intimidating quality in combat," p. 122. *So apparently even lizards do not adhere to the "lizard type"*.

As to the "cichlid type", Noble (1938:136) took exception to Lorenz's description. This classification has also been criticized by Tinbergen (1939c:53) for "the description of each type contains characters, and therefore criteria of different orders, such as: the mechanism of sex recognition, sexual reversibility, the necessity of inferiorism. Nevertheless, Lorenz's three types are very useful as a basis of a real classification, because he has used largely one criterion: the male's mode of sex recognition." He then points out difficulties, and concludes that most species will have to be classed as "cichlid" with releasers for pair formation in both sexes, while at one end of the series stands the lizard type with releasers only in the male, and at the other end the labyrinth fish type with releasers only in the female, the cichlid type "being a heterogeneous mixture of all kinds of intermediate forms", p. 54.

Lack (1940e:276) finds it "impossible to use "Lorenz's categories, "even as a basis for a revised classification."

Two contrasting forms of pair formation are described for fishes by Noble (1934, 1938, Noble and Curtis 1939); these fit fairly well Lorenz's second and third types.

> "In the fighting fish, *Betta* and the sunfish *Eupomotis*, the two sexes behave differently and sex recognition is accomplished in a simple manner" (1939:16). The "mechanism of sex recognition" in the jewel fish (a cichlid), on the other hand, is "far more complex", depending on the possession of a territory. "Slight differences in motion identify sex and species" (1939:42). "Hence, it is highly probable that in some fish, as in birds, sex recognition depends on the grosser movements of response to the gesturing of the territory-guarding male. In these fish and birds sexual ripeness, however, in a female is indicated by her willingness to enter a territory-guarding male's area and to remain there in spite of threats of intimidation. The display, therefore, serves primarily to reveal sexual ripeness in both fish and birds" (1939:43).

Before we discuss further the types of pair formation in fishes and birds, let us examine the subjects of sexual ambivalence and sexual dominance.

B. SEXUAL AMBIVALENCE

It is well known that under conditions of captivity homosexual unions are formed by many birds. If a female Dove "has been long unmated, she may herself have become almost as aggressive as a male" (Craig 1908); an exceptionally aggressive male Dove may cow another male to the point where the latter will behave like a female. Homosexual pairs often occur in captivity among Pigeons, Anatidae, and Parrots; they have been reported in Emus (Heinroth 1927), Griffon Vultures (Heinroths 1924-33), and other birds in zoos. Ruffed Grouse in captivity take on male or female behavior according to their state of "dominance" (Allen 1934). Although in one season a female Starling had fought her mate's extra wife, in the fall she "courted" a young female, and the following season both became mates of one male (Freitag 1937), as did Lorenz's 2 female Jackdaws that had formed a homosexual union. Lorenz points out that homosexual pairs rarely occur where there is much difference in the plumage of the sexes; apparently a male in full breeding plumage (*Prachtkleid*) cannot take the submissive role, the only exception being the Wood Duck (Heinroth 1910). Diebschlag (1941) found it easy to induce homosexual pairs among female Domestic Pigeons, but did not succeed with males.

Homosexual pairs seem to be very rare in the wild. They have been reported with 2 feral male Mute Swans (Ritchie 1926), and in 2 "pairs" of feral Rock Doves (Brackbill 1941).

Brian Roberts in his study of Penguins considers that the "conception of the neutral type in birds . . . is outwardly much nearer to the male than the female" (1940b:209), Lorenz (1935:328) states that in birds with the labyrinth fish type of pair formation "each individual has the tendency to develop the male type of behavior, and it is the stimuli coming from the sex partner that suppress male behavior in the female and give first place to female behavior." The female Bronze-winged Pigeon's behavior "is that of the male; it is merely *less energetic*" (Whitman 1919:17). With Penguins the "essential difference in the behavior of the sexes is that during the breeding season a male always tried to dominate weaker birds, while a female loses this dominating urge during the short period when fertilization must take place" (Roberts 1940b:213). This is well illustrated in the case of Schantz's female Song Sparrow that "became antagonistic to her mate after each set had been laid, remaining so until the young were well feathered" (1937:190).

In many species some of the characteristics of the opposite sex are latent in each individual. Where the female normally does not sing, she may do so occasionally (Chapter X). Where the female regularly incubates, the male may do so rarely—American Robin, Bluebirds, Reed Bunting, Spotted Flycatcher, Tree Swallow (Kuerzi 1941), Ruffed Grouse in captivity (Allen 1934), Silver Pheasant at Dr. Lorenz's, and others.

Although the male Song Sparrow never normally builds, he carries material in the symbolic building and in one instance is known to have built a nest by himself and later helped his mates build (Schantz). The female Song Sparrow has a weak song, seldom heard, but one bird sang loudly and well (Wetherbee 1935). Females can be decidedly aggressive towards other birds. Nevertheless, I do not see how homosexual pairing could ever occur in Song Sparrows, despite the fact that the plumage is the same. There is too great a difference in the behavior of the sexes. The same would seem to be true of many passerines where the male's signals are specialized, and particularly where dimorphism is present.

Lack (1940e) in discussing sexual ambivalence, states that "this behavior is extremely complex, and probably has a different basis in different cases, sometimes genetic, sometimes hormonal, and sometimes due to various types of external situation."

C. The Question of Dominance

All life is interpreted in terms of "despotism" by Schjelderup-Ebbe, preferably male despotism. "In almost all creatures (human beings included) the female is never so well disposed for pairing as when the male has absolute superiority" (1924b:36). "In animals female despotism constantly brings about degeneration through the hindering of pairing, thus operating *against* the increase of the species" (1935:960). Hingston believes that the key note of the animal world is hostility; with birds "the demonstration before the rival is hostile, the display before the female is hostile, the sex act itself is hostile" (1933:357). A. A. Allen independently decided that, "Domination and fear are the important principles in the development of secondary sexual characters and even in controlling the mating cycle" (1934: 198).

Differences between social and sexual dominance are mentioned by Noble (1939b), but nowhere does he clearly define what he means by each. "In many birds the dominance threat to the sex partner is given vocally" (1939b:268). Lack (1940e:278) tell us that, "The dominance theory postulates that at pair-formation the male in some sense impresses or overpowers the female, sometimes through aggressive display." The matter of "sexual dominance . . . needs clearer definition, and it is not nearly so widespread in birds as Allen (1934) implies. I cannot say more as I have not studied at first hand any species in which it occurs."

Lorenz (1940) gives photographs of the male Raven's postures, the function of which he believes to be the overawing (*Einschüchterung*) of the female, which is "fundamentally important for the suppression in her of masculine behavior". The first mate, that had been severely dominated by the male during her early youth, feared him during courtship and flew away, but his next mate showed no fear of him.

The Pigeon affords a good example of what has been called sexual dominance.

> "The male takes an aggressive attitude and compels the female to submit to him", writes Craig (1908:82). "A female regularly gives in to her mate, even though he may be cruel to her. If she is approached by other males, she suffers herself to be driven away from them by her jealous spouse. Professor Whitman tells me that even a female of the domestic pigeon, when mated with a male ring-dove (less than half her size), whom she could crush if she wanted to, gives in to her little husband with the same meekness she would show to a husband of her own species. But let the female be threatened, not by her own mate, but by a stranger, and she is changed at once from the lamb to a lion. That the female always yields to her mate is due to no severity on his part, for he is always restrained in his attacks upon her."

Although Noble insisted that "dominance" was shown in his captive Night Herons by the male's holding his head higher than his partner, Lorenz (1935) and R. P. Allen and Mangels (1940) deny the presence of dominance between the pair. With some species the evidence is confusing. With many Parrots the female is said to dominate except during the breeding season, when the male drives her to the nesting box—if this can be called dominance (Tavistock 1929). Female Shell Parakeets drove the males from the food; they "won 367 of the observed hetero-sexual contacts in these non-breeding flocks, lost 27 and engaged in 23 'no-decision' contacts" (Masure and Allee 1934b). With the Snow Bunting one of the pair (the male except in one case) was the "despot" in that it drove its partner from some tidbit found by the latter (Tinbergen 1939c:26).

> Male canaries "regularly dominate females except their own mates during time of breeding, when dominance is reversed for mated pairs", the criterion being number of pecks given and received (Shoemaker 1939b:404). However, the author mentions a "severe flogging occasionally given the mate by a male just previous to nesting. This may be immediately preceded or followed by the usual gentle pecking by which the females dominate their mates. The two types of contacts have no comparison in severity since in the former the male often held the female in its claws and dealt severe pecks at the head and eyes."

With the Song Sparrow, it is evident that the female normally "dominates" her mate to some extent, sometimes threatening him by opening her bill at him, or giving the threat-note and sometimes by pecking him, two females carrying such behavior to extremes, 4M's mate K200 and Schantz's female that threatened her mate when he was singing, drove him from the food and once seized him by the neck. I never heard the male give the threat-note to his mate (although 4M did so to K2), nor saw him peck her except rarely after an unsuccessful attempt at copulation. I never noted any quarrelling over food between the pair.

Is the male's pouncing an expression of dominance, or is it merely a display, a signal, "a method of securing a bond of attachment between two birds of a pair", as Noble (1939b:269) suggests in regard to this activity? It is distinctly a male-female behavior pattern. The female responds to it in different ways depending partly on its severity, partly on the identity of the pouncer and partly on her own physiological state. During the first few days when some pounces are severe attacks she fights back, and this is almost always true when the pouncer is not her mate. When the pounces are mild and come from her mate, she usually gives her chief sex note early in the season and the threat-note later in the season. The fact that 4M pounced on 1M's mate, K2, until her fourth nesting when she became excessively belligerent in defending herself and her nest from him, and then resumed pouncing on her after 1M had taken over the defense of his family, points to a relationship between pouncing and dominance. Also, 1M, dominated as he was by 4M, had never to my knowledge pounced on 4M's mate, K3, until after he had obtained momentary advantage over 4M and the latter absented himself for long periods; later—probably due to severe punishment—he feared both 4M and K3.

The suggestion has been made (Lack 1940e:277) that the male Song Sparrow dominates the female "in the sexual sense", but she dominates him "in the social sense". I do not see any meaning in "sexual domination" in regard to the Song Sparrow; during the preliminary, building and laying periods the female is as eager for copulation as her mate, and often more eager. This is true of many birds. The Herring Gull, according to Goethe's description (1937a:36) may be a species in which the male is sexually dominant.

A possible explanation of the symbolism of pouncing may be this: the male's role is guardian of his mate and young and he shows her his prowess in a realistic manner. The female with her activities of incubation and brooding, needs a strong protector and so do the young. Hence it is of biological value for the female to mate with an aggressive male. His "courtship" may be symbolic of his readiness to defend her and her family. At first she welcomes his display; later it annoys her. Like many instinctive actions it appears to be overdone at times. If this explanation holds, pouncing has become conventionalized to such an extent that it has little meaning in individual cases. We have seen that 1M was not bold in defending K2 under difficulties. One exceptionally unaggressive male, that sang little and whose presence was not particularly resented by his male neighbors, eventually had 2 mates at one time while several neighbors were mateless.

With birds that flock, the situation may be different. Lorenz believes that in birds that show the labyrinth fish type of courtship, sex recognition comes through the fact that males are attracted to birds inferior to them in the social order, and females to those superior (1935:328). With many birds the "peck-order" never appears after they are paired, because the mates never have differences of opinion to decide, but for the formation of the pair, social dominance by the male is an essential element, p. 334. The Jackdaw is an example.

This pattern is carried out by the Black-capped Chickadee; "where the winter-dominance relations were known, the male was dominant over the female when the two were in the winter flock." The criterion was that "females withdrew or were driven away when they came in close contact with males" as at a feeding station. "After pairs had formed," the male was not seen to "exert dominance over his mate" (Odum 1941b:323). On the other hand, with a pair of Blue Tits the male was usually dominant over his mate during the winter, but in early February "she definitely became the despot for a few consecutive days"; later "he resumed dominancy" (Colquhown 1942).

Here with Lorenz's birds and Odum's color-banded Chickadees we have social dominance playing a role in pair formation and a status of no dominance afterwards. With the Song Sparrow perhaps we can consider each partner *socially dominant* in certain respects, like Carpenter's Gorillas (see Chapter VII).

Social dominance is something that can be observed and measured; sexual dominance is a postulate that might well be discarded until thoroughly studied. If the male drives or pecks or pounces on the female, these activities are his signals that he is ready for pair formation or copulation. The female signals by posturing, trilling, etc. We do not have to say that one set of actions expresses dominance and the other submission. After all, in nature the female is free to come or go. If she really feared the male, she would stay away from him.

D. Tinbergen's First and Second Reactions

An excellent analysis of sex recognition preceding pair formation has been given by Tinbergen (1939c). With some birds with marked sexual dimorphism the reactions to males and females are different from the beginning. This is true with some Ducks, the Golden Pheasant and Maryland Yellow-throat (Noble and Vogt 1935), the Blackcock (Lack 1939a), Gould's Manakin (Chapman 1935) and others.

With others where sexual dimorphism is less marked or absent, the *same first reaction* is shown by the more active animal to both male and female; this is the case with the Northern Phalarope and Snow Bunting. "It seems to be of widespread occurrence," writes Tinbergen (1939c:47), "not only among birds (*Ciconia,* Heinroth 1924); Pigeons (Whitman 1919, Heinroth 1928), but among fishes, too (Fighting Fish, Lissmann 1932; Stickleback, ter Pelkwyk and Tinbergen 1937), and it has even been reported for the Cuttlefish, *Sepia officinalis* L. (L. Tinbergen 1939)."

The response of the reactor differs according to sex and breeding condition. An animal of the same sex in breeding condition displays in turn; male and female not in breeding condition usually flee, while an animal of the opposite sex in breeding condition typically remains and displays in a manner different from that of the actor.

The second reaction of the actor is typically: fight under the first condition; drive off or ignore in the second; and court in the third. This pattern agrees in many respects with the labyrinth fish type. Table XII shows the possible responses in a mollusk, a fish, 3 birds with some dimorphism (in one of which the female is the active partner) and 2 birds where there is no dimorphism.

TABLE XXII

"SEX RECOGNITION" BASED ON BEHAVIOR OF ACTOR AND REACTOR

b = breeding condition; n = non-breeding condition; o.s. = other species

	First Reaction						Second Reaction
Species	Sex	Status	Actor	Sex	Status	Reactor	Actor
Cuttlefish (L. Tinbergen)	♂	b	Displays	♂	b	Displays	Fights
				♂ ♀	n	Flee	Ignores
				♀	b	Stays	Copulate
Stickleback (Ter Pelkwyk and Tinbergen)	♂	b	Displays	♂	b	Displays	Fights
				♂ ♀	n	Flee	Ignores
				♀	b	Stays, special movements	Pair formed
Phalarope (Tinbergen)	♀	b	Displays	♀	b	Displays	Attacks
				o.s.		Stay	Ignores
				♂	b	Rustles wings	Pair formed
Snow Bunting (Tinbergen)	♂	b	Threatens	♂	b	Displays	Fights
				♂ ♀ o.s.	n	Flee	Ignores
				♀	b	Stays	Courtship display
Rooster (Domm and Davis)	♂	b	Waltzes	♂	b	Raises hackle	Fights
				♂ ♀	n	Flee	Pursues or ignores
				♀	b	Squats	Copulate
Pigeon (Craig)	♂	b	Displays	♂	b	Displays	Fights
				♂ ♀	n	Flee	Ignores
				♀	b	Stays, bows	Courts, drives
Song Sparrow	♂	b	Threatens (flies at)	♂	b	Displays	Fights
				♂ ♀ o.s.	n	Flee	Ignores
				♀	b	Stays, trills	Courts, pounces

In all these the fundamental pattern is the same. One animal—usually the male—***proclaims its sex and status;*** according to the reponse to its display, it then reacts to the newcomer as to a rival, an indifferent object or a potential mate. As Craig (1908:92) points out, "Each dove must, by its behavior, proclaim its own sex and induce other birds to proclaim theirs."

The table gives examples from 2 phyla, and 2 classes of one phylum (vertebrates) and 4 orders of one class (birds). It is extremely interesting to find this pattern occurring widely in vertebrates and even in an invertebrate. Craig (1921:274) says of Pigeons: "When a male meets a stranger belonging to his own species, provided this male has not learned by experience to discriminate the sexes, the only discrimination he shows is this: if the stranger fights, the agent treats it as a male; if the stranger refuses to fight, the agent treats it as a female. . . . Behavior of this sort is now known to be characteristic of a great many animals ranging all the way from the lower invertebrates to the Primates."

It is unexpected to find the domestic fowl in this category. Domm and Davis (1941), however, report, "The sex of a newcomer is determined by behavior. The rooster 'waltzes' . . . thereby inducing the newcomer to either squat or raise the neck hackle feathers. When a bird is introduced to a rooster, he at once pursues, seeking to determine its sex. If it is a receptive female, she squats for copulation. If, on the other hand, it is a male, it raises the neck hackle and thereupon begins a fight which settles its social rank in the group."

The actor's signals are his display: his evident possession of a territory in many cases, his song, bright colors, and special gestures. These serve as a warning to other members of the same sex and an invitation to a mate. The reactor, according to its sex or condition, shows its signals—challenge, avoidance, or approach. The challenge may be the same as that of the actor (cuttlefish, stickleback) or somewhat different (Song Sparrow, Snow Bunting, rooster). The potential mate usually has special signals—notes and postures in the Song Sparrow, movements in the stickleback, "bowing and showing herself off" in the Pigeon (Whitman 1919:28).

The male Song Sparrow on his territory probably gives the same first reaction to any new bird somewhat the size of a Song Sparrow: he flies at it. A male seeking territory puffs, sings and waves; transient Song Sparrows and most other birds leave, while a potential mate stays and trills and chatters. If she does this the moment she arrives, it may be that the male reacts to her at once as to a female (see example 2 in Appendix III); if so, his behavior would come under Tinbergen's first class where sex is discriminated immediately.

When a female Mockingbird joins a territory-holding male, both give a "peculiar rasping sound", the male pursues the female, sings softly, picks up twigs and runs "with head down, tail and wings spread" to possible nesting sites, giving a low *cluk-cluk* (Laskey 1933:31).

An interesting example of differential behavior to adult males and undifferentiated behavior to like-plumaged females and immature males is given by the Magnificent Bird of Paradise: the full plumaged male prepares a display grounds and calls loudly from its edge; when a bird in female plumage arrives, the male gives a "preliminary display", and if the visitor does not leave, he goes into the "horizontal display", upon which a female approached and copulation ensued, but an immature male attacked him and flew away. A mounted adult male, on the other hand, was attacked at once by the owner of the court (Rand 1940).

Still a third type shows a much longer identical reaction.

In the Common Tern "males and females both show exactly the same display during the first phase of their courtship, which may last for days, and this absence of a difference in behavior, together with the absence of morphological differences, probably makes it impossible for the birds to distinguish between the sexes" (Tinbergen 1939c:51). By collecting Gentoo Penguins, Roberts discovered that "*in the early stages* the initiative in courtship may be taken by birds of either sex. The behaviour of an individual bird gives no indication of its sex, for the activities are interchangeable" (1940b:203). Later only males were seen offering nest material. "The British Robin (*Erithacus rubecula*) has a long period of identical reaction of the sexes, so comes in the third group" (Lack 1940e:278).[1]

As to species that pair in flocks, Lack (1940e:279) suggests that, "the members of a pair gradually come together, using many small interrelated mutual actions, with intervals when they move apart again. I think it will prove exceptional to find pair-formation depending on a simple dominance mechanism or set of releasers."

In the Herring Gull the male of each pair was found to be larger than its mate (Goethe 1937a), and the same was true with the Yellow-eyed Penguin (Richdale 1941a), although there was much overlap in both populations. Although male Song Sparrows are normally larger than their mates, this is not invariably so.

In 166 matings involving 103 males and 111 females, the wing measurements of all the birds are known. Forty per cent (55) of the males had larger wings than any female, and 32 per cent (41) of the females had smaller measurements than any male. The wing measurement of the 14 largest males ranged between 68 and 70 mm., averaging 68.4; that of their 20 mates ranged between 60 and 64 mm., averaging 62.1. The wing measurement of the 14 smallest males ranged between 62 and 64 mm., averaging 63.6; that of their 23 mates between 60 and 65, averaging 62 mm. Four of these last females were larger than their mates, and this was true in one other pair. 4M, whose wing measured 67 mm. had 8 mates in which almost the whole gamut of female sizes was shown—from 58 to 65 mm.

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[1] In his "Life of the Robin" (1943 London) Lack has revised this opinion: "the hen in search of a mate persistently flies right up to the cock and does not retreat when he postures," p. 64; hence this species comes into Tinbergen's second group.

There was no tendency whatever for assorted matings according to size. This is natural, since Song Sparrows have plenty of differential behavior patterns for sex recognition.

Tinbergen's 3 groups may be summarized: (1) species with marked dimorphism that discriminate the sexes at the first reaction; (2) species with little or no dimorphism where the more active sex proclaims its sex and induces the other to do the same; (3) species where the process of sex recognition may be prolonged.

How do these types compare with Lorenz's categories? The second type agrees in some respects with the labyrinth fish type—display by male, and differential display by female; and the third type with the cichlid in which display is made by both. Tinbergen's first type does not, however, necessarily agree with the lizard type; probably it would come into the labyrinth fish class where Lorenz places dimorphic birds; in the cichlid type the sexes are nearly the same size and nearly the same color (1940:279). However, birds of the labyrinth fish type are sexually ambivalent, and Lorenz knows of only one case in which male homosexual pairs have been formed in strongly dimorphic species. I had considered Song Sparrows as belonging to the labyrinth fish type, but they are sexually ambivalent to only a small degree and the female is more or less dominant; perhaps they belong to the cichlid type, which, according to Tinbergen, includes forms in which the display of the sexes may be similar or very different.

In conclusion, it seems to me that Lorenz's classification is confusing, for he includes too many characteristics under a few heads. Tinbergen's types give a better basis to work upon. It is clear that we need many more detailed studies of pair formation—intimate studies of marked birds from the first moment of their meeting.

E. Personal Recognition of the Mate

Undoubtedly a great many birds recognize their mates personally by visual and/or auditory cues. Heinroth showed that Swans recognize each other by the face (1912a), and Noble found the same for the Flicker (1936) and also the jewel fish (Noble and Curtis 1939:22). Lorenz (1935:312) says that the features of the head play the most important role and after these the voice; Jackdaws came out of their nesting holes when they heard their mates' voices, but ignored those of neighbors. When Schjelderup-Ebbe (1923a) fastened hens' combs on the wrong side of the head, the birds were treated as strangers by the flock. The Heinroths once exchanged clothes in an attempt to deceive the Pheasant that courted Herr Heinroth and fought Frau Heinroth; the bird started to attack the dress, stopped, looked up at the faces, then flew at Frau Heinroth. Frau Heinroth and her sister changed clothes, but the Pheasant still knew his supposed enemy (1924-1933, III). A pair of American Robins whose young were subjected to daily weighings, greeted the experimenter with loud outcries no matter what was her costume, but ignored all other people (C. Nice 1941).

When banded birds were dyed—we are not told on what portion of the body—other individuals "took no notice of the strange appearance of the colored bird" (Butts 1927:336). Ring Doves, dyed on the breast, produced in most cases a marked reaction in their companions who first seemed frightened, then courted them, i.e., treated them as strangers (Bennett 1939). Watson found that coloring on the head brought forth a much stronger response than coloring on the neck (1908:220).

One Noddy Tern dyed red on the black neck feathers returned to its nest to incubate; its mate sat near the nest, pecked at it, then both nodded. After 40 minutes the mate crawled on the egg. A second Noddy was dyed red on its white head and eye-spaces; it was *3 hours* before its mate would take the egg. "Both the noddies and sooties in the vicinity of this nest were badly frightened by this bird." Two Sooty Terns were marked on the throat, breast, and spaces between the eyes, one with burnt sienna, the other with blue. Neighbors and mates were greatly disturbed, attacking and fighting the marked birds. Even a visiting Noddy showed a marked response. The birds were finally accepted by their mates "by reason of their persistance in their normal activities in the region of their nests. The 'recognition' through the interrelation of habits overcomes the disturbance produced by the changed visual situation" (Lashley 1915:79).

Herring Gulls were disturbed when their young were dyed, especially when the color was on the head (Goethe 1937a:87).

Kirkman, Goethe and Tinbergen mention the surprising distances at which Gulls recognize returning mates, sometimes by sight, sometimes by voice. Song Sparrow females certainly know their mates' songs in one season, but do they remember them from one year to the next? If so, a bird that joins a next-door neighbor will have to learn to disregard the songs of her former mate, in case he still survives.

How long do birds remember individuals? Schjelderup-Ebbe (1923a:80) says that hens have an excellent memory for places, recognizing an old home after several years, but that if a hen or rooster is absent 2 weeks and then returned, it will be regarded as a stranger. Mr. Nicholas Collias tells me that memory depends partly on the length of time fowl have been acquainted; they remember each other from a week to a month. White-throated Sparrows remembered each other after intervals of 11 and 17 days (Wessel and Leigh 1941), Black-crowned Night Herons for 22 days (Noble et al., 1938). As to Pigeons, 2 sisters that had formed a homosexual union were separated; they clearly remembered each other after 9 days, but after 26 days one seemed to do so, while the other did not (Whitman 1919: 115). Parrots have long memories for individuals. Jackdaws recognize members of the colony after many months of absence.

F. PROMISCUOUS TENDENCIES IN MONOGAMOUS SPECIES

For a great many species that are normally monogamous occasional cases of bigamy are reported (see Sunkel 1926, Verwey 1930, Portielje 1936, Tinbergen 1939c); these involve Hawks, Swans and many passerines.

At times there is antagonism between females, as reported for Montagu's Harrier (Dent 1939), Starlings (Freitag 1936, 1937), Long-billed Marsh Wren (Welter 1935), European Blackbird (Kochs 1935), and Nuttall [White-crowned] Sparrow (Blanchard 1936, 1941). Often, however, this is not true. Sometimes two females use the same nest—White Stork (Ringleben 1936); Red-breasted Merganser 2 years in succession (Ringleben 1936); European Sparrow Hawk (Hughes-Onslow 1925); Pied Flycatcher (Pollkläsener 1936); Whinchat (Wilcox 1920); House Sparrow (Pearse 1940); House Finch (Michener 1925); Cardinal (personal communication from W. A. Matheny). Occasionally the two mates nest side by side or very near each other—Swans (Portielje 1936, Ringleben 1936, Dewar 1936); American Robin (Brooks 1932).

There is not much information as to how these triangles come about. With Starlings and Wrens of some species, the male may start to guard a new nesting site and in this way get a new mate. Twice with the Song Sparrow it came about through a neighbor female having lost her mate while incubating. With the Nuttall Sparrow 2 females " lost their mates before the start of laying. . . . Each stayed on her own area and subsequently mated with a neighbor which already had one mate" (Blanchard 1941:19). One female whose mate spent most of his time with his new mate, joined her neighbor; her former mate came and twice fed her young. A potential case of polygamy turned into a divorce; a "male became so interested in a neighboring widowed female that a bereft male was able to carry off his mate" (1941:37).

In the 2 cases where I was able to follow the history of nesting where a Song Sparrow male had 2 mates at one time, success was small (see Nice 1937:88-89).

G. SEX RECOGNITION AT COPULATION

Sex recognition at copulation is a different matter from pair formation. "The major stimulus in most species is simply that the female keeps still" (Lack 1940e:280).

Many males have been reported as attempting copulation with mounted specimens of their own or other species: Blackcock (Lack 1939a), Golden Pheasant (Noble and Vogt 1935), Ruffed Grouse, House Wren, Yellow-breasted Chat (Allen 1934), Cowbird (Friedman 1929), European Robin (the Heinroths 1924), Red-winged Blackbird, Northern Yellow-throat (Noble and Vogt 1935), Gould's Manakin (Chapman 1935) and others.

Yearling Red-winged Blackbirds in Noble's and Vogt's experiments copulated with a wide variety of species, both dull and brightly colored, including male Cardinals and Blue Jays, but 2 year-old males as a rule responded only to females of their own species. It is a question as to whether this greater discrimination of the older birds was due to learning or maturation.

Some birds, however, are not sexually stimulated by a mount—Gentoo Penguin (Roberts 1940b), Black-crowned Night Heron (Allen and Mangels 1940), Common Tern (Noble and Vogt), Flicker (Noble 1936), Magnificent Bird of Paradise (Rand 1940:14), Song Sparrow (Chapter XII, also Noble 1936, Allen 1934). With the Flicker and Song Sparrow special notes are necessary before a bird will have the meaning of a female.

Dr. Lorenz told me that only pure-bred Mallard ducks are pursued by Mallard drakes and forcibly copulated with, although hybrid Mallard ducks were as attractive as mates to the drakes as were the pure bred birds. The pattern that releases copulation is different from that bringing about pair formation.

H. Do Birds Discriminate Sex?

"Birds are not sex conscious," writes A. A. Allen (1934:198) on the basis of his observations on captive Ruffed Grouse, "that is, they do not discriminate between the sexes as such. Courtship displays, including song, are one form of intimidation."

Concluding from their series of experiments with mounted birds, Noble and Vogt (1935:286) state in regard to the Red-winged Blackbird and Northern Yellow-throat, "These highly dimorphic birds are therefore sex conscious at this season in that they respond differentially to sex when only visual cues are available to them."

Lack (1940e:279) says: "In the British Robin (Lack, 1939) one cannot speak of sex recognition at any stage of the breeding cycle. In pair-formation, the unmated male treats intruding males and mated females alike, but reacts differently to an unmated female. How he differentiates an unmated from a mated female is unknown, but since pair-formation takes some time, discrimination is evidently difficult. . . . In other small passerine species, for example the Song Sparrow, *Melospiza melodia* (Nice 1938), the male reacts similarly to all strange females, whether mated or unmated, hence the problem here is genuinely one of sex discrimination, which in the Song Sparrow where the sexes are alike in plumage, depends primarily on a special call of the female. In other species, for example the chaffinch, *Fringilla coelebs* (Lack, Ms), it depends on plumage difference."

With the Gentoo Penguins, at first both sexes offer nest material, later only males do so (Roberts 1940b:209). "It seems probable that the birds had not learned to distinguish the sexes as such, but that the birds of a pair, originally established by trial and error, had come to recognize each other personally."

Tinbergen (1939c:83) points out that: "The recognition marks that enable the bird to discriminate between the sexes . . . need not necessarily be morphological structures, even in species that show morphological sexual dimorphism, as in the Ruffed Grouse, where different behavior of male and female enables sex discrimination. Allen's conclusion, based on this species, that birds do not discriminate between the sexes, is therefore rejected."

I. SUMMARY

1. With some birds the recognition of possible mates is an inherited matter, with others the mating preference is acquired.

2. Lorenz describes 3 types of pair formation in birds: lizard, labyrinth fish and cichlid fish. This scheme has been criticized by Noble, Tinbergen and Lack.

3. Noble suggests that "in some fish, as in birds in general, sex recognition depends on the grosser movements of response to the gesturing of the territory-guarding male."

4. In many species some of the characteristics of the opposite sex are latent. It has been suggested that the "neutral type in birds" is nearer the male than the female.

5. Social dominance can be measured, but sexual dominance remains a matter of interpretation. With some birds social dominance may play a part in pair formation, but afterwards there is no dominance. Instead of saying the male dominates the female by pouncing, pecking, or driving her, we can consider these activities the male's signals that he is ready for pair formation or copulation, etc.; the female signals by posturing, trilling, etc.

6. Tinbergen suggests 3 types of pair formation: (1) species with marked sexual dimorphism that discriminate the sexes at the first reaction; (2) species with little or no dimorphism where the more active sex proclaims its sex and induces the other to do the same; (3) species where the process of sex recognition may be prolonged.

7. Table XXII illustrates the second of these methods of sex recognition in a mollusk, a fish and 5 birds of 4 orders.

8. Mates may be recognized personally by voice or appearance, particularly by characters of the head and face.

9. Hens remember individuals for a week to a month; Parrots and Jackdaws have much longer memories.

10. In many normally monogamous species occasional instances of bigamy are reported.

11. Males of some species will copulate with mounted specimens, but others require more signals than quiescence if a bird is to have the meaning of a female.

12. Many birds respond differentially to the sexes, hence may be said to discriminate the sexes.

CHAPTER XVII

The Nest

When the female Song Sparrow starts to build the nest, the male begins to sing again. Often the awakening song reappears the same day that the nest is begun, but at other times it comes a day or two later. During the day the male may or may not sing a great deal. Flight songs are fairly frequent during the building of the first nest. There is much pouncing, and copulation is frequent, particularly while the female is carrying nesting material.

A. Choosing the Site

The Song Sparrow pair goes about together searching for nest sites, twitching their wings and giving soft notes. Undoubtedly the female tries out possible situations by nest molding, and perhaps the male does likewise. Since young males may nest-mold when 2 to 4 months old, it may well be that the adult male does it when assisting his mate in the choice of a nest site.

That the male often has influence in this choice seems probable to me from the history of the nest sites of a number of males, that had different mates each year. It must be remembered that every territory appeared to me to afford a multitude of nesting sites.

1M and 23M kept much the same territories for 3 years. With 1M 3 sites were favored, 2 being chosen 2 years in succession and one 3 years. These nests were never in exactly the same spot, but were placed within a radius of 3 meters or less. The record for 23M is less complete, only 6 nests having been found; the first nests in 1930 and 1932 were in approximately the same spots, and the same was true of the second nests in these years. 4M nested in the west half of our garden from 1928 through 1931, shifted further west from 1932 to 1934, and returned to his old territory in 1935. Three locations were known to have been chosen twice: for the first nests in 1929 and 1931, the third nest in 1930 and 1935, the fourth in 1930 and second in 1935. 50M's first nests in 1931 and 1932 were in an unusual place, a meter above the ground in the vine on our porch; in 1933 the vine was not used. See also the account below of Schantz's nest-building male.

Although in these cases the male seems to have had considerable influence in the choice of sites, this certainly was not the case when K2 followed one of her young into 4M's land and built her fourth nest there; for a while 4M's vigilance was relaxed and 1M and K2 had gone "nest-hunting" in the hedge where she later built her nest.

There appear to be 2 chief requisites for a nest site for a Song Sparrow—secure support and concealment. Since nesting starts in April, normally the only situations on Interpont offering these characteristics are on the ground; here under tufts of grass, weed stalks or thistles, and often in a natural depression, nine-tenths of the nests of the first attempt have been situated. The Song Sparrow, however is not "bound to the ground" as is the Vesper Sparrow or a Lark; when security of foundation and concealment are afforded in bushes, small evergreens, vines or piles of flood debris, it readily nests up to a meter or a meter and a half above the ground. A female Puget Sound Sparrow showed even greater contrast between the sites of her first and second nest—on the ground and 9 meters above (Blanchard 1941:46).

In my experience a later nest was never placed lower than an earlier one. It was also always placed at some distance from the first, in 44 cases ranging from 9 to 50 meters, and averaging about 23 meters. In some cases where a territory possesses one outstandingly attractive nesting site, Song Sparrows have been reported as using the *same nest* twice in a season (3 cases of Eastern Song Sparrows, Nice 1937:93), while a pair in northeastern Columbus *raised 4 broods in one season in the same nest* (Schantz 1937).

B. BUILDING THE NEST

On Interpont the female Song Sparrow always built the nest alone. In only one case (4M on Apr. 30, 1935) did I ever see a male even picking up and dropping material after his mate had started to build the nest. He never accompanies her on her trips for materials, but usually sits watching her as she gathers it and takes it to the nest.

Nest building typically takes place early in the morning and as a rule is carried on quietly and secretively, although K2 in building her first nest in 1929 was demonstrative, as was K150 in 1933, who answered each one of her mate's songs with a trill or chatter as she worked. K2's periods of attention and inattention during 9 hours of observation Apr. 6-8 corresponded well with those of incubation—15, 20, 23 minutes of work, interrupted by absences of 5, 7 and 8 minutes. During periods of attention she brought a load every 2.3 minutes on the first 2 mornings, but averaged one in 5.8 minutes on the third morning.

K200 in 1935 was far more deliberate. If we compare 4 hours on the first 2 days of building with both pairs we find that on Apr. 6 and 7, 1929, 1M pounced 4 times and copulated with his mate 8 times; K2 brought 54 loads, trilled 45 times and chattered 23 times. On Apr. 20 and 21, 1935, 4M pounced and copulated with his mate 10 times; K200 carried 18 loads, trilled 10 times and chattered 5.

The nest is usually pretty well completed in 2 days and lined on the third and perhaps the fourth. A nest may be started from 3 to 13 days before the first egg is laid; 5 days are probably more typical, corresponding to the length of time it takes for the development of an egg (Nice 1937:111). The start of nest building in the Song

Sparrow roughly corresponds with the beginning of rapid growth of the ovum (Riddle 1911) which normally begins 5 days before the egg is laid. In Chapter XI of Volume I (Nice 1937) charts and tables are given illustrating the start of laying in relation to temperature. Chart XIV gives data on temperatures 5-7 days before the laying of the first egg and before the start of general laying; these dates correspond well to the start of building. Nest building at the beginning of the season is stimulated by high temperatures and inhibited by low ones.

An interesting case of "A Nest-building Male Song Sparrow" is given by Schantz (1937); this bird lived as a bachelor from the spring of 1933 to the summer of 1934 in northeastern Columbus, spending much of his time in a small red cedar where "he began a nest. When it was half completed, he ceased building and roosted on it during the remainder of the year. . . . During the next spring he built an excellent nest a few inches higher in the same cedar, but still no mate came to it." In mid-summer he obtained a mate and nested "a half square to the north. . . . Very early in the spring of 1935, he began a third nest several inches above the last one. Soon a mate came, and they moved to a neighbor's yard where they both built a nest in a brush-pile. This was hauled away after the eggs had been incubated for two days, whereupon the birds returned to the cedar and completed the first nest. *In it they raised four broods,* relining it three times." The male roosted in the cedar all winter, and the next spring he and a new mate built another nest in it.

This male was exceptional, in building 2 incomplete nests and one complete one by himself and also in helping his mates build 3 nests. One element in the case seems to have been his strong attachment to the cedar in which he roosted much of the year; this tree offered favorable nesting sites, and his latent nest-building ability, appearing in most male Song Sparrows in the symbolic manipulation of material, developed through practice when he was mateless in 1933 and 1934. He was a zealous singer. In 1936 he suffered from a despotic mate, as described in Chapter XVI.

From my experience with banded females on Interpont, of some of which I knew the exact age, and many of which were present several years in succession, I came to the conclusion that a Song Sparrow builds her first nest as quickly and expertly as she does her last, and that there was no evidence of improvement in building more secure nests, nor in concealing them more effectively. Nor was there evidence of some birds consistently surpassing others in these 2 prime requisites in nest building.

With birds that build very elaborate nests there is some evidence of improvement with age, as in Baltimore Orioles (Williams 1934) and Oropendolas (Chapman 1928). With Tree Swallows, nests of immature females were less fully lined with feathers than those of older birds (Kuerzi 1941:19). Whether this facilitation comes through learning or maturation is undetermined; Lorenz (1932:65) is inclined to the latter view.

Other aspects of nest building of the Song Sparrow—structure, weight, position, security, time spent at the nest in building, and building of old and young—are discussed in Chapter X of Volume I (Nice 1937).

C. Nest Building in General

A bird's nest may range from a mere *place* to a hanging cradle or an oven constructed of mud.

> "There would seem to be a vast difference between digging a hole in warm, moist sand, as we see a turtle or a maleo doing," writes Herrick (1935:137), "and the weaving through the unremitted effort of many days of a beautiful pouch like the oriole's, so admirably adapted through its form and position for protecting the young and adult birds; but if the essence of nest-building is providing for the off-spring in the sense of affording them protection, the fundamental building instinct is not wanting in reptile or megapode.
>
> "Nest-building of one kind or another is found in all classes of vertebrates, and the guarding and fighting propensities at breeding-time are as strong in some of the fishes as in the birds; but though the practice is clearly of ancient origin, it is by no means universal. In every case it seems to be related to the needs of the animal and its young and to be a refinement of the more simple means of securing protection through concealment, as seen in many reptiles."

1. *Methods of Protection*

Adult birds protect themselves by escape, concealment, threat, and attack. Eggs and young must be protected in situ by concealment, inaccessibility, proximity to powerful neighbors, and by cryptic behavior of the adults, while later threat, deflection and attack may play a role. The first 4 methods will be very briefly considered here, the last 3 will be discussed in Chapter XX.

A certain amount of safety may be ensured through instinctive choice of nest site and through instinctive modes of nest-building.

Inaccessibility of nest-site is clearly attained on islands, on or in cliffs, on ends of branches, in thorny growths, etc. Defense through neighbors may be effected in various ways; through their own species for Terns, Gulls, Willets, Avocets, etc.; for Tufted and Eider Ducks on Finnish Islands through Terns and Gulls (Fabricius 1938, Hartman 1938); for Geese from foxes, large Gulls and Ravens through Snowy Owls and Peregrine Falcons (Grote 1938); for Warblers, Vireos and Tanagers from Jays and squirrels through Coues' Flycatcher (Howard 1904); for various passerines through wasps and stinging ants in Africa and South America (Myers 1929, 1935, Beebe 1910, Moreau 1942b), for Grackles, House Sparrows, etc., through large Hawks; for many birds through human beings.

As to the construction of the nest, inaccessibility may be effected in many ways: excavations in banks and trees, woven nests with small openings, mud nests with small openings, thorny twigs for nesting material, etc. Concealment is evident in nests that are arched over, well hidden in cover, etc. Camouflage plays a part in nests such as those of the Hummingbirds and Gnatcatchers (although several of the Blue-gray Gnatcatcher found in Oklahoma failed to harmonize, Nice 1932b).

Cryptic behavior of adults is evident in the instinctive stillness near the nest, and the refusal to approach the nest in the presence of an enemy. Protectively colored females are hard to flush from their nests (Woodcock, Bustards, Nightjars, Short-eared Owls), except in a few cases where the eggs themselves are protected by cryptic coloration.

> "There is among birds a striking general coincidence between highly specialized cryptic resemblance and highly developed crouching instincts, both on the nest and at other times, the birds which allow the closest approach of an intruder being usually those which are best concealed by their coloration. This relation between appearance and activity reaches its zenith in many widely unrelated kinds of birds (and indeed in many groups of animals besides birds), in every type of environment, and in each of the five continents—whether the resemblance is to stone or sand, to the patterns of tangled grasses or of fallen foliage, to the trunks of trees or the stems of reeds; whether it occurs in the barren tundras of Siberia or the fertile forests of Guiana; whether it relates to the orders Passeres, Ciconiiformes, Galliformes, Anseriformes, Gruiformes, Charadriiformes, Psittaciformes, Strigiformes, or Caprimulgiformes. It was one which was sufficiently general to lead Beebe [1917] to base his estimate of the colour-status of forest species in British Guiana on the actions of the birds themselves at the approach of danger. He says: 'A bird which flew at once, either to a point of vantage where it could see clearly about it, or flying on out of sight was plain evidence of lack of protective coloring, at least in its own estimation. If it squatted or "froze" either for a moment or until we had crept up to within a few feet, I felt that it unconsciously, but surely, counted upon being overlooked, or confused with its surroundings'" (Cott 1940:131-132).

2. *Nest Building*

There is great variation in the part played by the sexes, as pointed out by Stresemann (1927-34:343) in his review of the subject in which examples are given from all over the world. In some the male pays no attention whatever; in some he accompanies his mate on her trips (Snow Bunting, Chaffinch, Titmice, European Nuthatch); in some cases he brings the material to his mate who arranges it (Doves, Penguins, Grey Heron, Little Gull), while in others he builds the foundation and perhaps the outside of the nest while his mate puts in the lining (some Old World Warblers, some Wrens, Penduline Tit, some Weaver-birds, the Crimson-crowned Bishop-bird), or occasionally makes the whole nest (Baya and other Weavers).

The more elaborate the nest is, according to Stresemann, the more apt it is to be relegated to one sex. Anseres never carry material to the nest site, merely molding what they find in place.

There is little information on the subject of searching for a nest site. Craig describes the behavior of the pair of Ring-doves (1909) and Mourning Doves (1911)—the trial of suitable spots, the special postures and nest-calls (Nice 1931c). With the Corn Bunting, "The hen usually spends some hours in site-selection and is closely accompanied by the male, which frequently perches near her and indulges in vigorous bursts of song, scoldings and wing-quiverings" (Ryves 1934a). Willet pairs hunt for nest sites together or separately; on May 3 Vogt (1938:32) noted of one male "that it seemed he could scarcely go near a tuft of grass without exploring its possibilities." Observations have been made on nest-site hunting by the American Robin (Meuli 1935), European Goldfinch (Geyr 1939), and Northern Phalarope (Tinbergen 1935).

Bringing of nesting material often stops with the laying of the first eggs, but sometimes that is not true. Snow Buntings finish the lining after the first egg is laid (Tinbergen 1939c:32) and so do Black-capped Chickadees (Odum 1941b), Crimson-crowned Bishop-birds (Lack 1935), young Tree Swallows (Kuerzi). With Cormorants, Gallinules, Herons and Falconiformes material may be brought throughout nest life; with some of the Falconiformes—Eagles, Goshawks, Mississippi Kite and others—green twigs are brought.

With the Black-headed Gull bringing material after the eggs are laid is usually a "substitute reaction" when the mate refuses to leave the nest. "It may be said with some truth that the size of a Black-headed Gull's nest is largely determined by the number of times it is prevented from sitting on its eggs" (Kirkman 1937:78). One of the Gulls—a female in immature plumage—showed an over-development of the nest-material carrying instinct, building up a large pile of stuff at the site of the nest; "the only purpose it answered was to supply a convenient store of nest material that neighboring gulls could plunder with less risk than the nest proper," p. 78. Over-exuberance in the use of nesting material—an abundant supply of colored yarns—has been reported for the Baltimore Oriole, Kingbird, Cedar Waxwing and Robin (Williams 1934), Least Flycatcher and Robin (Herrick 1935:251).

Herrick discusses the question as to "why the birds react so strongly to such artificial materials and why they use so much more of them than they need. . . . I can only suggest that in instincts as important as those concerned with the making of nests, some of the elements are possibly at times greatly overstressed" (1935:253-254). It may be that a bird has a certain amount of energy that normally goes into building its nest; if part of its work is greatly lightened—in this case the procuring of materials—the normal amount of energy expended results in a much larger mass of material than would occur under natural conditions. With some species the nest building impulse is so strong in the males that they construct "dummy nests", as in the Long-billed Marsh Wren and European Wren. With the House Wren this behavior would seem to be a method of claiming all possible nesting sites within or near the territory.

Few detailed studies have been made on the process of nest building. Herrick (1911, 1935) has done the most work on the subject, describing particularly the technique of the American Robin, Red-eyed Vireo and Baltimore Oriole. After discussing the different materials used by the Robin in different regions he suggests that birds inherit *"definite ways of working, with a predisposition to draw from their environment any available materials suited to their methods and style"* (1939:248). Lorenz (1932) discusses instinct and learning in nest building, stating that at first his Ravens and Jackdaws picked up and flew with all kinds of objects, but that young Storks and Night Herons recognized the proper materials from the first.

In reviewing this subject, Laven (1940a) points out that the starting point of study should not be the nest itself, but the bird, how specifically it behaves under greatly differing environmental conditions and how wide individual variations and skill show themselves to be.

With the Tricolored Red-wing, Emlen (1941) found that the nest-building period could not be artificially lengthened or shortened; the introduction of eggs or young into a partially built nest did not call forth incubating nor feeding behavior, nor were eggs laid any sooner than usual if a complete nest was substituted for an incomplete one. When the lining was removed, no new material was added. When "nest construction was interrupted or delayed by natural factors the birds commenced laying without regard to the incompleteness of their nests."

D. THE MEANING OF THE NEST

Since birds lay eggs that have to stay in one place, and these may hatch into young that also cannot leave for a while, the attention of the parent or parents is focussed for some time on one spot. That the nest site becomes "an area of great emotional valency" is emphasized by Roberts for the Gentoo Penguin (1940b:201). It may be defended before a piece of material has been brought, as pointed out for the Black-winged Stilt (Yeates 1941), Arctic Skua or Parasitic Jaeger (Jourdain 1936-37), Pigeon (Whitman 1919), Raven (Lorenz 1940), Brown Thrasher (Sherman 1912) and Nuttall Sparrow (Blanchard 1936). Copulation takes place on the nest with many species—Penguins, Herons, Storks, Gallinules, Bayas, sometimes American Robin and others.

As to recognition of the nest, Lashley (1915) writes in regard to the Sooty Tern: "Individual characters of the nest and egg do not play any important part in orientation. The birds react positively to any nest at the chosen site." They are "very greatly disturbed by a lateral displacement of only a few inches", and "adjustment to changes in the height of the nest is not made any more readily than to changes in the horizontal position." If the position of a Ring Dove's nest is moved, the birds fail to recognize it (Whitman 1919:160). Meise (1933) moved the nest of a House Sparrow with small young a short distance, and although the bird must have seen the nest-box, yet he did not go to it, but fluttered around the former site; the author considers this evidence of the importance of kinesthetic memory in nest-location among colony breeders.

According to Kirkman, "a nest is any receptacle for its eggs into which an animal has put work. Thus the patch of rock on which the Guillemot (*Uria troille* [L.]) lays its eggs is not a nest; a scrape in the soil is, even though it remains devoid of lining" (1937:71).

The attachment to the nest site and the nest may become so great as to overshadow the attachment to mate, eggs or young. In regard to the White Stork, Schüz (1936:102) writes, "one often has the impression that it is first the nest that is defended and second the mate." With Black-crowned Night Herons "the nest is of great importance as a bond between the members of the pair . . . the nest or nest site exerts a far stronger influence on the birds than does the contents" (Allen and Mangels 1940:21). A heron sat on wooden blocks in its own nest rather than on its eggs in an artificial nest next to it. Noble and Lehrman (1940:37) make the interesting suggestion that, "In both Herring Gull and passerine bird, the extensive work which has gone into the nest construction seems to take the attention of the bird away from the biologically more significant object." (See the account of the Linnet and her nest in Chapter XIX.)

The nest may still retain much of its meaning after the young have left. A Black-throated Green Warbler female flew about protesting when the observer climbed the hemlock to inspect the nest from which the last young had left 10 minutes before (the Nices

1932). 1M and K2 drove off a Cowbird from their first nest which they had deserted that morning because of disturbance to its contents. "After the young have left the nest the male [Flicker] may still defend the nesting hole" (Noble 1936). The emotional valency of the nest site is shown by the fact that it was defended by a pair of Herring Gulls even when the young were not there (Portielje 1928).

E. SUMMARY

1. Male and female Song Sparrow both have influence in choosing the nest site.

2. Building is normally by the female Song Sparrow, but in one case a male built.

3. There was no evidence that the Song Sparrows benefited from experience in making their nests more secure, nor in concealing them more thoroughly. Yet with some birds that build elaborate nests, there is some evidence of facilitation with age either through learning or maturation.

4. The function of a nest is protection of the eggs and young. This may be furthered through instinctive choice of inaccessible nest-sites, or of sites near powerful neighbors. In nest-construction inaccessibility and concealment may play a part. Cryptic behavior of the parents is an instinctive response of many birds in reference to the nest.

5. There is great variation in the part played by the sexes in nest-construction.

6. Bringing of material may stop after the eggs are laid, or it may last through nest life. Sometimes it is indulged in to an extravagant degree.

7. The nest-site becomes an "area of great emotional valency", and the attachment to the nest-site or nest may become so great as to overshadow the attachment to the mate, eggs, or young.

CHAPTER XVIII

The Eggs

In Volume I, 3 chapters are devoted to the subject of eggs: The Start of Laying, The Eggs of the Song Sparrow, and Incubation. In the present chapter the incubation pattern of the Song Sparrow will be briefly touched upon and comparisons made with other species. The recognition of eggs by the parents will also be discussed.

A. Egg Laying

This is Stage V in the Song Sparrow nesting cycle. The eggs are laid, one each day, early in the morning. The male sings much, copulation is frequent, but pouncing has practically disappeared. Incubation usually starts the day before the last egg is laid.

B. Incubation

There is a close bond between the Song Sparrow pair, but their roles are sharply differentiated during Stage VI.

1. *The Part of the Female*

As with the majority of the Fringillidae the female alone incubates. (The males of the Rose-breasted Grosbeak, White-throated Sparrow [Snyder and Lozier 1930] and Reed Bunting [Haverschmidt 1937] sometimes incubate.[1]) She stays on the nest from 20 to 30 minutes and off the nest from 6 to 9 minutes, this rhythm being correlated with hunger. The total number of periods off the nest *per day* varied from 14 to 39, while the total percentage of daylight hours spent on the nest ranged between 70 and 80 (see Chapter XII, Nice 1937). She trills to answer her mate, but the chatter is not heard. In 3 cases eggs that were slightly injured were removed by the bird. When off the nest, she often drives away birds of other species. Incubation usually lasts 12 to 13 days.

2. *The Part of the Male*

The male guards the territory. He sings a great deal, giving the awakening song regularly and occupying himself with song while his mate is on the nest. Pouncing and copulation are almost never seen. He keeps in close touch with his mate, calling her off the nest many times a day with a "signal song", i.e., after a period of foraging in the grass he flies to a perch usually within 6 meters of the nest and gives one or more songs suddenly and loudly. His mate often comes off the nest at once, but sometimes she trills and remains.

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[1] For an excellent discussion of behavior involved when males are very exceptionally found on eggs see B. H. Ryves 1943 An Investigation into the Role of Males in Relation to Incubation. Brit. Birds. 37:10-16.

In 30 hours of K2's first incubation two-thirds of her departures from the nest were in answer to 1M's signal songs. 1M gave no signal song to his mate during 2 storms that each lasted an hour, nor did he give it at the usual 20 to 25 minute interval on one occasion when boys were near the nest. Males have called their mates off when I have been within 5 meters of the nest, in which case the females refused to return until I had withdrawn to a greater distance. Once in such a situation a male called off his mate, then began to *tchunk* at me.

When the female leaves the nest, the male usually remains near it for a few minutes and then joins his mate, often accompanying her when she returns; he thus alternately guards both the nest and her. He rarely visits the nest during incubation; 1M did so twice in 30 hours during K2's first incubation, and once in 17 hours during K7's first incubation. Only 3 times have I met other males at nests during this stage.

3. *Incubation with Other Species*

The origin of incubation, according to Whitman (1899) may have come from (1) the disposition to remain with or over the eggs, "probably bound up with the physiological necessity for rest after a series of activities tending to exhaust the whole system," (2) the disposition to resist enemies, (3) periodicity.

a. Share of the Sexes

Probably in the majority of birds both sexes incubate. This is usually the case where both sexes have similar plumage, although there are many exceptions, since only females regularly incubate with the Tyrannidae, Muscicapidae, Troglodytidae, Paridae, Buntings and American Sparrows, most Corvidae, most Turdidae and many others. With Common and Spotted Sandpipers only males incubate as a rule.

If there is sexual dimorphism, usually the less brightly colored partner incubates—the female in Hummingbirds, Pheasants and Icteridae, the male in Phalaropes, Button-Quails, Painted Snipe. There are a few exceptions, for the strikingly colored male Rose-breasted Grosbeak and Paradise Flycatcher assist in incubation. Some Fruit Doves (*Ptilinopus solomonensis, P. rivolii*) have striking dimorphism, yet, as with all Columbidae, the male incubates in the day-time (Mayr, letter).

Where both sexes are conspicuously colored, the nest is often in a cavity—Kingfishers, Bee-eaters, Barbets, Trogons, Cassiques, Parrots, Puff-Birds, Motmots, Toucans, Woodpeckers, Starlings, Sheldrake, European Robin, etc. In such cases both sexes often incubate, but this is not always so. "With many small egg-rich Waxbills, the pair incubates together in the roomy spherical nest often for hours at a time, not only at night, but also in the day (*Estrilda melpoda* and *E. astrild*)" (Stresemann 1927-34:385).

b. Length of Periods On and Off the Nest

Where both parents incubate, the spells on the nest may be very short: 7 minutes with the Lesser White-throat (Löpmann 1934), 5 minutes or so with the Black-winged Stilt (Yeates 1941), 2-15 minutes with the Bush-Tit (Addicott 1938) and 15-40 with the Blue-gray Gnatcatcher (Nice 1932b). There may be a regular division of the 24 hours as with Columbidae, the female incubating from late afternoon to the middle of the morning, the male during the middle of the day. With the Ostrich the male spends the night on the nest, the female the day. The male Woodpecker regularly incubates at night, and often more in the day time than does his mate (Pynönnen 1939, Sherman 1910, Steinfatt 1937b). With some birds either partner may be on at night, as with the Willet (Vogt 1938). Noddy Terns relieve each other at about 2 hour intervals, while Sooty Terns stay on a whole day at a time (Watson 1908). Black Oystercatchers, when incubating and caring for chicks, change places at low tide, i.e., every 12 hours (Webster 1941).

With some birds the periods on the nest are long, as for instance: Murres 16-24 hours (Johnson 1941), Wilson's Petrel 2 days (Roberts 1940a), Leach's Petrel 4 days (Gross 1935), Fulmar 4 days (Richter 1937), Yellow-eyed Penguin 1-5 days (Richdale 1941a), Rockhopper Penguin 4-10 days (Roberts 1940b), Royal Albatross 3-14 days (Richdale 1942).

Where only one bird incubates, the matter of the rhythm of incubation is of much interest. Some birds leave the nest only once a day, as the Bob-white, or twice as Mallards (Girard 1941). With passerines the number of times the female leaves the eggs during a day varies greatly: Ovenbird 5-13 (Hann 1937), Cardinal 11-12 (Schantz, letter), Song Sparrow 14-39 (Nice 1937:125), House Wren 27-43 (Baldwin and Kendeigh 1927), while Bussmann (1933) gives data for 4 European species studied with his terragraph—Song Thrush 20-21, Common Redstart 30, Wryneck 40 and Pied Flycatcher 90. European Dippers left 21 and 28 times (Eggebrecht). Steinfatt gives figures for all day incubation for 4 species: European Nuthatch 24, Marsh Tit 17, Chiffchaff 17, 34, Hedge Sparrow 20,22.

Periods off and on the nest are of considerable interest. In Table XXII data are given on 21 individuals of 10 passerine species whose incubation rhythm was recorded from a minimum of 7 hours to a maximum of 11 days, the table representing a total of some 47 days of observation. The birds are arranged in order of length of periods *off* the nest.

TABLE XXIII

AVERAGE PERIODS ON AND OFF THE NEST DURING INCUBATION IN TEN PASSERINE SPECIES

Length of Periods On and Off in Minutes
(Incubation by Female Only)

Species	Average period off	Average period on	Percentage of time on nest	Length of observation	Author
Song Sparrow	5.7	19.3	73	6 days	Nice 1937[1]
Song Sparrow	6.0	30.5	80	17 hours	Nice 1937
Marsh Tit	7.1	37.9	84	12 hours	Steinfatt 1938c
Song Sparrow	7.8	24.9	76	11 days	Nice 1937[1]
Song Sparrow	7.8	30.0	79	30 hours	Nice 1937
European Dipper	7.8	29.8	77	All day	Eggebrecht 1937
Song Sparrow	8.0	20.0	71	24 hours	Nice 1937
Chiffchaff	8.2	19.6	70	All day	Steinfatt 1938a[2]
Chiffchaff	8.2	49.1	85	All day	Steinfatt 1938a[3]
European Dipper	8.5	32.0	79	All day	Eggebrecht 1937
Becard	8.5	12.0	60	1½ days	Bent 1942[4]
Sulphur-bellied Flycatcher	8.5	17.0	67	7 hours	Bent 1942[4]
Song Sparrow	9.0	27.0	75	21 hours	Nice 1937
Song Sparrow	9.2	26.5	74	3 days	Nice 1937[1]
Scarlet Finch	9.2	48.5	84	All day	Steinfatt 1937d
Song Sparrow	9.3	36.1	80	5 days	Nice 1937[1]
American Robin	11.0	44.0	80	37 hours	Schantz 1939
European Nuthatch	11.3	31.1	73	All day	Steinfatt 1938e
Hedge Sparrow	12.6	29.4	70	All day	Steinfatt 1938b
Hedge Sparrow	16.5	30.0	63	All day	Steinfatt 1938b
Song Sparrow	16.5	42.4	72	4 days	Nice 1937[1]

[1] Records taken by potentiometer by Drs. Baldwin and Kendeigh in Cleveland, Ohio.
[2] Third day of incubation; sunny, warm.
[3] Different female; 11th day of incubation; foggy, then sunny.
[4] Observations by A. F. Skutch in Central America.

The periods off the nest range from 5.7 to 16.5 minutes, the median being 8.5 minutes, while two-thirds of the cases fall between 7 and 9 minutes. The range of the 9 Song Sparrows is 5.7 to 16.5 minutes, the median 8 minutes. The range of the 12 birds of the 9 other species is 7.1 to 16.5, the median being 8.5 minutes. It seems as if *8 minutes was a favorite period for small passerines to stay off the nest.*

As to periods on the nest, they range from 12 to 49.1 minutes with a median of 29.8. If the 2 tropical species—Becard and Sulphur-bellied Flycatcher—with 12 and 17 minutes on the nest are omitted, the minimum of the 19 temperate zone birds is 19.3 minutes, the median 30 minutes. Thirteen cases range between 19 and 32 minutes. An inverse correlation between length of periods on the nest and temperature is shown in a number of cases: the 2 tropical species in the table and the Chiffchaffs, Hann's Ovenbirds (see Bird-Banding, 9:57) and my Song Sparrows (Nice 1937:123), but with Baldwin's and Kendeigh's Song Sparrows, the warmer the weather, the longer were periods on and off (Nice 1937:125). As to periods off the nest, with the Ovenbirds and Song Sparrows they were longer in warm weather than in cold.

The percentage of time during daylight that the eggs are covered ranges from 17-90 with the White-rumped Swift (Moreau 1942a), and 31-66 with the Rough-wing Bank Martin (Moreau 1940) to practically 100 with Columbidae and many sea-birds, Herons and others. As to the 10 passerine species in the table, their percentages run from 60 to 85 with a median of 75. (Three other percentages fall within the same range—Yellow-headed Blackbird 63.9 (Fautin 1941), Linnet 78 (Steinfatt 1937f) and Ovenbird 82.5 (Hann 1937). In a study of the European Wren in Holland, females were found on the nest 54 per cent of the times visited during the first brood and 80 per cent during the second; the female has to spend more time searching for food early in the season than later; the average incubation period in April lasted 17.5 days, in July 14.5 days (Kluijver et al., 1940). A female Lyre-bird incubated her single egg for 7 weeks before it hatched, but was off the nest from 7-8 hours each day (Campbell 1941); an egg placed under a fowl hatched in 4 weeks.

c. Length of Incubation

The classical study on "The Relation between Bird Weight, Egg Weight, Set Weight, and Length of Incubation" was published in 1922 by Heinroth. The following birds have very long incubation periods: Procellariiformes, Falconiformes, Alcidae, Psittaciformes and Trochilidae. The following have rather long periods: Phalacrocoracidae, Ardeidae, Ciconiidae, Charadriiformes, Coraciiformes, Strigiformes, and Micropodidae. Anatinae have short incubation periods and so do Picidae despite their protected nesting sites. "Very long incubation periods, especially with altrices, are always to be regarded as somewhat primitive, and have persisted where the brood is subject to few dangers. Long incubation periods are usually correlated with slow development of the nestlings," p. 285. Fresh eggs take less time to hatch than stale eggs; the last egg is the freshest and often hatches in a shorter space than the others. (A set of 8 Emu eggs hatched in a span of 4 days, although the last 4 had been laid during the first 13 days after incubation had begun [Fleay 1936].) In the incubator eggs usually hatch one-fourth to half a day sooner than in nature. It is impossible to hasten development to any appreciable extent, but it may be considerably delayed.

How long will birds incubate over the normal time? Whitman (1919) found that Pigeons will not incubate overtime, and this is correlated with formation of pigeon milk in the crop. One Song Sparrow incubated 16 days, another 24 (Schantz 1937), while a Catbird incubated 22 days (Latham 1936) and Black-crowned Night Herons in captivity for 40, 49 and 51 days, instead of the regular 22-24 days

(Noble and Wurm 1942). Some birds incubate for extraordinarily long periods: a Peregrine Falcon 61 days (Schiermann 1925), Black-headed Gull 75 days (Kirkman 1940b), a Lapwing 88 days (the Nethersole-Thompsons 1942b), a Kiwi in a London zoo 4 months (Stresemann 1927-34:394).

On the other hand, it has been found that if incubating birds are given eggs ready to hatch, the parents as a rule respond to the stimulus of the young and care for them, the incubation period being thus very much shortened or entirely suppressed. This was true with K201, whose foster eggs hatched 3 days after her own set was complete, and with a pair of Song Sparrows given Yellow-breasted Chats' eggs (Young 1895). In Emlen's series of experiments with Tricolored Redwings, the normal incubation period of 11+ days was reduced by the introduction of other eggs to 6, 5, 3, 2, 1 and 0 days. Nestlings "2 to 3 days of age were introduced into 10 nests where the laying phase was just being completed. In 2 of these the old birds deserted, in the other 8 the strange nestlings took precedence over the eggs, and the nest owners passed directly from laying into the feeding-the-young stage." The author concludes: "The development of breeding behavior in the Tricolored Redwing is closely regulated by physiological factors from the start of nest-building through the initiation of incubation. During the rest of the cycle, however, the rate of development is largely controlled by external situations associated with the nest" (1941:218). Allen and Mangels (1940) concluded from their experiments on interchanging eggs and young of the Black-crowned Night Heron that the adults accept very small young "innately", but must be conditioned to larger young.

d. Incubating on Empty Nest

Some birds have been reported as brooding on the nest before any eggs were laid—Skylark, Mistle-thrush and Chaffinch, also 2 Rooks in *November* (Brown 1924). Peregrine Falcon, Owls, Buzzard, (*Buteo buteo*) and Kestrel (Owen 1940). Others have been found incubating without laying—Rook, Hedge Sparrow, Long-tailed Tit and Green Woodpecker, while a Great Tit, robbed on May 24-25 continued to occupy the nest till June 10 (Owen 1940). A Pigeon will sometimes fail to lay, but "incubates the empty nest and exchanges with her mate as punctiliously as if she actually expected to hatch something out of nothing" (Whitman 1919:89). A hand-raised Robin laid in captivity, but her eggs disappeared; she brooded the empty nest and when taken off by force, "She bites my fingers and fights" and "utters all the alarm cries and notes that a bird does out of doors when disturbed" (Scott 1902a).

An interesting case of this behavior is reported by Davis (1941c). A pair of Eastern Kingbirds built 3 nests in succession and deserted each one without laying any eggs. "Four days after the first nest was completed she started to 'incubate' the empty nest. About four days is the normal interval between the completion of the nest and the start of incubation. The behavior of the female was identical with that of a female incubating eggs. She 'incubated' for 15 to 25 minutes; the male guarded in her absence and greeted her in typical manner when she returned," p. 166.

In all these cases of incubating empty nests the bird (or birds in the case of the Pigeons) carried on the physiological rhythm, although one of the prime elements in the external situation was missing.

4. *Role of the Non-Incubating Mate*

The males of some species pay no attention to their "mates" after copulation has taken place. But wherever a pair is really formed, the male usually plays a significant role even if he does not share in incubation. This may be guarding the territory, nest, and mate as in a very large number of species. Sometimes the male's role is to attract attention of the enemy to himself and lead it off (as in Geese and Ptarmigan).

Sometimes the male feeds the female on the nest. This may be largely token feeding that strengthens the bond between the pair, as in Titmice, Old World Flycatchers, a few Wood Warblers. In others there is a real contribution to the nourishment of the female as in Shrikes and various Falconiformes. In the Hornbills the male brings all the food to his imprisoned mate and the young. This subject was treated in detail by Lack (1940b), and further records appeared in *The Auk*, Jan. 1941:56-60. It is of interest to find how widely spread this behavior is, occurring sporadically in families where it seems normally absent.

Sometimes the male drives or urges his mate back on to the nest, as in Parrots (Travistock 1930), Herring Gull (Goethe 1937a), Pigeons (Whitman 1919), Crimson-crowned Bishop-bird (Lack 1935), Corn Bunting (Ryves 1934), Dickcissel (Crabb 1923), Nuttall Sparrow (Blanchard 1941). With one of the Button-quails the ***female drives her mates*** back to their duties of incubation (Stresemann 1927-34: 379).

Diebschlag (1941) interprets this as a matter of dominance with Pigeons, considering that the male is driving his mate out of his sphere of influence. However, the explanation might be different. A bird instinctively responds to certain situations; the situation eggs-in-nest implies mate-on-nest-much-of-the-time; if the second element in the situation is not functioning he is disturbed; if his mate has disappeared he starts to sing (for her or another); if she is around, he tries to get her into the appropriate situation. That birds have some feeling at times for appropriate behavior in their mates is shown by the attacks of an overworked mother Dipper on her lazy mate, after which he worked harder (Eggebrecht 1937), and by a Bank Swallow on its mate that was attempting to dig a hole where a stone obstructed the passage (Selous 1901:328).

C. RECOGNITION OF EGGS

Experiments have shown little evidence of recognition by birds of their own eggs.

Rensch (1925) experimented with passerines in Europe: 2 species accepted their eggs when painted red, while 3 deserted; when sets were exchanged between species some were accepted and some were not. Single eggs of other species were often rejected, while in one case a Whitethroat incubated the 3 eggs of a Lesser Whitethroat and threw out her own.

On the basis of his wide experience with parasitic Cuckoos in Europe and Asia, Baker (1942) marshalls much evidence as to discrimination of eggs; for instance, the incidence of desertion of parasitized nests by normal hosts of the Khasia Hills Cuckoo was 8 per cent in 1642 cases and by abnormal hosts 24 per cent in 298 cases. He concludes:

> "The evolution of adaptation between the eggs of Cuckoos and their normal fosterers is brought about by the constant destruction, by the latter, of the Cuckoos' eggs most unlike their own and the survival of those most like them. Adaptation has been evolved in size as well as in general appearance," p. 179.

A very different situation is found with the Cowbird that shows no specialization for parasitism in the size or color of its eggs. If we take the 15 most common fosterers according to Friedmann's book (1929), and consider the matter of resemblance in color, we find considerable similarity with 3 species, not too great difference with 5, but striking contrast with 7. As to resemblance in size, there is little difference in 4 cases, some difference in 2, and a great difference in 9. Only two of these species often reject the Cowbird egg: the Yellow Warbler whose own eggs are decidedly smaller, but not very different in color from those of the parasite, often builds over the strange egg; the Yellow-breasted Chat whose eggs are "very similar to those of the Cowbird" in size and markings, usually deserts a parasitized nest.

It looks as if Old World passerines are more selective in the matter of eggs than those in the New World. Five families are represented by these 15 most common victims of the Cowbird: Tyrannidae (1), Vireonidae (3), Compsothlypidae (5), Turdidae (1), Fringillidae (5); only the last two occur in the Old World; they are parasitized to some extent.

Gulls (Kirkman 1937, Goethe 1937a, Tinbergen 1936b, Noble and Lehrman 1940), Terns (Marples 1934, Tinbergen 1936b), and the Black-crowned Night Heron (Allen and Mangels 1940) have been shown not to recognize their own eggs.

Kirkman (1937:98) writes in regard to the Black-headed Gull: "A complete normal incubating reaction will result from the presence of two sets of conditions, both of which are indispensable, namely an internal drive or urge to brood together with an external situation in the form of an effective nest or nest substitute containing at least one egg or a substitute for that egg, the substitute being of any colour, shape, size, material, or smell, provided that its shape does not cause discomfort, that it is not too large to sit upon, or is not so small that it sinks into the material of the nest." Lashley suggests (1938:455), "The adequate stimulus of the egg may thus be defined as a rounded object of certain size and texture, and this, in the setting of the nest, elicits specific retrieving, cleaning, and brooding behavior."

Murres or Guillemots make no nests; they do know their own eggs which are strikingly marked and they are strongly attached to them. "Eggs out of place are returned by their owners to the old nest site, and are usually completely ignored by strange birds," writes Johnson (1941:163) in regard to the Atlantic Murre (*Uria aalge aalge*). "Two different pairs of birds at different times incubated broken eggs and empty shells or pieces of shells. This indicates that the birds may rapidly adjust to a change in the character of their eggs." Dawson (1921:1506) describes a California Murre (*Uria aalge californica*) retrieving and incubating its egg that had been broken by Gulls.

With Gulls, Terns, Geese, Rails (Pettingill 1938), and some others there exists an instinct to retrieve eggs outside the nest. This activity has been analyzed as to its elements of instinct and taxis in the Greylag (Lorenz and Tinbergen 1938).

Whitman (1899) experimented by removing the eggs of several of his Pigeons, placing them 2 inches outside the edge of the nest. The Passenger Pigeon returns to the nest, looks at it, "sits down as if nothing had happened. She soon finds out, not by sight, but by feeling that something is missing." She "leaves the nest after a few minutes without heeding the egg." The Ring-necked Dove puts her head down "as if to feel for the missing eggs." She may leave after 20 minutes "with a contented air as if her duty were done", or she may try to roll *one* egg back into the nest, staying content with this. The Domestic Pigeon generally tries to get *both* back; "failing in this, she resigns the nest with more hesitation than does the ring-neck", p. 335.

It is typical of instinctive reactions that the animal need not perceive their function or end; with most birds there is no need for them to recognize their eggs; it is simply enough for these birds that they recognize the nest which in nature is fixed. But where eggs may be moved in the natural course of events, the individual is able to recognize its own eggs, as in the Murres. Even in this case the bird has retained the universal attachment to the site, for moved eggs are brought back to the accepted site.

D. SUMMARY

1. The female Song Sparrow incubates for 20 to 30 minutes at a time, staying off the nest from 6 to 9 minutes; this rhythm is correlated with hunger.

2. The male guards, singing a great deal, and calling his mate off the nest with signal songs.

3. In the majority of birds both sexes incubate; where this is true, periods on the nest may vary from 5 minutes to 5 to 14 days.

4. When only one sex incubates, the bird may come off once a day, or as often as 90 times a day; between 20 and 30 times seems to be typical for many passerines. In 7 species of 6 passerine families, the average period off the nest ranged from 7-9 minutes.

5. The percentage of the daylight hours that the eggs are covered ranges from 31 with a Swallow to nearly 100 with Doves; in 9 passerine species it ranged from 64 to 84.

6. Very long incubation periods are primitive and have persisted where the eggs are subject to few dangers.

7. Some birds will incubate a long time over the normal period.

8. If eggs nearly ready to hatch, or nestlings, are given to birds just starting to incubate, incubation may be greatly shortened or suppressed entirely.

9. Cases are reported of birds incubating empty nests.

10. The non-incubating mate often guards the territory, nest and mate; he may feed his incubating mate and he or she may drive the other back to the nest.

11. Experiments have shown little evidence of recognition by birds of their own eggs; usually it is the nest site that is recognized. Murres, however, that build no nest, do know their own eggs, and show a strong attachment to them.

CHAPTER XIX

Care of the Young

Both Song Sparrow parents cooperate in the care of the young, the female brooding and feeding them, the male feeding them. Both attend to nest sanitation and both defend them. Singing is much reduced; the awakening song is given irregularly. (During May 1934 I noted that 4M gave it about two-thirds of the time while caring for young.)

That the care of the young is the most strenuous period in the life of both parents is shown by the fact that they lose some 9 per cent of their weight at this time (Nice 1937:27). The Eastern Tree Sparrow shows an even greater loss in Manitoba while feeding young—"almost 20 per cent for the males and 10 per cent for the females" (Heydweiler 1935). Parent Noddy and Sooty Terns became emaciated (Watson 1908).

The young are cared for by one or both parents for about 4 weeks from hatching; the first 10 days of this period are spent in the nest—Stage VII; the last 20 are spent in or near the territory—Stage VIII.

A. Brooding

Brooding with Song Sparrows is by the female alone, although the male may stand over the young for as much as 6 to 8 minutes at a time (1M with his first brood in 1928 and third brood in 1929), even though there was no question of protecting them from the sun. It seems to be a general rule that the bird that incubates the eggs, broods the young.

Table XI in Volume I (Nice 1937) shows that in 3 Song Sparrow nests the young were brooded about two-thirds of the daylight hours on the first day, about half the time for the next 3 or 4 days and perhaps a third of the time on the sixth day with little brooding after that. With an Ovenbird the proportions on the first 4 days were two-thirds, one-half, one-third and one-twentieth (Nice 1931b); with a Black-throated Green Warbler two-thirds, two-thirds, one-half and one-third; the development of both these species is more rapid than that of the Song Sparrows.

In regard to the Wire-tailed Swallow, Moreau (1939b:125) says: "For the first three days the young in all the nests were brooded much as the eggs had been, but after that the amount of brooding varied greatly between the nests." With the Rough-wing Martin the young are brooded as much as the eggs for the first week after hatching (Moreau 1940:243).

With Song Sparrows, Wood Warblers, Wrynecks (Bussmann

1941) and others, more brooding takes place during cold weather than warm.

Sometimes "shading" the young from the sun is an important function of the parent; here the adult stands spread out over the nest. The somewhat different positions taken by male and female Brown Thrashers are shown by Gabrielson; the male "sat on the edge of the nest with his feathers ruffled up . . . affording very poor protection for the young, as compared with the female. She spread her wings, ruffled her feathers, and stood in such a position as to completely shade the nest" (1912:82).

That this behavior is not necessarily released by the sight of the discomfort of the young, but may be a direct response to the sun is shown by an observation by Charles (1909:30) on American Robins nesting on a window sill.

> "The sun shone directly upon the nest for about an hour each day, during which time the female brooded in striking attitude. At one time when the young had been weighed in a bowl and the bowl had been placed upon the sill close to the nest preparatory to returning the nestlings, the mother appeared and brooded for some time upon the empty nest, utterly indifferent to the presence of the young in the bowl."

B. Feeding the Young

In general the male Song Sparrow does the major part of the feeding as long as the female is occupied with brooding; in the second half of nest life they may feed equally or either may surpass the other.

1. *How Does the Male Know the Young Have Hatched?*

Since the male so seldom visits the nest, it is a question as to how he knows that the young have hatched. Is it by seeing his mate carry food? Howard describes the situation with the Yellow Bunting that may not assist in feeding until 3 to 5 days after the young have hatched:

> "He sees her leave the nest in order to collect food for the young and follows, waits while she seeks it, returns when she returns, follows her even to the thicket, and, when she enters, flies to the oak and sings. Again he sees her leave; again he follows, chases and worries her, hampering her routine; but he can neither feed nor brood the young. Four days pass before this male carries insects in his bill, but thereafter he brings food and cleans the nest regularly," (1929:27).

In 1929 I obtained some data on this question.

July 5. At 9:02 one of 4M's young was lying between the broken halves of the shell; the other eggs had not hatched. K3 returned to the nest and did not leave until 9:45; probably she did not meet 4M during her 8 minute outing. She returned at 9:53 and left silently at 10:22. 4M had been singing nearby for 9 minutes; he darted after her. The nestling gaped. At 10:25 4M appeared with nothing in his bill, sang twice near the nest, *went in to the nest and left;* at 10:26 K3 returned with an empty bill. At 10:29 4M appeared with a small insect and the baby apparently received its first meal, 1½ hours after hatching. He fed 3 more times in 46 minutes and 4 times in 1¾ hours in the afternoon. So far as I could tell K3 did not feed at all during the period I watched. I was not in a blind, but in the open 6 meters from the nest.

July 7. K2 left her nest at 7:24; I found one egg had hatched. 1M came near and *tchunked,* but did not go to the nest. K2 returned and did not leave again until 7:58. At that time I was trying to find a snake that had been coiled up at the base of the bush, and I did not see the meeting of the pair. Both came to the nest at 8:02, flipping their wings; 1M left and returned in 4 minutes with the first meal.

In 1930 I watched the newly-hatched young of 1M and K7 from a blind. 1M came to the nest at 9:46 and looked in, remaining about a minute; at 9:55 he brought food. This may have been the first time he knew of the hatching.

My theory is that the female shows excitement, probably by flipping her wings; the male visits the nest and the sight of the young induces him to feed.

When a Henslow's Sparrows eggs hatched, the female, instead of "leaving with her usual low flight . . . mounted to a height of about twelve feet in the air, uttering animated twitterings as she swerved over a clump of shrubbery" (Hyde 1939:38); this looks like a device for stimulating the male to come to the nest.

Under like circumstances the female Bonelli's Warbler, instead of flying 50 meters along the ground, mounts straight up into the tree tops, where her mate is, flips her wings and gives little notes. The male at once responds to this new behavior; he follows her closely and tries to feed her, but she avoids this and sits with food in her bill. The male's ground-shyness prevents his feeding the young for some hours (Heilfurth 1935).

A curious thing happened in 1935: as I went to visit 204M's nest at 5:20 P.M., there was 204M with a grub in his beak; his mate was on the nest, but no eggs had hatched. Later when I passed by, he was there again, examining the eggs. The next morning two had hatched.

A male California Thrasher was seen carrying insects to the nest at the beginning of incubation! (Sargent 1940). A male Ovenbird, as shown by the itograph record, came to the nest each morning on the 9th, 10th and 11th days of incubation; on the 12th he was seen bringing food (Hann). A female Chough regurgitated food into the nest and gave the food call 1¾ hours before the first egg was pipped and 8¾ hours before it hatched (Schifferli and Lang 1940).

2. *The Rate of Feeding*

The rate of feeding typically increases with the age of the young. It varies greatly from species to species.

a. The Rate Per Hour

The results of 137.5 hours of observation on the feeding of 7 broods of Song Sparrows are shown in Table XXIV.

Table XXIV

RATE OF FEEDING PER HOUR AT SEVEN SONG SPARROW NESTS

Nest	Number young	First 5 days				Second 5 days				Total			
		Hours	♂	♀	Total	Hours	♂	♀	Total	Hours	♂	♀	Total
Mousley	3	6	......	......	6.5	3[1]	......	......	12	9	......	......	8.3
Haldeman	3	......	......	......	......	16[2]	4.0	12.3	16.3	......	......	......	......
1M & K1	2	18	4.6	2.7	7.3	......	......	......	......	......	......	......	......
1M & K2	4	17.5	5.8	0.2	6.0	21.5	12.4	5.2	17.4	39	9.4	2.9	12.3
1M & K2	4	31	4.7	2.0	6.7	9	14.3	5.4	19.7	40	6.9	2.7	9.6
1M & K7	4	10.5	6.6	4.4	11.0	3	8.7	15.3	24.0	13.5	7.1	6.7	13.8
17M & K20	6[3]	......	......	......	......	2	10.5	14.0	24.5	......	......	......	......
Total		83	......	......	......	54.5	......	......	......	101.5	......	......	......
Average	3.7	......	5.2	2.0	7.2	......	9.7	8.3	17.8	......	7.9	3.4	11.1

[1] 7 days old.

[2] 6 or 7 days old; all day observation.

[3] 5 Song Sparrows and 1 Cowbird, all 7 days old.

The rate of feeding for the first 5 days of nest life ranged from 6 to 11 times an hour, averaging 7.2 times; for the second 5 days from 12 to 24.5 times, averaging 17.8. The results from 101.5 hours where observations were made in both the first and last halves of nest life range from 8.3 to 13.8 and average 11.1 times an hour for the whole period.

There is considerable agreement in the different samples. Four of those in the first half of nest life range between 6 and 7.3; the fifth case that amounted to 11 involved an unusually zealous female, K7. In the second half there is one low record—12, but this was based on only 3 hours' observation of birds 7 days old; three medium records—16.3-19.7—, and 2 high—24 and 24.5. These last 2 are based on short periods of observation, only 2 and 3 hours; in one K7 was again involved, while in the other there were 6 young in the nest. This nest had the distinction of raising 5 Song Sparrows and a Cowbird (Nice 1930d), apparently the only such case on record.

As to the totals, those for 1M and K2 in May and 1M and K7 are probably the most representative. Mousley's samples of 3 hours each were taken when the young were 3, 5 and 7 days old, so are not representative of late nestling life. 1M and K2's nesting in July has no data for the last 2 days of nest life. If the 7.2 times an hour for the first half and 17.8 for the second half are averaged, each being given equal value, the result is 12.5 times an hour for the whole period. This may well be more representative than 11.1, for the number of hours in the table spent on the first half of nest life is almost double that spent on the second half. Comparing 7.2 with 17.8, we find the average rate of feeding during the last half of nest life two and a half times as rapid as during the first half.

b. Increase with the Growth of the Young

It is clear that with the growth of the young there must be an increase in the amount of food brought after the first few days. This may take the form of more frequent trips or larger amounts—larger insects and more of them—brought each time. With many species that stay in the nest only a short time, this increase is consistent throughout nest life. This is shown in Table XI in Volume I (Nice 1937) where K2 in July increased from 3 feedings an hour on the first day to 9 an hour on the 9th; K7 in May from 1 feeding an hour to 15 on the 8th day, while 1M's average for 5 broods started at twice an hour on the first day and finished at 26 times an hour on the 11th day.

A steady increase in rate of feeding throughout nest life is shown in the Ovenbord (4 nests Hann 1937; 2 nests Nice 1931b), Black-throated Blue Warbler (Nice 1930c), Maryland Yellow-throat (Shaver 1918), Blue-gray Gnatcatcher (Nice 1932b), Henslow Sparrow (Hyde 1939:42), Wren-tit (Erickson 1938) and others.

Marked increase in feeding activity is shown in a number of species studied by Steinfatt by means of 2 all day records, one usually taken early in the nest life, the other late: Spotted Flycatcher (1937e), Chiffchaff (1938a), Willow Warbler (1939c), Thrush-Nightingale (1939b), Europeon Nuthatch (1938e) and Hedge Sparrow (1938b). This was also true of Eggebrecht's Dippers.

With species that stay in the nest until ready to fly there is typically a steady increase in number of meals brought for the first week or 10 days after which a "plateau" is reached.

This was true of the Song Thrush—3-4 feedings an hour at first and 19 at the 11th day and afterwards (Siivonen 1939), Wrynecks (Bussmann 1941), Great Tits and European Redstarts (Bussmann 1940a, 1940b) and Starlings (Kluijver 1933). With this last species there was some decrease the last 2 or 3 days. With the Rough-wing Bank Martin the feeding "rates increase slowly for about the first ten days", after that remaining much the same for the next 14-17 days (Moreau 1940:243). With the Silvery-cheeked Hornbill the number of meals brought by the male "increases a fortnight after the eggs have hatched" and decreases "a fortnight before the family emerges" (the Moreaus 1940:243). An increase and decrease is also shown in the Kestrel (L. Tinbergen 1940). With the Wire-tailed Swallow, "After a slow rise, comparatively stable feeding rates were attained at each nest during the last week of fledging" (Moreau 1939b: 125); in the first week feeding occurred about 10 times an hour, in the second about 14, in the third about 25. Robins watched by Charles (1909) fed 3 young as follows on the 6th, 7th, 8th, 13th and 14th day: 66, 85, 85, 94, 102.

The two broods of Robins studied by Schantz (1939:161, 163), on the contrary, showed little change in the rate throughout the nestling period: in the first brood with 3 young 82 feedings when the young were 2-3 days old, and 83-99, averaging 90, in 9 all day feedings during the rest of nest life; 81 when the 4 young of the second brood were 1-2 days old and 84-113, averaging 92, during the following 11 days of nest life.

Careful studies of the increasing amount of food brought to young Starlings were made by Kluijver (1933:138) by means both of the terragraph and by placing a collar around the necks of the young for a few hours each day and collecting each meal with forceps. The average weight of a feeding to one young was 144 mg. on the first day, and 853 mg. on the tenth; each feeding amounted to about 1/80 the weight of the young, but in one case where the female alone cared for the young, some feedings equalled ⅛ the weight of the nestling. At first the young were fed *half their weight each day, later 7/6 their weight each day.*

When my 3 European Redstarts were 7 days old I fed them 26.5 grams of ant pupae, which came to about 2/3 the total weight of the birds (39 grams). The 44 excreta weighed 12.5 grams, about 1/3 the weight of the birds and ½ the weight of the food.

Northern Flickers fed their young by regurgitation about 10 times the first day and 4 or 5 times as often later; at 19 days one feeding amounted to 1/16 the weight of the young bird; during a day the young consumed their full weight of food (Sherman 1910:151). A brood of Ivory-billed Woodpeckers were fed 30 times a day at first, 15 times later (Tanner 1941).

c. The Part Played by Male and Female

The amounts fed by male and female Song Sparrow are shown in most cases in Table XXI. In the 4 instances in the first half the male outdid the female, but in 3 out of 5 cases in the second half the opposite is true. It is probable that in the majority of cases while the female broods the young, the male will do the larger part of the feeding; later, however, the individuality of the birds plays an important role. K2 during her May and June nestings in 1929 fed the young very little during the first half of nest life, but did better in this respect in the July nesting and also the following year. (The June nesting in 1929 is not included in the table since the birds were disturbed by carpenters near their nest.) K1 and K7, on the other hand, were zealous in feeding young; the greater activity of K7 than K1 is perhaps due to the larger brood of the former. (K1's nest was destroyed by some predator.) Haldeman's female fed 3 times as often as did her mate. The average rate of feeding of 1M during 110.5 hours in 3 years was 7.4 times an hour; two-thirds of the hours came during the first half of nest life. It should be noted that male Song Sparrows usually bring larger portions, larger insects and more of them—than do their mates. The same thing has been noted in a number of birds: Black-throated Blue Warbler (Nice 1930c), Myrtle Warbler (Nice 1930a), Black and White Warbler (Smith 1934), Black-throated Green Warbler (Pitelka 1940), Blue-gray Gnatcatcher (Nice 1932b) and others.

1M also differed from K2 in taking food from the feeding shelf to the nestlings. He started taking bread to the June brood when they were only 4 and 5 days old: at first he did this only occasionally, but by the time they were 8 and 9 days old half his meals in 3 hours consisted of this artificial food. He also brought them Canary seeds at this time. He first took bread to the July brood when they were 5, 6 and 7 days old, a third of the feedings in 4 hours on this and the next day consisting of this easily obtained provender.

d. Number of Objects Brought and Number of Young Fed at Each Trip

Some birds habitually bring only one object at a trip: Gnatcatchers (Nice 1932b), one of the Black-throated Green Warbler females (Nice and Nice 1932), Red-breasted Flycatcher (Steinfatt 1937a). Others bring whole mouthfuls (Ovenbird, Starling, Robin, the other Black-throated Green Warbler female), while still others may bring one or more (Song Sparrow, Great Tit [Bussmann 1940b]). Figures on 5 species—Catbird, Brown Thrasher, Red-winged Blackbird (Gabrielson 1915b), Myrtle Warbler (Nice 1930a) and Maryland Yellow-throat (Shaver 1918) show the number of objects brought ranged from 104 to 167 per cent of the number of trips, the average being 1.37 objects per trip. In 1928 1M brought at least 32 insects in 19 trips to small young, an average 1.7 per trip.

Kluijver (1933:62) gives the average number of objects brought per trip by Starlings for 17 days: for the first 4 days it averaged 2, after that it ranged between 2.7 and 7.3, the median of the 17 being 3.6. Steinfatt (1937b) found the male Great Spotted Woodpecker brought an average of 4 insects to his young at each trip. A male Eastern Tree Sparrow had 45 insects in his bill at one time (Baumgartner 1937). As many as 80, 220 and 686 insects have been taken at one time from the gullet of an Alpine Swift (Bartels 1931:19).

As to the number of young fed at each trip there are a number of records from observers who watched from blinds: Song Sparrow (Haldeman), Towhee, Meadowlark (Esten), Catbird, Brown Thrasher (Gabrielson) Maryland Yellow-throat (Shaver); the average per nest ranges from 1.06 to 1.7, the average of all nests being 1.3 young fed per trip. This probably varies according to the age of the nestlings. With the Wren-tits all the young were fed at each trip at first, but later only one or two at a time (Erickson 1938:292, 295).

e. Rate of Feeding Throughout Nest Life

To return to the hourly rate of feeding throughout the nest life, Table XXV gives data on 10 passerine species for which there is a large amount of information.

TABLE XXV

HOURLY RATE OF FEEDING THROUGHOUT NESTLING LIFE WITH TEN PASSERINE SPECIES

(The feeding of the first three and last two species were mechanically recorded)

Species	Number of young	Age in days	Number of hours watched	Rate per brood	Rate per young[1]
Great Tits[2]	9	3-15	195	39.7	4.4
Starlings[3]	4-6	1-20	510	22.0	4.4
Common Redstart[4]	5	5-16	180	19.3	3.9
Bank Swallow[5]	3-5	2-12	56	17.1	4.3
Wire-tailed Swallow[6]	2	2-19	63	16.7	8.4
Yellow Warbler[7]	3	0-10	145	16.5	5.5
Maryland Yellow-throat[8]	3	0-8	98	12.6	4.3
Song Sparrow[9]	2-6	0-10	137.5	11.4	3.1
Robin[10]	3	3-15	140	6.4	2.1
	4	2-13	174	6.6	1.7
Ovenbird[11]	2	0-8	128	2.4	1.2
	3	0-8	128	2.3	0.8
	5	0-8	128	4.3	0.9
	6	0-8	128	5.2	0.9

[1] Assuming that only one bird is fed each time. [2] 13 full days (Bussmann 1940b). [3] Average of 2 nests; 34 full days (Kluijver 1933). [4] 12 full days (Bussmann 1940b). [5] 7 hour samples of 8 nests (Stoner 1941). [6] 200 minutes each day (Moreau 1939b). [7] 96% of complete nest life (Bigglestone 1913). [8] 75% of complete nest life; one nestling a Cowbird (Shaver 1918). [9] See Table XXIV (Nice). [10] 10 and 12 full days (Schantz 1939). [11] Complete record for all 4 broods (Hann 1937). In the last brood 2 nestlings were Cowbirds.

The records range all the way from 2.3 times an hour per brood to 39.7 times. The highest rate coincides with the largest number of young. (This nest of *Parus major* affords one of the highest daily rates recorded—793 meals when 11 days old.) Assuming that only one bird is fed each time, it will be noted that, with one exception, from the Great Tits down to the Maryland Yellow-throats the number of meals given per young bird per hour is much the same—slightly over or under 4. The Song Sparrows with 3.1 make a lower showing than they should because of the preponderance of records from the first half of nest life. The Wire-tailed Swallows have the highest individual records of any—8.4 an hour; early in the nest life each parent "usually fed more than one young bird"; later they brought food "for one young bird only."

The Robin shows a distinctly lower rate—about twice an hour per bird, while the Ovenbird is the slowest of all—less than once an hour per bird. Both of these species bring very large mouthfuls at one time. Ovenbirds and Song Sparrows are about the same size; apparently the former brings about 4 times as much food to its young at one trip as does the latter.

Hann (1937:218) assumes that 2 Ovenbirds are fed on each trip; this gives 21, 24 and 25 meals per bird per day except at the nest with only 2 young where the figure would come to 38. The average number of meals per day for the first 3 broods of Ovenbirds during the last half of nest life comes to 33.7. Starlings during the early part of nest life were fed 33 times a day by Holzapfel (1939:527); when nearly ready to leave, about once an hour. I gave my hand-raised Song Sparrows 28 and 34 meals a day when 7 to 9 days old, and 27 meals to the Redstarts at 6 and 7 days. In nature during the latter part of nest life each Song Sparrow should get from 70 to 100 meals per day, which, of course, are much smaller than those given to hand-raised birds where the attempt is made to satisfy each bird at each session.

How much adaptation is there to larger or smaller broods? There is some adaptation in the rate of feeding, but often less than would be expected. The adjustment may occur largely in the amounts brought, a matter not easy to measure.

So far we have been considering passerines that gather food, largely invertebrates, and feed it directly to the young. It is a different story with those birds that feed by regurgitation, for here few visits and large feedings are the rule, as the following all-day records show. Six Linnets, 6-8 days old, were fed 50 times (Steinfatt 1937f); 4 Rose-breasted Grosbeaks, 6-9 days old, were visited 79 times by the parents and 208 individual feedings given (Esten); a brood of well-developed Red-shafted Flickers were visited 43 times in contrast to a brood of Red-naped Sapsuckers about the same age whose parents made 238 trips (Shirling 1927).

The rapid rate of feeding with passerines is correlated with rapid development of the nestlings. In contrast to small passerines that need to be *well fed* at 30 to 45 minute intervals throughout the day, many birds thrive on a very different regime. A pair of Alpine Swifts fed their 2 young about 3 weeks old 24 times, each being fed about once an hour (Bartels 1931:17). A single White-rumped Swift may be fed only 4 times a day (Moreau 1942a). Fulmars are probably fed once a day (Richter 1937); the male Crowned Eagle brings food once or twice a day (Maclatchly 1937); Royal Albatrosses are fed once or twice each day to the age of 3 weeks, after that not every day (Richdale 1942); while 4 young Wilson's Petrel's normally fed each night, survived 3, 5, 11 and 20 days of starvation when snow covered the burrows (Roberts 1940a).

3. *The Role of Experience*

There is some evidence of facilitation in parental responses of the Song Sparrow through experience.

K2, apparently a young female, fed her first and second broods very little during the first half of nest life in 1929. The third brood, however, (July 1929 in Table XXI) she fed from the start, her rate being twice an hour in contrast to 0.2 times an hour. The following year she also fed her young from the start.

1M in 1928 brought some very large insects to his 2-3 day young of the first brood, at one time spending 7 minutes trying to get his offering disposed of. In 1929 and 1930 he brought small insects to small young.

It is a pity that there was not time to watch carefully the activities of Song Sparrows known from banding or character of the song to be nesting for the first time.

In regard to Tree Swallows, Kuerzi gives 2 tables that bear on this subject. Table XX shows the "reproductive efficiency" of 10 pairs in which one or both birds were fledgling returns. "Their average efficiency of 75.0% is fully as high as the more adult birds" (1941: 39). His table XIV gives "Data on Feeding Rhythm of Four Pairs"; in two of these the females were "1st year", in two they were adult; the age of the males was unknown except for one fledgling return (1st year) mated with a young female. During 8 hours of watching it was found that the young females were greatly outdistanced in feeding rate by their mates, but that the adult females outdid their mates.

C. NEST SANITATION

The excreta, enclosed in mucous sacs, are usually eaten during the early part of nest life, but later they are more commonly carried away. At a nest of Song Sparrows about 6 days old, watched all day by Haldeman, the female swallowed 7 sacs and carried off 34, the male swallowed 3 and carried off 30; the number of excreta disposed of amounted to 28 per cent of the number of trips made (1931:401). The total number of times 1M carried excreta during 124 hours of care of 7 broods from the 3rd to 11th day amounted to 24.5 per cent of the number of trips with food.

I calculated this percentage for 35 studies on 28 species ranging from 16 to 145 hours of observation or even longer (Moreau 1939b, 1940); they vary from 8-10 per cent with the Wire-tailed Swallow (Moreau 1939b) to 66.6 per cent with the Meadowlark (Esten); 18 range from 20 to 28 per cent, while the median of all is 25 per cent. This may be a little low, as in some studies it may be that the number of excreta that are swallowed is underestimated. With the hand-raised Redstarts at 6 days the percentage of excreta to feedings was 52. Steinfatt says that the number of excreta becomes proportionately fewer during nest life, apparently because of more thorough digestion (1938a); this seems to be the case in some studies—Chiffchaff (Steinfatt 1938a), Thrush-Nightingale (Steinfatt 1939b), Maryland Yellow-throat (Shaver), Catbird and Brown Thrasher (Gabrielson).

Of 112 sacs of excreta removed from a brood of Brown Thrashers, 104 were taken from the bird just fed (Gabrielson 1912:90). In Shaver's 9 day study of 2 Maryland Yellow-throats and a Cowbird, only 6 of the 314 excreta were "voided by a nestling other than the one just fed" (1918:8). Food stimulates excretion, but not every time, as the Reeds (1925) believe: "The young bird, then does not take food until the previous bolus has been digested." This would necessitate 100 per cent disposal of excreta in comparison to trips with food.

"The functions of nest-sanitation are two-fold, one to prevent contamination of the young birds, their food, and the brooding parents, and the other in many cases to prevent the nesting-site being made conspicuous by accumulated droppings" (Blair and Tucker 1941:208). An early paper on this subject was written by Herrick (1900), who mentioned the mucous encapsulation of the feces in passerines and woodpeckers, and suggested in regard to the swallowing of the sacs, "since digestion in the young is an imperfect process, the substance may serve as a kind of predigested or partially digested food." Selous (1933) devotes a chapter to "The Origin of Domestic Cleanliness in Birds" in which he conjectures that "the first motive" was "the gustatory one."

Blair and Tucker speak of 3 stages: swallowing; removal; and later, evacuation of the young on or over the nest edge. They give 2 instances of "spring cleaning" in Pied Flycatcher and Wryneck: "on the day after the nestlings flew the parent birds returned and cleaned up every particle of excrement, leaving the nest-box clean" (1941:241). Biting of the anal region of the young as a stimulus to defecation has been reported for Flickers (Sherman 1910), Wren-tits (Erickson 1938), and Wrynecks (Bussmann 1941). Smith (1941) speaks of parents' tugging at down on the nestlings' back.

That nest-sanitation is a purely instinctive act is pointed out by the Heinroths (1924) who found a nest of the European Jay with a pile of excrement on the rim; apparently the male roosted above the nest on which his mate was incubating.

Birds have a strong impulse to remove foreign objects from the nest while it contains young; the disposal of excreta is a specialized form of this instinctive activity.

"Egg-Shell Disposal by Birds" is discussed in general and in detail by the Nethersole-Thompsons (1942a), in particular as to "how, when and why the egg-shell loses its status to become a redundant, if not undesirable, body in the nest." An amazing variety of responses are described.

D. RECOGNITION OF YOUNG

A striking example of conditioning to a situation and of failure to adjust to a change even when young were involved is given by Howard in "The Nature of a Bird's World" (1935:42-44).

> "Here is a Linnet's nest in which the eggs are hatching. It is 6 A.M., in a few hours all will be hatched. Ten A.M. comes and one egg is still unchipped; so I remove it that it may not confuse the parent or obscure the experiment. Then I place a forsaken Linnet's nest against the real nest and transfer the young.
>
> 10:14 A.M. The hen broods the empty nest.
>
> 10:16 A.M. She raises herself, looks at the young and squats again.
>
> 11:14 A.M. The cock settles on the forsaken nest and feeds the young, staying six minutes to clean the nest.
>
> 11:45 A.M. She leaves.
>
> 11:55 A.M. Both return: she bends her head to the bottom of the empty nest, holds it there, and then broods emptiness; he feeds her, goes to the young and flies away.
>
> 12:00 P.M. She rises, feeds the young by regurgitation, cleans the nest and broods the young.
>
> 12:09 P.M. She moves to brood the empty nest.
>
> 12:12 P.M. She flies off.
>
> 12:20 P.M. She returns to brood the empty nest.
>
> So the stupid bird broods over an hour on emptiness. I do not mean that she alone is stupid; her race is stupid, for one broods a vacant nest and works her feet to turn the eggs that are not there; another, like the Reed Bunting, springs up and down on the bottom of the nest to make the young stretch up for food and behold, they are not there; another like a Hummingbird, goes through the movements of shaping the nest though no nest is there. . . . If I had not moved the young into a strange nest I should not have known that when she broods and when she feeds her young she lives in different worlds. By 'different world' I mean that each internal state has its own external world. Brooding is an internal state, its external world the nest. While the Linnet is away I move her young into a strange nest and she broods the empty nest. Well, did she not find a site for the nest, build it, and for near a month live in a nest world? Think of the force of habit and her action does not seem strange; but think how accustomed she must have become to the eggs by sitting on them, by using her feet to turn them, by spreading her feathers to cover them, and her action does seem strange and needs something more than habit to account for it. She cannot know her young, which she has felt but never seen, in a nest she has never seen. But emptiness—that should trouble her!"

That many passerines have no *instinctive* recognition of their own young is clearly shown by their readiness to adopt Cuckoos and Cowbirds. Song Sparrows with fresh eggs were given Yellow-breasted Chat eggs nearly ready to hatch; the foster parents raised the young Warblers (Young 1895). In another case Song Sparrows raised Kingbirds; after leaving the nest the Flycatchers did not seem to relish some of the meals given them (Strong 1891).

However, some parasites in the Old World closely "mimic" their hosts. In Africa with some of the Whydahs (*Viduinae*) the young resemble the hosts in the coloring of the inside of their mouths and also in their first plumage. The Asiatic Koel (*Eudynamis*) parasitizes Crows and Starlings—its young are black; the Koel of North Australia parasitizes hosts that are brown, its young are brown (Stresemann 1927-34:428-9).

It is clear that many passerines do not *learn* to recognize their young while in the nest.

When 1M's young in June 1929 were 5-7 days old, I exchanged them for a few hours with a brood of House Sparrows about the same age, but very different in appearance, for the latter were still naked. Both sets of parents fed the changelings.

In experiments with Black Phoebes Kinsey (1935) was able to get nesting birds to accept newly hatched young in place of fresh eggs, young ready to leave in place of small young, half grown young in place of young ready to leave, and young ready to leave in place of slightly incubated eggs. One pair, however, would not accept eggs in exchange for half grown young.

"The stimulus for feeding-the-young behavior is normally the presence of nestlings calling for food in the nest, or of fledged young similarly calling in the nest vicinity" (Emlen 1941:217). "The identity of the nestlings in the nest is apparently of minor importance in the Tricolored Red-wing, for no difficulties were encountered in transferring young from nest to nest up to the end of nestling life. . . . Advanced (9 days) nestlings were successfully established in place of 3-day-old young in one nest and 2-day-old young in another. . . . Two-day young were introduced into one nest when the rightful young were 10 days old and the attending pair was thus induced to feed nestlings for 17 consecutive days. Feeding behavior in one nest was discontinued with the removal of the 2-day-old introduced nestling, then resumed 7 days later when the rightful eggs hatched."

The passerine bird responds first to what is *in the nest;* here form, touch, motion, color and faint sound are stimulating. If a small nestling gets outside the nest, the parents do not recognize it. Song Sparrows never attempt to push back into the nest one of their young pulled out by accident, although they will remove dead young *from* the nest. Passerines in Europe let their own offspring, ejected by a nestling Cuckoo, perish before their eyes. The same was true of a young Black Stork that got out of the nest on to the rim (Siewert 1932).

"With the absence of a proper response on the part of the young, the parental instinct disappears" (Howard 1907-14:86). The nestling must play its part. A number of cases have been recorded where parents ate their dead young—Black-throated Blue Warbler and Red-eyed Vireo (Harding 1929), White Stork (Schüz 1936), and Hobby (Friedmann 1934:31), while a mother Marsh Hawk picked up a dead nestling and fed it to its brothers (Breckenbridge 1935).

It is clear that this lack of personal recognition of young is widespread among birds with altricial young: Columbidae, Falconiformes and others (Heinroth 1938a), Herons (Allen and Mangels 1940), and probably many others. *So long as the parents respond to what is in the nest, there is no need for personal recognition.*

As the young grow older, their vigorous calls incite parental care even outside the nest. When using Cowbirds as bait in traps for catching foster parents, I found the nestling had to be at least 7 days old in order to call sufficiently loudly to induce the Song Sparrows to enter the trap (1933a). I once returned 12-day old Song Sparrows to their parents (with whom I had left part of the brood): the active individual was at once adopted; the other that was ailing and quiet was ignored. A pair of American Robins in Columbus fed a young stranger recently out of the nest along with their own brood of about the same age; Heinroth (1938a:35) reports this as characteristic of the European Blackbird.

Song Sparrows probably recognize their young personally some days before they become independent. 4M drove 1M's young several days before he drove his own young that were some 2 days older and 1M reciprocated. Lorenz (1935:292) believes that Corvidae (except for the European Jay) that lead their young for some time come to know them personally.

Heinroth (1938a:32) points out that although most birds will accept a strange egg, if the chick that hatches is too different from the foster parent's species in appearance, voice or behavior, it will either be ignored or treated as a nest enemy. However the Eagle Owl (von Korff 1938) raised ducklings, and the Great Horned Owl (Holland 1926) and Short-eared Owl (Dubois 1923) chicks.

Many parents know their precocial young after a few days, although not as early as the young know their parents (Lorenz 1935:292). Gulls and Terns soon know their own young, in some cases by voice as well as appearance. When Terns have been given eggs or young of other species, they sometimes have brooded the young, but failed to feed them. Common Terns hatched Roseate Terns, but the begging note of the latter apparently was too weak to induce feeding behavior (Palmer 1941); Little Terns hatched Kentish Plover which hunted food for themselves (Goethe 1939). However, a pair of Common Terns raised a Herring Gull; it showed no escape behavior and failed to develop the specific scream (Kuhlemann 1939). Common Gull eggs, given to Black-headed Gulls, were hatched and the young raised, and 79 banded (Schüz 1939). Grey Herons hatched Stork eggs (Blockey 1939) and Black-crowned Night Herons Snowy Egret eggs (Allen and Hickey 1940), but in neither case were the young raised.

"There is good evidence," writes Lashley (1938:452), "that animals without previous experience may give specific reactions to biologically significant objects and that the recognition or discrimination of these objects may be quite precise." If Sooty Terns were given eggs of a related species (Noddy Tern) "to hatch they would invariably reject the foster children within a short time after hatching, throwing the chicks out of the nest and sometimes killing them. Strange chicks of their own species were accepted during the first few days of brooding. The chicks of the two species did not differ greatly in appearance, yet the discrimination was certain. I was unable to discover the sensory basis of the reaction, beyond getting indications that it depended upon a complex of stimuli, not wholly visual. The history of these birds was of course unknown but the number of individuals observed, considered in relation to the death rate of the colony, makes it certain that some at least were dealing with their first brood."

In regard to fish, Noble and Curtis (1939:45) found that "cichlids which have had no previous brooding experience will adopt and rear young of other species", but experienced cichlids will not do so. They will "adopt other young of their own species provided there is a difference of not more than 2 days between the ages of their own and the introduced young."

E. HELPERS AT THE NEST

In Chapter VI cases were mentioned where young of the first brood helped feed young of later broods. It occasionally happens that a bird of one species will feed young of another species, either in the latter's own nest or after leaving it. A male Bluebird fed House Wrens, a male Scarlet Tanager fed Chipping Sparrows (Forbush 1925), a male Junco fed Bewick Wrens (Williams 1942b), a male Song Sparrow fed Robins (Twombley 1934), all while their mates were incubating. Here the young of a neighbor stimulated the males to premature feeding activity. Other instances are given where birds feeding their own young also feed other young, or where a bird that perhaps has lost its own brood persists in feeding young of other species despite the antagonism of the parents. After it has left the nest, the young Cuckoo is often fed by birds that did not foster it, and this is occasionally true of the Cowbird.

When I brought the 13 and 14 day Song Sparrows and 17 day Cowbird from Michigan to Chicago on June 28, 1939, I wondered whether Y would feed them. The Song Sparrows never begged to him, although the Cowbird did. Y did not feed them, yet he evidently had a preliminary impulse to do so, for he carried mealworms about for considerable periods, mouthing and crushing them. On June 30 he treated mealworms in this way for 5, 10 and 18 minutes, on July 1 for 12 minutes. This behavior soon disappeared.

Caged Song Thrushes, European Robins and other birds near the end of the normal nesting season will carry mealworms about, as if trying to feed them to non-existent young (Heinroth 1938a:36, Lorenz 1935:293).

With a few species "unmated helpers" seem to be of fairly regular occurrence. Skutch (1935) describes this behavior in 3 Central American species: at 5 nests of the Central American Brown Jay, which does not become mature until 2 years of age, from one to 5 yearling birds were in attendance feeding and guarding the young; with the Black-eared Bush-tit, where there is a preponderance of males, extra males assist in nest building and feeding the young, from one to 3 at each nest; with the Banded Cactus Wren from one to 2 helpers were present. With the Long-tailed Tits in Europe there are many records of several birds feeding at one nest. With the Bush-tit in California a third bird often helps in nest-building, incubating, feeding and brooding the young (Addicott 1938). A helper has been recorded while Chimney Swifts feed young (Day 1899, Sherman 1924), and also with Bicknell's Thrush (Wallace 1939). Extra birds of either sex have been seen feeding at nests of the Tree Swallow (Wetherbee 1933a, Bent 1942), European Barn Swallow (Moreau, R. E. and W. M., 1939), Violet Green Swallow (Shirling 1935), and Bluebird (Wetherbee 1933b). A second Black Redstart in better plumage than the father, helped feed young and clean the nest; the parents were not hostile, but were disturbed and "their efficiency in feeding the nestlings was impaired" (Ashby 1942:203).

F. SUMMARY

1. The bird that incubates the eggs, broods the young. The newly hatched young may be brooded nearly as much as the eggs, but brooding decreases regularly, depending partly on the weather, and practically stops by the time temperature control is established.

2. Both parents may shade the young from the sun. A Robin shaded her empty nest while her young lay in a bowl beside her.

3. Where the male does not assist in incubation, it is a question as to how he knows when the young have hatched. With the Song Sparrow the male has been seen to examine the nest before he starts to feed. With some other species the female changes her behavior at this time.

4. The rate of feeding typically increases with the age of the young in birds that leave the nest early; in those that remain until ready to fly, there is apt to be no increase after about 10 days.

5. Table XXIV gives the results of 137.5 hours of observation on the feeding of 7 broods of Song Sparrows; the rate of feeding for the first 5 days of nest life averaged 7.2 times an hour, for the second 5 days 17.8; the average for the whole period was 11.1 times an hour. The rate increased in the last half

of nest life 2½ times over that in the first.

6. With the increase in size of the young, more food is brought, either more frequently or in larger amounts.

7. The part played by male and female depends partly on circumstances, such as the brooding of the female, and partly on the individuality of the birds. In a number of species males are apt to bring larger portions than are females.

8. The number of objects brought at a trip varies greatly.

9. At 6 nests of passerines watched from blinds the average number of young fed at each trip was 1.3.

10. Table XXV gives data on the hourly feeding rate for 10 passerine species throughout the nest life; these range from 2.3 times an hour for Ovenbirds to 39.7 times an hour for Great Tits. This nest of *Parus major* affords one of our *highest daily records*—793 meals brought to the 9 young when 11 days old.

11. Assuming that only 1 young is fed each time, in 7 of the species each was fed about 4 times an hour.

12. Many young passerines seem to need 20 to 30 full meals per day, although in nature many of them may get 3 times as many small meals.

13. Where feeding is by regurgitation, the number of trips are fewer.

14. 1M and K2 showed evidence of facilitation with practice in parental activities.

15. In 35 studies on 28 species the percentage of times excreta were removed in terms of number of feeding trips ranged from 9 to 67 per cent, the median being 25.

16. Passerines and many other birds with altricial young do not, as a rule, know their young in the nest personally either instinctively or through learning; they respond to what is *in the nest;* form, touch, motion, color and sound stimulate parental activity. Outside the nest, pronounced sound and motion are stimulating.

17. Some birds with precocial young seem to recognize them instinctively; others come to know them in a few days.

18. Birds sometimes respond to the begging behavior of young of other species by feeding them. In some species instances of one or more "unmated helpers" seem to occur fairly regularly.

CHAPTER XX

Defense of the Young

Concern of the parents typically increases with the growth of the young, reaching a climax at about the time the young leave the nest. Where both parents care for the young, they may be equally solicitous, or one or the other may show the greater concern. Sometimes this difference is specific (as the male in some of the Limicolae, the female in others); sometimes it is individual.

In many species the male shows a strong tendency to *defend* the young, even if he does little or no feeding of them. This is true with the European Wren, that seldom feeds the young in the nest, but feeds and defends them as soon as they leave, expressing his excitement with continued "ticking" (Kluijver et al. 1940). See also examples later in this chapter under "Attack".

A. LURING THE YOUNG

The function of the different activities by which parents at times induce their young to follow them usually can be interpreted as an attempt to bring the young into positions of greater safety. This is apparent in many cases, but not at first thought in those cases where parents coax young out of the nest. Here, also, when young are able to leave the nest, it is advantageous for them to be outside and separated, for then the whole brood would not be lost to a predator.

Song Sparrow young leave so early in life that it is probable their parents seldom have the occasion to lure them from the nest. There are 2 instances, however, of adults trying to get young birds already out of the nest, to follow them to places of safety.

I was watching from a blind a nest with 8 and 9 day old young; I placed near the nest a 12 day hand-raised bird; the pair fed it and tried to lure it into cover. A parent would put its bill into the bill of the young bird, then withdraw it quickly; sometimes the bill held food, sometimes it seemed empty.

A tame male Song Sparrow tried to lure his young from the hands of the Schantzs (1937). "He brought food close to them and then hurriedly ran a short distance across the lawn. He then looked back, and, seeing he was not followed, repeated the performance. Over and over dozens of times, he tried, but in vain, for the young were imprisoned in our hands."

The most dramatic luring which I ever witnessed was that of a female Black-throated Green Warbler trying to get the last young bird from the nest the day after the first two had left; by offering food and withdrawing it, by holding it up out of reach, and by dangling it in front of the little bird, she was able to get it out of the nest tree to the ground and finally into a little pine tree 15 meters from the starting point (the Nices 1932, Nice 1939a).

Luring the young out of the nest has been reported as an occasional happening with a number of altricial species.

Little Flycatcher: a female enticed a fledgling "to hop along the ground by getting near him, uttering a tender trill and fluttering her wings" (Bennett 1934).

Barn Swallow: a pair "flew slowly on hovering wings back and forth through the shed . . . uttering soft, coaxing notes" (Smith 1936). In England one pair, when the young were ready to leave, "fed very irregularly and most visits were feints" (the Moreaus 1939).

Tree Swallow: "Within a day or so of the fledglings' leaving, the adults definitely attempted to coax the young to leave. They could be seen flying to the boxes without apparently carrying any food. The adult would perch at the opening for a moment, flutter off, and then return" (Kuerzi 1941:34).

Prairie Horned Lark: a female coaxed the last bird from the nest by holding food before it (Pickwell 1931).

Spotted Flycatcher: parents put food into the mouth of the last nestling, then withdrew it (Steinfatt 1937e).

Bonelli's Warbler: the male entices part of the brood up into the trees by holding food before them and calling (Heilfurth 1935).

Yellow Warbler: female alighted on tree and held food a foot or 2 above newly-fledged young (Cottam 1936).

Ovenbird: one female "went through the motions of feeding when she had no food" (Hann 1937:186).

House Sparrow: the male sometimes lures young from the nest with attitude and notes usually used to lure the mate to the hole chosen for the second nesting site; he also pretends to feed (Daanje 1941:25-26).

Red-eyed Towhee: a male tried to lure a fully grown young Cowbird from an orchard to a rose-bush (Neff 1926).

Wryneck: young are sometimes stimulated to leave by parents' not bringing food near the end of nest-life (Bussmann 1941).

Bald Eagle: at the end of one nesting (but not of others), the young were given almost no food; the female brought a fish near and flew off with it, thus inducing the last bird to follow her (Herrick 1934:174-175).

Nighthawk: the female "would back off or fly a short distance" away with a tempting morsel (Gross 1926:43).

Luring the young with pretence of feeding has also been reported for some precocial young: Common Terns coax their young to follow them by holding their bills before them and then drawing back (Goethe 1939:46); Little Terns do the same by holding a fish before the young and then retreating (Goethe 1939:54). A different technique was observed by Yeates (1936) with a Stone Curlew, where a blind had been placed over newly-hatched chicks; a parent "tried to lure the young away from the tent by brooding a few feet from them, her brooding patch being fully fluffed out."

A social method of getting young to safety is shown by the Common Gull: when 2 to 3 week old young are frightened they take to the sea; if the water is calm, the adults pay no attention, but if it is rough, 20 to 30 adults settle on the water in a semi-circle around the young and swim towards them, some splashing the water with their wings, thus driving them back to land. When the young are Herring or Black-headed Gulls, the Common Gulls often attack them (v. Töne 1939).

It is clear that parents of many species at times lure their young by movements, calls, pretence of feeding, and with food as bait. Such behavior is not often seen, but it evidently is latent in the instinctive equipment of many species of different orders.

B. REACTION TOWARD ENEMIES

This subject is treated in Chapter XXI largely from the standpoint of the adult Song Sparrow as an individual; here we will consider the behavior of parent birds. Birds react differently to different enemies, and also react differently according to the stage of the nesting cycle.

In his interesting paper on the Chiffchaff, Treuenfels (1940:521-523) describes the behavior of the Phylloscopi in relation to enemies in the territory: "ground enemies"—man or dog—elicit "alarm notes" during the nesting season, but are ignored at other times; harmless flying birds are ignored or elicit a brief warning; but the appearance of a dangerous flying enemy induces the Warblers to freeze. Everything that approaches the nest is a "nest enemy"; small birds are driven off, while a shrew was attacked. Much the same could be said for the Song Sparrow.

The common responses to the approach of enemies near the nest or young are giving warning cries, leading the enemy away, threat, mobbing, and attack.

1. *Warning Notes*

Warning notes are not given by birds as "warning" in the usual sense; the birds are not telling their young or companions of danger, they are expressing their own fear. A bird "warns" when alone. They "warn" more readily when they have young, and especially (with passerines) rather large young, for at this time they are in a state of heightened sensibility.

The *tchunk* is given by both parent Song Sparrows at the approach of person, cat or dog, while there are eggs or small young in the nest. When the latter are nearly ready to leave, or have just left, both birds, and especially the female, use a great variety of notes—

tik, ick, yip, jib, etc., when an enemy is near. The young respond to these notes by silence. I have often noted this response on the part of the young of Wood Warblers (Nice 1932a, the Nices 1932).

Chiffchaffs just before and after leaving the nest become silent on hearing their mother's alarm notes (Treuenfels 1940:520). Young Arctic Three-toed Woodpeckers kept up a buzzing noise except when a Red-breasted Sapsucker "flew past the nest just as one of the parents sounded a harsh, clicking alarm call some distance away" (England 1940). The Brown Towhee gives a *tsink* that induces fledglings to freeze even at the age of 43 days (Quaintance 1941). Nuttall Sparrows warn young with a faint *tit* note; when 7-9 days old "they respond to it by stopping their food cries and crouching down" (Blanchard 1941:29).

An interesting observation was made on the European Avocet by Makkink (1936:61): "about the time when the eggs hatch, the Avocet gets a second alarm-call, by means of which practically only gulls are signalized and pursued. For man, mammals and other birds apart from gulls the ordinary alarm-call is sounded. . . . The 'gull-cry' has been taken to be a part of the hereditary equipment, which enables the Avocet to announce its chief natural enemy."

After the young Song Sparrows came out of hiding at the age of 17 days, I have twice noted the male giving the fear note *tik-tik-tik* when I approached the young. Each time the young bird became silent.

2. *Deflection, Distraction Display or "Injury-Feigning"*

The instinctive response in face of danger to eggs and especially to young of drawing attention to the adult and away from the offspring, is usually termed "injury-feigning". It would be better to call it "nest-protecting display" (Murphy 1926) or distraction display.

In the Song Sparrow *this display does not simulate injury.* The bird runs about close to the intruder holding its wings stiffly erect and its tail depressed. This was the typical response of parent Song Sparrows when young of 6 to 7 days old shrieked while being banded. Once I saw it in a mild form when the eggs had just hatched; the female flushed from the nest, ran down the bank next me and then ran along with wings raised. Whenever I banded young just ready to leave the nest, the parents gave the distraction display. The 204s gave it when I took their 9 day Cowbird out of the nest and the bird screamed.

One Song Sparrow was caught 4 times between the age of 23 and 31 days.

23 days: catch Blue in trap. 204M *tchunked* at me. 204f was probably on her nest with her second set. Blue was silent.

25 days: catch Blue and 204M in trap; Blue screeches. 204M *tchunks* in the other part of the trap. 204f comes dashing over, giving a note like *puh puh puh,* and running about nearby, but not with uplifted wings.

28 days: catch Blue in trap; it screams, holding its wings up. Parents give vigorous distraction display. 204M gives a song, my only instance of singing under such circumstances.

31 days: catch Blue in trap; it screams. 204M comes *tchunking*, but is very calm in comparison to 3 days earlier.

In Pelham in August 1940 I tried to catch by hand a Song Sparrow that had just left the nest. It ran in among the bushes and both parents came rushing to the scene, the presence of 3 birds instead of one proving so confusing to me that I lost track of the fledgling.

Distraction display in some form or other has been noted in a very large number of birds, mostly non-colonial ground-nesters. I have found records for 13 orders and among the passerines 16 families. These are listed in Appendix V.

At some 200 nests of Mourning Doves in Oklahoma, I found that the "broken wing" ruse was never shown at about 30 per cent of the nests; a few birds "showed it throughout the nesting cycle, but most exhibited it only when the young were half or nearly grown" (1923:57). In its extreme form, the birds "throw themselves on the ground near the intruder and flutter about as if seriously injured. More often . . . the bird flies some distance, perhaps 10 to 30 yards, flutters a little on the ground, stops and waves its wings, then walks along waving its wings, making little flights into the air and then again walking along flapping its wings; in these cases the pretence of injury has degenerated into a mere form," p. 37.

Some authors (Hudson 1920, Dewar 1928, Friedman 1934, and Mousley 1937a) have considered that "injury--feigning" is a "compromise between fear and reproductive emotions" (Friedmann 1934), "the result of conflicting emotions" (Mousley 1937a). But most observers think otherwise. Lack, however, suggests that this may have been the *origin* of the display (1941).

The fullest discussion of the subject is that by Jourdain (1936, 1937). Besides quoting a great array of instances, he points out that, " 'Fear,' in the sense in which we use it of ourselves, hardly enters into normal bird life. . . . Man does not normally inspire fear in birds; they are quite aware of his limitations and keep out of his reach, but that is all" (1936:68). When an enemy approaches a nest on which a bird is sitting, the bird may do one of 3 things. If the enemy is formidable and resistance is useless, the bird flies away. If it is one where "the safety of the eggs or young can be secured by leading the attacker, generally a small mammal, away from them by slowing down her movements while keeping just, but only just, out of range," then "injury-feigning" may be shown. If "the intruder is known to be harmless, but may injure or destroy nest or young by crushing or treading on it," then attack is used. The Curlew (*Numenius arquata*) flies up in the face of a grazing sheep. A Killdeer did the same with a horse or cow, but flew to meet man and dog "from afar, indulged in all the broken-winged helplessness with which we are familiar and led the enemy far from the nest before returning to it" (Taverner 1936).

A Lapwing used threat, attack and finally deflection in attempting to drive sheep from his nest (Nethersole-Thompson 1940). A Wood Duck through "feigning injury" enticed a Red-shouldered Hawk from the vicinity of her brood (Saunders 1937). Deflection tactics have been reported as displayed by Stone-Curlews before a blind in which the young were hidden (Yeates 1936), and by a Ringed Plover before artificial eggs placed on the rim of its nest (Koehler and Zagarus 1937).

The ruse has been successful with coyotes, foxes, stoats, weasels, dogs, cats (Jourdain) and man (Erickson). From his experience in Australia, Chisholm (1936) suggests that it might "have developed from encounters with reptiles and small mammals."

The situation predator-near-nest releases this nest-protective display, the function of which is to call attention to the parent and away from the young. If the predator follows the bird, the stimulus continues until the predator is no longer near the nest. If the predator remains by the nest, the stimulus is increased and the bird returns to display near the predator until the response tires. The bird certainly does not consciously imitate a sick or wounded individual. The display is part of the bird's repertoire of instinctive actions, yet it is not employed absolutely blindly; the bird responds to different enemies differently, and its subsequent behavior differs according to the response of the enemy. The intensity of the reaction typically increases during the nesting cycle. Some birds, as Mourning Doves (Nice 1922-23), and shore birds may show it with eggs, especially well-incubated eggs. With many birds, both precocial and altricial, it is at its height when the young are leaving the nest.

3. *Threat*

Song Sparrows sometimes use on other species that come near their nests techniques normally used on their own species. They puff up at Cowbirds and use *zhee* occasionally at Juncos, Cardinals and once (K3) at a baby rabbit. Three times they seem to have attempted to intimidate human beings. The tame male whose young were being held by the Schantz's, after vainly trying to lure the young, rushed at Schantz "with open bill and spread tail, making a hissing sound." (His third attempt was the distraction display.) Both 4M and 204f came near me and uttered notes like *puh puh puh* when I had trapped their young.

Nethersole-Thompson (1940) describes "three different methods of nest-defense—threat, deflection and attack directed by the same bird [Lapwing] within the space of a few minutes." The male was incubating "chipping" eggs as a sheep and lamb approached the nest. "The Lapwing rose and, with wings fully raised and shaken, he ran right up to the sheep. All the time he called persistently a shrill *peet-peet-peet,* normally associated with sexual excitement. In this display, as in the 'injury-feigning' performance, the white underwing surface with its dark edges contrasts vividly with the darker plumage." As the animals took no notice, the bird rose and several times struck the lamb. "This also failed to move the sheep, and the Lapwing next squatted and employed the 'injury-feigning' antics . . . one wing was outstretched and shaken as if broken while the other was alternately raised, shaken and lowered." The threat display was once directed at this author "by a bird with young which I surprised while cycling."

The Texas Nighthawk when on the nest goes through a spectacular intimidation display with wide-open mouth and spread wings to a human being approaching on all fours, but leaves the nest with "distress simulation" when approached by a person on foot (Pickwell and Smith 1938). A male Dusky Poorwill showed much the same attitude to human intruders except that he spread his tail "showing all the tail spots", and gave "a low guttural hiss" (Aldrich 1935:51).

A Spotted Sandpiper shown in a movie film gave an intimidation display with wings held straight up in the presence of a ground squirrel, an entirely different attitude from that taken in the distraction display, where the male "curled itself, as it were, into a little ball" (Mousley 1937a). Carl Maslowski's film of the Black-necked Stilt shows deflection behavior by both parents before a flock of sheep, but threat by the female when facing a new-born kid. A Mourning Dove will sometimes raise its wing and stay on its nest until the observer can almost reach it. Occasionally an Alpine Swift instead of leaving its young, will remain, flapping its wings and snapping its bill; this behavior was also seen in a 3 weeks old bird (Bartels 1931:22). Bitterns, Owls, Doves and others put on intimidation displays. Titmice and Wrynecks habitually hiss when disturbed on the nest.

"Warning Displays" among different animals, vertebrate and invertebrate, are discussed by Cott (1940:208-225). He describes "Displays depending upon an increase in size," "Sudden exhibitions of conspicuous colour," "Advertisement by movement" and "Warning sounds". The Lapwing exhibition utilized all four of these techniques, the Song Sparrow's (when he rushed at Schantz) all but the second, the Poorwill's all but the third. Cott points out that warning sounds are not loud because the enemy is near.

4. *Mobbing*

The tendency of small birds to "mob" an owl, snake, or occasionally a quiet Hawk, has been mentioned in Chapter VII. Bolles (1890) used to take his pet Barred Owl that had an injured wing out-of-doors to test the effect on the bird population; there was much more response in summer than in winter, the birds that reacted most strongly being Thrushes, Vireos, Catbirds, Thrashers, Ovenbirds, Woodpeckers, Crows and Blue Jays. This mobbing tendency occurs throughout the breeding season at the same time that territory is rigidly held.

With Snow Buntings, while the presence of human beings "caused disturbance in one or two pairs at the same time, an Arctic Fox was surrounded by quite a flock of screeching birds" (Tinbergen 1939c:60). Yellow-headed Blackbirds leave their nests and territories to mob an enemy when an alarm call is given; once an American Bittern was severely attacked (Fautin 1941:116).

With the Wren-tit a "loud, continuous *krrr* . . . is a scolding or mobbing note. . . . If a jay is discovered in the territory, the pair follows it and both birds utter this sound continuously until it leaves. The jay seems quite indifferent. The same note was used to mob a sharp-shinned hawk that was perched in an oak. Once a snake appeared to be the cause" (Erickson 1938:304).

"Many species of Gulls and Terns—in the manner of passerines heckling an Owl—will mob an enemy, diving at it, spraying it with excrement, and even attacking," writes Vogt (1938:35). "Some of the shore-birds (Bent and others), will repel invaders in much the same way. The Willet, whose territorial intolerance has already been described, disregards all territorial boundaries when repulse of an enemy is involved. Dogs running through the nesting grounds . . . are followed by a motley mob of screaming, darting Willets that join the group from long distances. This, then, would seem to be normal behavior for many species of this interesting family. One needs to see nothing more than the hasty retreat beat by Crows to surmise its effectiveness, for Willets."

The Marples devote a Chapter in their book on "Sea Terns or Sea Swallows" (1934) to "Attacks and Defence", describing how Common and Arctic Terns mob in flight and drive off Gulls, Crows, Rooks, Herons, Hawks and man. Goethe (1939:46) tells how when he went near a great swarm of non-nesting Common Terns in the evening they swooped upon him silently and tried to drive him off with a strange noise made by their wings, somewhat as Starling flocks behave towards a European Sparrow Hawk.

Concluding from his experiments with a Blue Jay that was shown a Great Horned Owl mount, Rand (1942) suggests that "the conflict of exploratory tendencies and avoiding tendencies, resulting in substitute or irrelevant screaming, may be what is known as 'mobbing a predator.' "

5. *Attack*

The only enemies which I have seen a Song Sparrow attack are other birds—in particular Cowbirds, and small snakes, which were greatly disliked by K7, but ignored by her mate 1M (Nice 1939a).

Many birds, however, do attack intruders. Mockingbirds strike cats, dogs and even a box turtle, while many swoop at and occasionally strike human beings—Brown Thrashers, Swallows, Hawks, Owls, Skuas, Gulls, Terns, and many others.

Lorenz writes that the male in many Phasianidae pays no attention to the young unless they are caught by an enemy, when he at once comes to their rescue. Golden Pheasant and Muscovy Duck males in late summer will attack anything that catches any bird of their species (1935:302). At the Kellogg Bird Sanctuary in Michigan a Whooper Swan started to attack a young hand-raised Canada Goose, but was in turn attacked by an adult male Canada Goose.

Some birds that nest colonially seem not to recognize enemies until the latter are at their own nests, as Black-crowned Night Herons (Allen and Mangels 1940), Cormorants and others. With such birds colonial nesting does not function for defense as effectively as with species that recognize danger from afar and go to meet it.

C. Break-up of the Family

When the young Song Sparrows become independent at the age of about 4 weeks the family bond dissolves. The 204s were greatly concerned over their 28 day-old young, but much less so 3 days later. 1M alternately fed and pecked his young when they were 28 to 30 days old. Although they fluttered their wings when meeting him at the feeding station for a day or two longer, 1M gave them nothing more, being occupied at this time with a new family.

If a new brood is being started, the mother takes less and less interest in the fledglings, soon leaving them entirely to the care of the father. In 1929 K2 fed her first brood till they were 20 days old and her second till they were 15. The longest periods of feeding observed in the case of females have been 25 days from hatching by K111, 26 and 27 days by K7, and 28 days by K14 with her last brood.

It seems to be the rule with birds that raise more than one brood for the family to break up as soon as the first young can care for themselves, but the bond may be prolonged with the last brood (Sherman 1924). This is certainly true of Cardinals. The break-up probably occurs more or less spontaneously, although in some cases there is certainly some pressure from the parents. Song Sparrow parents drive off their own full grown young as readily as strangers. A pair of Lichtenstein's Orioles drove full-fledged young away from the new nest being built (Skutch 1935). Flocks of Chickadees have been found not to consist of "family parties" (Butts 1931, Odum 1942). The resident Nuttall [White-crowned] Sparrow feeds its young till 32 to 35 days old, the migratory Puget Sound [White-crowned] Sparrow till 25 to 28 days (Blanchard 1941).

In some species the family may stay together throughout the summer or even longer. This is sometimes true of Bluebirds, while Wren-Tits stay together for 6 or 7 weeks (Erickson 1938). With tame Greylag Geese young stay with their parents until a new family is started the following spring, then rejoin the parents in fall and remain with them until winter when they find mates of their own (Heinroth 1912a).

D. SUMMARY

1. Parents of many species occasionally lure their young to places of greater safety by movements, calls, pretense of feeding, or with food as bait.

2. Warning notes express the bird's own state of feeling. Young often respond to such notes by silence.

3. In the so-called "injury-feigning" the bird does not consciously imitate a wounded individual, nor is it a victim of conflicting emotions. This nest-protective or distraction display is widely spread through Class Aves, having been reported in at least 13 orders, and in 16 families of Passeriformes. It is an instinctive response to the situation predator-near-nest and it functions to draw the attention of the enemy from the nest or young to the parent that later escapes.

4. Intimidation displays in both vertebrates and invertebrates utilize one or more of these features: increase in size, sudden exhibition of conspicuous color, movement, and warning sound.

5. Mobbing of an Owl or snake occurs with passerines, while many birds, from Yellow-headed Blackbirds to Terns and Willets, by mass action drive off potential enemies.

6. Many birds attack nest enemies, even though the latter are much larger than they. Some males that customarily pay no attention to their young will defend a young bird of their own species when it is attacked.

7. With many passerines the family bond dissolves as soon as the young become independent at about 4 weeks.

CHAPTER XXI

Enemy Recognition

The subject of reactions to enemies has been discussed for the young bird in Chapters II to IV, and for the parent bird in Chapter XX, while some responses to warning of other birds were mentioned in Chapter VII. Now it is pertinent to ask how a bird knows an enemy. In analyzing this problem, I will describe the behavior of the Song Sparrow when alarmed, tell of the observed responses of some passerines to predators, and mention briefly some experiments on enemy recognition. The recognition of the adult Cowbird as an enemy by its hosts is a problem by itself.

A. BEHAVIOR OF THE SONG SPARROW WHEN ALARMED

Three stages of fear may be distinguished in this species:

Stage	Note	Postures
"Alarm"	*tchunk*	Crest raised; tail raised and flipped; wings flipped; restless change of location.
"Fear"	*tik*	Feathers compressed; neck elongated; body crouched.
"Fright"	*tik-tik-tik*	Flies and hides; if caged, flutters in attempt to escape; pants with open bill.

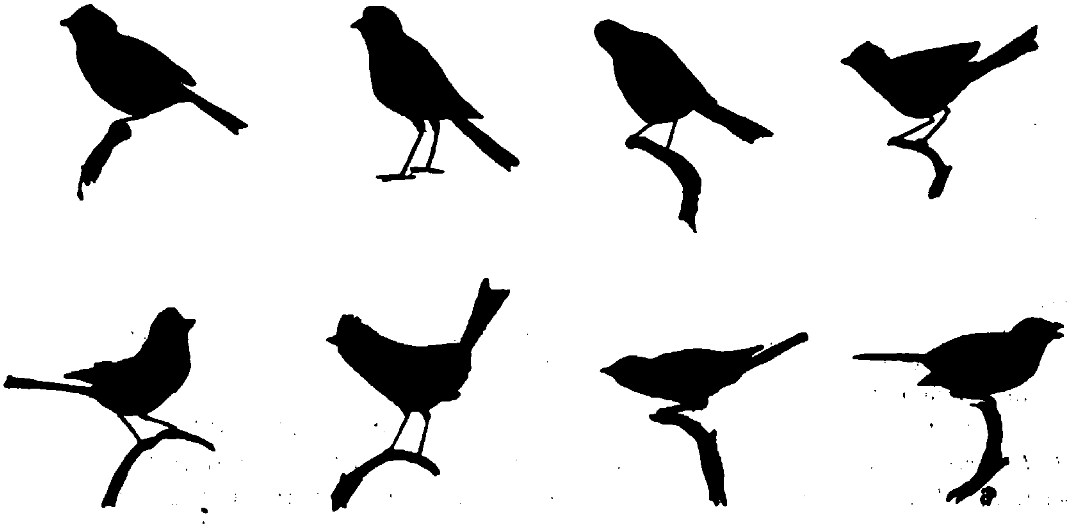

FIGURE 5. *Attitudes of Song Sparrows in Alarm, Fear and Fright. From left to right (upper row): 1, unalarmed; 2, alert; 3, turning head to look; 4, 5, alarm (wings and tail flipped); 6, strong alarm; 7, fear; 8, fright (panting).*

These descriptions show "alarm", "fear" and "fright" in their extreme form; in milder cases some of the characteristics are not exhibited. All the characteristics of the first stage except the raised crest may be shown separately in situations that obviously have nothing to do with alarm. *Tchunk* is the "ordinary" note of the male Song Sparrow on his territory, sometimes it seems to express self-assertion, sometimes it is a sign of disturbance and often appears to have an element of "protest" in it.

With the hand-raised males it was often given while bathing; here it might be considered vocal self-assertion while temporarily hampered by wet feathers. It is seldom heard from the female except during the nesting season; she often gives it after leaving the nest while incubating, and utters it more vigorously upon the approach of an enemy to her nest.

Raising the crest with the Song Sparrow typically expresses some alarm or apprehension; it is diagnostic of the underling with the hand-raised birds. (With the Nuttall White-crowned Sparrow raising its conspicuously marked crest is a threat, and this is true of the Goldcrest (Lack 1937).) Wing- and tail-flipping may accompany "pleasurable" excitement, as when the pair hunt for a nesting site, or visit the nest when the young have first hatched.

The rate at which the notes are given, and the kind of note given, vary with the degree of excitement.

When searching for a nest containing newly hatched young, I came within a few meters of it; the female gave 48 *tchunks* and 5 *tiks* in one minute. I left, walked 50 meters and hid; the bird then gave 32 *tchunks* in a minute. When the nest was visited 2 days later, the female gave 56 *tchunks* in a minute; as soon as I was out of sight she gave 35 in a minute.

A month later a cat was seated within 8 meters of the nest of this pair containing 6-7 day young; at first the cat was looking at the Song Sparrow, later it turned its back. In 3 consecutive minutes one of the parents gave 51 notes a minute: in the first minute 1 *tchunk* and 50 *tiks*, in the next 15 *tchunks* and 36 *tiks*, in the third 47 *tchunks* and 4 *tiks*.

A mounted Barred Owl was fixed near a tangle in which were an adult Song Sparrow and young recently out of the nest. The parent gave 64 *tiks* in the first minute, 63 in the next and 65 in the third.

The first bird showed alarm: strong alarm at my proximity with 56 *tchunks* a minute, moderate alarm immediately after my departure with 32-35 a minute. The second bird showed fear of the cat at first with approximately 51 *tiks* a minute, and later alarm with about the same number of *tchunks*. The last bird showed fear of the Owl with 64 *tiks* a minute.

On the basis of a series of experiments carried out with the hand-raised birds, Song Sparrow "alarm" seemed to fall into 3 fairly distinct classes: 10-15 *tchunks* a minute showed weak alarm; 25-30 a minute, moderate alarm, and about 50 a minute, strong alarm (Nice and ter Pelkwyk 1941:203).

B. REACTIONS OF PASSERINES TO PREDATORS

The responses already mentioned in previous chapters will not be repeated here. Rather some detailed observations on reactions to specific predators will be given for the Song Sparrow and other passerines.

1. *The Song Sparrow and Predators*

Predators affecting Song Sparrows may be reptiles, mammals and birds. It was not often on Interpont that I saw encounters between Song Sparrows and their enemies.

a. Reptiles

Although I believed that the rather abundant snakes on Interpont took somewhat of a toll of eggs and nestlings, I had no direct proof of the fact, and it was seldom that I saw the birds and snakes together. In 1929 1M reacted with curiosity to a 60 cm. garter snake coiled beneath his nest with newly-hatched young; he hopped around it and gave it a peck. The next year his mate attacked small snakes near her nest. Garter snakes 30 and 70 cm. long were shown to Y within a meter of his cage and the smaller one allowed inside it; he craned his neck, but showed no alarm.

b. Mammals

Rabbits on Interpont were ignored by the Song Sparrows, except that once K3 gave the threat note to a young individual near her nest. A large black-and-white rabbit that hopped about next Y's cage induced fright; later when it was quiet Y showed moderate alarm.

Dogs were ignored unless they came too near the nest, when *tchunk* was given. (Dogs several times destroyed nests with eggs or young and once or twice killed the incubating female.) Active dogs brought into the study induced fright in Y at first, but later he came to ignore the chow puppy that was a frequent visitor.

Cats on Interpont were consistently greeted with *tchunks* at the rate showing strong alarm; these *tchunks* were taken up by all the Song Sparrows in the neighborhood. Once parents with young 10 days out of the nest gave *tik-tik-tik* to a cat. As already mentioned hand-raised Song Sparrows nearly 4 weeks old paid no attention to cats. None of the birds have reacted to cats (or grey squirrels) seen out of the window. Cats and kittens placed near the cage induced weak alarm. During the summer of 1940 Y stayed on the screened porch at Mrs.

Dorothea Ewers' home; on several occasions she heard him give ***tik tik,*** whereupon she went out and chased a cat from the railing. That fall he was more disturbed than he had been before when kittens were placed next his cage.

People are usually greeted with *tchunk* when they approach the nest, but when the young are nearly ready to leave or have just left, both parents use *tik* and a variety of miscellaneous notes. Occasionally in winter a Song Sparrow *tchunks,* if startled by a person's sudden appearance. *Tik-tik-tik* may be given in reference to persons by a male soon after he has been joined by a mate, by a male if his young approaches the person, and once by a female when her Cowbird foster-child was approached by an observer. 1M and K2, and also 4M were fearless in relation to me; the first two would even come to meet me in hopes of being fed. The hand-raised birds apparently make no distinction between persons. Twice, however, when I came to the cage wearing black glasses and offered Y an insect, he kept to the furthest corner of the cage.

c. Birds

Twice Bronzed Grackles were noted near Song Sparrow nests, the parents of which were reacting with strong alarm. When a Blue Jay screamed outside the window, A froze, while Y became very alert and soon started to *tik*. The hand-raised birds apparently react to birds flying outside, possibly Gulls; for they suddenly give *tik-tik-tik* and hide. Once we saw that a Starling flying rapidly past was the cause of the fright.

As to Hawks, the Song Sparrows were usually indifferent to the nesting pairs of Sparrow Hawks (*Falco sparverius*). Once in March they gave *tik-tik-tik* when a pair appeared; in November they gave *tchunks,* in February and October they stopped singing, and once when a Hawk flew at 2 fighting males, they hid. They stopped singing and many gave *tik-tik-tik* as a female Marsh Hawk flew over. To a Sharp-shinned Hawk, they gave *tik-tik-tik,* hid and remained frozen for some minutes.

2. *Some Others Birds and Predators*

Some birds are reported as having different notes for different dangers. The Jungle Fowl has one note for an air enemy, another for a ground enemy; the responses of the bird and its companions differ accordingly (the Heinroths 1924-33). The European Avocet has a general alarm cry and a special "gull-cry" that appears when the eggs are laid; "it is uttered everywhere when an Avocet meets a gull" (Makkink 1936:49). The House Sparrow has 2 danger notes—the ***kewkew*** call in response to cats and people, the *krüü* call, given at the appearance of the European Sparrow Hawk (*Accipiter nisus*) and other Hawks; this is followed by a dash to cover. This last note is sometimes given upon the approach of a person when the males are occupied with a "Social-song" assembly; it is suggested that hiding from a Hawk and not wanting to leave may be somewhat analogous (Daanje 1941).

The Snow Bunting called *weee* and remained on the ground when a Falcon appeared; they also called *weee,* but fluttered around people, dogs and Arctic foxes; the calls might have sounded different to the Buntings, but it might have been that "the behavior of the warning birds influenced the others' reactions" (Tinbergen 1939c:41).

Henslow's Sparrow is said to have a "hawk call" which "differed from the alarm note given" to the human intruder (Hyde 1939). I used to consider *tik-tik-tik* a "hawk call", until further experience showed that it was given to various enemies under stress of a strong stimulus. Tinbergen says that in the European Blackbird "the different alarm calls correspond to different degrees of danger only" (1939c: 41). Brown Jays in Mexico give a note like a hiccup while examining a motionless hunter, but, at the slightest *movement* of the strange object, break forth into screams (Sutton and Gilbert 1942).

The strength of instinctive rather than learned fear is pointed out by Sherman (1910:155) in regard to her Flickers that nested in a box in the barn in which there were peep-holes for observation and a door for removal of nestlings: "Generally the sounds that aroused fear in this species were made by some one back of their nest, yet the bird always sought the hole and looked for the cause of alarm outside. Even after two seasons of experience with the five-fingered terror that entered the hand-hole so often, and removed their young, they failed to learn to look for any disturbance from that direction. Another illustration similar to this is the careful inspection of the hole before entering it at night, a Screech Owl or other enemy might be lurking there."

A curious observation by Heinroth with his hand-raised birds is the fear that some of them show towards certain colors. A young Yellow Wagtail, a Yellow Bunting and a Meadow Pipit were much afraid of different shades of blue, while most of the other birds in the room feared red (1917). One of a brood of Red-backed Shrikes, a Jackdaw and a Cockatoo feared blue, while Tree Pipits feared red (the Heinroths 1924). There was no evidence of fear of any color with the hand-raised Song Sparrows, nor the Bobolinks, but a pair of Goldfinches, taken from the nest at the age of 2 days by Wm. E. Schantz and brought to Chicago in the fall, flew wildly about whenever a dark-blue box top was shown to them. Some other blue objects also elicited signs of fear. Mr.

Schantz experimented with his other pair of hand-raised Goldfinches and found them afraid only of black paper.

C. EXPERIMENTS ON ENEMY RECOGNITION

A review of the experiments on this subject was given in the paper mentioned above (Nice and ter Pelkwyck 1941). The most important of these were made by Strauss (1938b), Krätzig (1939, 1940), Lorenz (1939), Goethe (1937b), Tinbergen (1938-39) and more recently Rand (1941c). Mrs. Laskey has given me information in regard to her hand-raised Mockingbird: when 3 months old he gave alarm cries as a Screech Owl came into a nearby tree; he showed a pronounced fear reaction to a dead Screech Owl and to a live Saw-whet Owl.

Descriptions of our experiments and their results are given with 3 sample charts in the paper on "Enemy Recognition by the Song Sparrow." Here they will be briefly summarized.

The experiments started with showing a mounted Barred Owl. After finding that this induced strong alarm or fright in the Song Sparrows and Goldfinches (and the same was true a year later with the hand-raised Bobolinks), we tried mounts of various foreign birds. Finally in an effort to discover what it was about the Owl that induced so much greater reaction than any of the other objects, Mr. Pelkwyck ingeniously constructed and painted models of Owls, one the same size and shape as the mounted Barred Owl, the "best" model, and many others, a few of which are shown in Figure 6. Cardboard models were also made of other birds. At first each object was shown for 15 minutes, but most of the tests lasted for 3 minutes. All models were placed on the Victrola.

FIGURE 6. *Cardboard Models of Owls. From left to right: 1, model at half scale; 2, 'head' model; 3, 'best' model; 4, 'head' model without eyes; 5, 'outline' of 'head' model; 6, model with shading on the sides.*

All the objects were shown in the study except that sometimes the birds met the Barred Owl perched on the piano in the front room. When exhibited in the study the Owl usually provoked strong alarm, but later in the course of the experiments it induced only moderate alarm. In the comparatively unfamiliar environment of the front room, however, this mount invariably provoked strong alarm. Interestingly enough, the piano still had a strong Owl tone even without the Owl, and both birds reacted with moderate or strong alarm on first coming into the room. After more than 4 months Y was still conditioned to this spot. He had last seen the Owl on the piano on May 24; he spent the summer with Mrs. Ewers and did not enter the front room again until October 1. He at once showed strong alarm with crest and tail raised, keeping his eyes on the end of the piano. He gave 148 *tchunks* in 3 minutes, left the front room, and gave 9 more before he returned to the study.

Lorenz's Ravens became conditioned against places where they had been frightened (1935:205). Mrs. Laskey's Mockingbird gave alarm notes in the dark; the lights were turned on, and he was seen looking at the spot where the Saw-whet Owl had perched 10 minutes before. The biological value of this conditioning against places where an enemy has been met is evident.

The Hornbill and Grouse evoked strong alarm in these Song Sparrows at the first showing, moderate and weak alarm later. The Kite and Falcon produced moderate alarm, as did the cardboard models of all species but Owls.

In general Y reacted to the "best" model and "head" model almost as intensely as to the mounted Owl when shown in the study, i.e., moderate alarm. Covering the eyes of the best model made little difference. A piece of cardboard of the same shape as the "head" model (the "outline") brought no response. So there was a remarkable difference between the results with the painted and unpainted models. (I will quote a paragraph from our paper. The number of *tchunks* cited are for periods of 3 minutes.)

"We attempted to analyze this difference and in this way to find the essential features in the owl. The 'head' model without eyes evoked moderate alarm (*104 tchunks*). The 'head' model placed upside down brought 75 *tchunks*. Reactions were similar to a model of which only the left half was painted (77, 82 *tchunks*). A model with only some shading on the head evoked 53, 27 and 0 *tchunks* and when eyes were added no reaction was given. A model with only some shading on the breast brought 13, 66 and 0 *tchunks*. A model with a dark border around the outline evoked no reaction, but a similar model with some shading along the outline, so that it seemed to be rounded brought 94 *tchunks* (Fig. No. 6). A piece of cardboard of the same size as the 'head' model was gradually changed and shown at intervals. *Eyes, bill and disks around the eyes brought no reaction, but as soon as some shading was added that gave contour to the model, Y showed* *moderate alarm, uttering* 85 *tchunks*". (In experiments with hens on space perception Benner [1938] found that the most important criterion is the shadow, which if artificially removed leaves the object disregarded.)

The last regular test was made Oct. 13, 1940. On Mar. 13, 1941, I showed Y the best model for a moment; he immediately responded with *tchunks*. Thirteen months later, and 19 months after the full tests, on Apr. 26, 1942, I placed the *outline of the best model* on the victrola; Y at once showed moderate alarm, giving 106 *tchunks* in 3 minutes. Since before this he had been almost indifferent to "outlines" of models, having given 31 *tchunks* in 3 tests and no reaction in 10, this would appear to be a test of *memory* of former experiences rather than reaction to the model of an Owl.

D. RESPONSE OF THE SONG SPARROW TO THE COWBIRD

Song Sparrows habitually respond to the presence of Cowbirds on their territories with vigorous *tchunks*. As the female nears the nest the pair frequently attacks her. Records of alarm over Cowbirds on Interpont ranged from Mar. 29 to July 14.

Some sample entries from 1929 will be given.

Mar. 30. A female Cowbird spends about 10 minutes in 1M's territory. 1M and K2 *tchunk* continually, following her closely in trees, on burdocks and on the ground. K2 seems more zealous than 1M. 4M and K3 are also *tchunking*. 1M flies to trough to drive off 4M; returns within a meter of Cowbird with tail spread. K2 utters *zhee*.

Apr. 3. Male Cowbird comes within a few centimeters of 1M and K2 feeding on the hillside; one of the pair pecks him in the breast; he leaves.

Apr. 4. 1M is carrying nesting material; a female Cowbird appears on a nearby bush. He drops his stuff and looks as if he might attack her.

Apr. 8 (3rd day of nest-building). A pair of Cowbirds in the center maple; female goes near the nest site. K2 hurries to meet her, giving *zhee, zhee*.

Apr. 9. All 4 Song Sparrows *tchunk* at female Cowbird. Later she is on a post; 4M and K3 *tchunking*. She descends to ground, the birds attack her. She leaves.

Apr. 10. Female Cowbird near 1M's nest; 1M and K2 *tchunk*, both rather puffed out.

Apr. 11. Female Cowbird comes looking for the nest; leaves chattering when she sees K2 on it.

Apr. 12. (At 8:12 I come out, examine the nest, find only one egg in it where there should have been 3; the birds had evidently deserted it.) 9:00. A female Cowbird comes to the big burdock; 1M and K2 *tchunk* more and more, she goes to the nest, stays about 15 seconds, comes out, the Song Sparrows rush to attack her, giving *shees*. She flies off. K2 examines nest, comes right out again. I examine it and find no change.

How do Song Sparrows know that the Cowbird is an enemy? In 1929 1M had nested the year before, but I believed K2 to be a young bird; her behavior might have been conditioned by his. In 1935

121M, known from the character of his songs to have been hatched in 1934, was markedly disturbed by courting Cowbirds high in the ash on his territory from Apr. 18 on. The next day both he and his mate *tchunked*. Their nest was not started before the 22nd. Once I saw 4M and his mate attack a Cowbird in the presence of one of their young that was 6 weeks old.

Two tests with mounted female Cowbirds were made with Y, both in the fall; he showed moderate and weak alarm to this mount and moderate alarm to a mounted Starling.

The Ovenbird is heavily parasitized by the Cowbird, yet they "do not recognize the Cowbirds at sight as enemies" (Hann 1937:201). The female Cowbird "will frighten the [Ovenbird] owner from the nest if she happens to be there first" (Hann 1941:220). As to American Redstarts (*Setophaga ruticilla*), "Males were silent in the presence of female Cowbirds, but females reacted with sharp hisses, a rapid snapping of the bill and much spreading of the tail" (Hickey 1940).

It seems to me that antagonistic reactions to Cowbirds depend on conditioning, sometimes perhaps during early life as in the instance mentioned above with 4M's young, sometimes from behavior of mates or possibly neighbors, and sometimes from personal experience of the Cowbird's insistence on visiting nests. In regard to the attacks by birds on the Koel or Black Cuckoo in Australia, Chisholm (1933:390) suggests "that the potential fosterers attack cuckoos because they recognise them, in some degree, as *meddlers* at nests, without appreciating what that meddling portends."

E. Discussion of the Problem of Enemy Recognition

How much is inborn in enemy recognition and how much is learned? Is fear generalized, so that the bird largely has to learn what *not* to fear, or are some rather specific patterns innate?

There is some evidence of inborn patterns in regard to form and movement from the experiments of Goethe, Krätzig, Strauss, Tinbergen and Lorenz, mentioned above, where mounts and models, both stationary and moving, were shown to hand-raised birds. Lorenz (1935) states that Magpies instinctively recognize predators, but that Jackdaws do not; also that a hand-raised House Sparrow reacted violently when he first saw an Owl.

Berndt, on the other hand, describes the warning notes given by several species of birds when a bat flew about in full day-light, and suggests that here and with the mobbing of Owls, the response is to the "unusual and unknown" (1940). One November I saw Song Sparrows with raised crests hopping about a sycamore, inside a hole in which Starlings were making a constant wheezing noise. In Australia a number of passerines mobbed a teddy bear with glass eyes (Sedgwick 1940). Hertz (1926:35) wrote of her tame Corvidae that every new object aroused fear; if the object appeared to be harmless, fear changed into curiosity and then into aggressiveness.

On the basis of his extended series of experiments with hand-raised Curve-billed Thrashers, Rand writes, "The experiments with the Screech Owl provide no evidence for a recognition of the Owl as such. . . . Instinctive recognition seems to be nonexistent, and the size, strange shape, plus certain activities of the Owl, bring about the responses" (1941c:240). "Enemies were not recognized as such; the Thrashers responded to some non-enemies as to some enemies. These responses usually combined exploratory acts and fleeing acts, sometimes a display and once pugnacious activities. Which type was dominant, with the exception of the snake display, appeared to depend not only on the size of the object, its familiarity or otherwise, but also greatly on its activity in relation to the Thrashers. Thrashers *probably* had to learn what not to fear," p. 242.

Apparently the Song Sparrow recognizes enemies by both inborn and learned patterns. In nature the behavior of the adults must be of great importance in the forming of conditioned patterns in the young. As pointed out in Chapter IV, simultaneous presentation of a natively inadequate stimulus (cat, Cowbird) and the unconditioned stimulus (alarm of the adult) may result in conditioning to the originally inadequate stimulus.

The birds may learn from personal experience or from responses of others what is *not* an enemy. Our experiments showed decrease of reaction when nothing happened after the enemy had been shown (see also Strauss 1938b). A similar process may be involved in the absence of alarm shown at rabbits and often for Sparrow Hawks (*Falco sparverius*) in nature.

I think we are safe in saying that a bird instinctively reacts with caution to new, strange, large, and rapidly moving objects. Whether the Owl merely comes into the category of new and strange is a question; with some birds this may be true, but our experiments with the Song Sparrows we felt could not be explained without postulating an inborn pattern.

F. SUMMARY

1. Three chief stages of fear may be distinguished in the Song Sparrow, postures and notes being different in each.
2. The raised crest in the Song Sparrow is characteristic of alarm, but in

some species with brightly marked crests it denotes threat.

3. "Alarm" in the Song Sparrow may be sub-divided into weak, moderate and strong alarm according to the rate at which *tchunks* are given.

4. One female Song Sparrow attacked small snakes near her nest; a wild male and Y treated sizeable garter snakes with curiosity.

5. Rabbits on Interpont were ignored, dogs evoked alarm when near the nest, while cats evoked strong alarm wherever seen. People usually evoked moderate alarm when near nests.

6. Sparrow Hawks (*Falco sparverius*) usually cause little concern, but to an Accipiter the birds gave *tik-tik-tik* and hid.

7. Jungle Fowls, Avocets and House Sparrows have 2 danger calls, corresponding to different dangers and inducing different behavior.

8. Some birds show fear of blue, and some of red.

9. Experiments on enemy recognition by the Song Sparrow were made with mounted birds and cardboard models. The mounted Barred Owl and models of Owls induced stronger reactions than did the other objects.

10. Tests showed a remarkable difference between results with painted and unpainted models. Eyes, bill and disks around the eyes brought no reaction, but as soon as some shading was added that gave contour to the model, Y at once showed alarm.

11. The memory of circumstances connected with strong alarm persisted after 4 to 19 months, a response that has definite biological value.

12. Antagonistic reactions to Cowbirds would seem to depend upon conditioning, sometimes perhaps in early life, sometimes later.

13. "Unpleasant" experience with an enemy will intensify the reaction, while indifferent experience will weaken it.

14. Some observers believe that fear is generalized and the bird has largely to learn what *not to fear*. Others believe that certain fears are inborn in some cases.

15. It is probable that most animals instinctively react with caution to new, strange, large, and rapidly moving objects.

16. Our experiments led us to conclude that Owls are recognized by Song Sparrows largely through an inborn pattern, Hawks through their rapid movements, and cats and Cowbirds through conditioning.

CHAPTER XXII

Innate and Learned Behavior in the Adult

With all the incredible diversity of animal life on the earth, at the same time there is a fundamental unity. *The basic needs are the same; it is the means by which they are satisfied that differ.*

Unicellular organisms react to all classes of stimuli to which higher animals react (considering auditory stimulation as merely a special case of mechanical stimulation)," writes Jennings (1906:26). They show perception, discrimination, choice, attention, fatigue and desire for food, and they react negatively to powerful and injurious agents. They show the beginnings of intelligence, which "is commonly held to consist essentially in the modification of behavior in accordance with experience," p. 334. They also seek mates. "The seeking of mates appears to be the fountain head of both social behavior and self-consciousness" (Jennings 1941:17).

Chapter IV dealt with innate and learned behavior in the young bird. In this chapter I intend to treat very briefly the same subject as regards the adult bird. As a natural sequence there follows the question of the sum of those learned actions that are passed on from one generation to another in birds and infra-human mammals, forming a kind of primitive culture. Finally a cursory view will be given of the instinctive behavior patterns throughout the vertebrate series with special emphasis on man.

A. THE BASIC NEEDS OF ANIMALS

All animals have the same basic needs: nutrition, protection, and reproduction. They need to eat, and to avoid being eaten, and they must have progeny. Food is essential for growth and continued life. Protection is necessary both from enemies and the elements. The demands of reproduction have profoundly modified the structure and habits of animals above the protozoa.

Birds and human beings are visual and auditory animals. Birds and infra-human mammals are nearer to human beings emotionally than intellectually. "In animal life, as in human life, emotions are of the utmost importance" (Craig 1922:359).

B. INNATE AND LEARNED ACTIVITIES IN THE ADULT SONG SPARROW

"The bird is certainly no reflex machine," writes Heinroth (1938a: 151). "Its behavior arises to a degree from a chain of instinctive actions that is not completely closed; the gaps are filled in through profiting from personal experience, thus through intelligent action. The more gaps there are, the better intelligence can develop." We might say that innate behavior patterns guide the bird in general, but that many details are left to experience. Learning in one sense is a matter of the elimination of unfruitful and inappropriate responses.

Some innate and learned elements in some of the major activities of the adult Song Sparrow are listed in Table XXVI.

TABLE XXVI

INNATE AND LEARNED ELEMENTS IN SOME OF THE ADULT SONG SPARROW ACTIVITIES

Activity	Innate Elements	Learned Elements
Anting	Rubbing ant on primary	Ant as object, probably from taste
Following Reactions	Response to species call note; suggestibility	Social-companions
Responses to 'Warning'	Response to alarm note and fleeing behavior	(Gulls learn to recognize alarm notes of Terns; react more to warning from one neighbor than another)
Social Attack	Response to notes of others; probable response to Owl	Cat and snake as enemies; also Cowbird
Social Dominance	Dominance-subordination behavior	Position in hierarchy
Awakening and Roosting	Response to light; recognition of roosting places	Particular roosting places
Song	Use; form; awakening song; flight song	Quality; (form learned with some species)
Habitat Selection	Response to key aspects	Particular places
Territory Selection	Confining fighting behavior to a certain region	Singing posts, boundaries, roosting and feeding places, neighbors
Territorial Defense	Threat-posture, challenge	Used in reference to boundaries and individuals
Pair Formation	Sex recognition through notes and behavior; pouncing, copulation	Personal recognition of mates (in some birds, species recognition; facilitation in copulation, as in Doves)
Nest Building	Choice of site, technique, selection of materials	(Facilitation in some birds, possibly from experience)
Incubation	Response to eggs in nest	
Feeding Young	Response to young in nest, later out of nest	Some facilitation
Defense of Young	Response to enemy near young	Recognition of Cowbird and cat
Enemy Recognition	Partly innate	Partly learned through example and experience

In most cases the gaps that are filled in through experience are concerned with the object of the instinctive reactions. Occasionally a bird will find a new technique for itself; in the following cases elements of learning were "clearly manifest in feeding technique carried on in the wild": a Lazuli Bunting pulled grass heads to a fence wire and held them there as he picked out the seeds (Miller 1939); a Fiscal Shrike in East Africa attached itself to a Roller, swooping at it and making it drop grasshoppers which the Shrike caught in midair (Moreau, R. E. and W. M., 1941b). (With species such as Man-of-War Birds, Skuas, Bald Eagles, etc., where such robbing is a regular means of support, elements of an innate pattern are not to be ruled out.)

C. PRIMITIVE CULTURE IN BIRDS AND MAMMALS

It is often thought that with animals below man, because of their lack of articulate speech, one generation cannot profit from the experience of another. Many animals do, however, pass on knowledge through unconscious teaching.

1. *Nutrition*

There is little information on how much choice of food is based on instinctive recognition, on individual trial and error, and on following the example of companions. That this last method is sometimes a factor in a social bird is shown by the lag in the adoption of new foods planted for Bob-white and Wild Turkeys, for it is sometimes several years before these are used (Stoddard 1938:9).

In Zurich during the first World War when it was forbidden to feed bread to birds, the Black-headed Gulls came into the city and begged on people's porches. "The bread-card-years are long past, but the habit has persisted for more than 15 years although the necessity for it is no longer present. From one winter to another it was perpetuated," younger birds learning the habit from the example of older ones (Noll 1934:185).

2. *Protection*

Primitive culture as regards protection has chiefly to do with recognition of enemies, but may also involve habitat selection, and perhaps covey size in the Bob-white.

a. Enemies

We have seen in Chapters II, III, IV and XXI that many birds do not recognize enemies instinctively. They learn much as to what to fear and what not to fear from their own experience, and partly from example of parents and social-companions. Antonius, director of the Schönbrunn Zoo (1939) found no "inborn fear of snakes in apes and monkeys, but as with man it is a matter of training in these uncommonly excitable and suggestible animals. In the band this comes about—of course entirely unconsciously—through the example of the alarm calls and excitement of the adults," p. 295. Seton (1909) points out the ease of trapping and poisoning wolves in the early days of the cattle industry, and its difficulty later; in some manner fear of these dangers has been transmitted to the wolf population. With this social animal it might well be that the disastrous experience of one member of a pack would make such an impression on the other members that caution in similar surroundings would become a tradition.

b. Habitat Selection

In his interesting article on this subject, cited in Chapter XII, Miller (1942:34) writes: "Habits and associations with respect to environments and particular landmarks are passed on non-genetically from generation to generation. Cultures or societies are formed in higher vertebrates, as indeed in humans, and temporary barriers are set up." With flocking Corvidae "Traditional roosting places are used and learned by successive generations", as "stressed by Emlen (1940) and Cushing (1941a)."

c. Covey Size

In discussing the uniformity of covey size of Bob-whites over a number of years in various places, *"sometimes despite profound modifications in food and cover relationships," Errington* (1941:99) concludes: "The likeliest mechanism behind these toleration phenomena seems to be dominance by veteran individuals that have their own ideas as to what constitutes desirable or safe numbers of birds in specific habitats. As long as the habitats are fairly well filled each winter, there should be a greater chance of 'traditions' being retained, either through continued presence of dominant old birds or through successors having had previous local experience." As to numbers of Chickadees at a winter feeding station, Hamerstrom (1942) attributes the increase at established stations to "tradition". "Instead of repeating this random building up from a fresh start, the territory begins its second winter with a nucleus of old-timers."

3. *Reproduction*

The recognition of species is often a matter of association in earliest youth with older birds (see Chapter XVI). As to courtship and copulation techniques, there is doubtless facilitation at times from the example of other pairs and experience of older mates. My hand-raised Bob-white never went through the proper courtship display as described by Stoddard (1931), and he rarely called his young mate to food. Craig's (1914) male Ring Doves raised in isolation and my hand-raised Mourning Doves (1931c) had difficulty in acquiring the technique of copulation and its accompanying ceremonies.

D. INSTINCTIVE BEHAVIOR PATTERS THROUGHOUT THE VERTEBRATE SERIES

We have seen that all animals have the same goals of sustenance, safety, and the perpetuation of their kind. Actions of all depend partly on innate patterns and partly on learning; with some animals behavior is almost entirely natively determined, but with man the instinctive behavior is more or less smothered and training is of tremendous importance. Much of man's rapid advance is made possible by his faculty of articulate speech and the consequent body of culture handed down from generation to generation. Nevertheless, we must remember that man is an animal and that his *instincts provide the foundation of his behavior.*

"At the fish level," writes Noble (1939a:120), "at least four of the principal components of social life in the highest vertebrates had already developed: (1) group attraction, (2) dominance-subordination behavior, (3) suggestion, and (4) parental service". (All of these also appear in some of the invertebrates.) Fish, reptiles, birds and mammals respond to the movements of other individuals. "Already at the frog level, voice had important functions both in attracting females and repulsing males" (Noble 1931). "It could also be used to warn companions or frighten enemies" (Noble 1939a:119). Voice is highly developed in birds as a means of social control (Craig 1908), and in some mammals. Territorialism is found in a great many fish, lizards, mammals and birds. Some of the methods of pair-formation are analogous in a number of vertebrate classes, and here we may include some insects and mollusks. Dominance is found throughout the vertebrates and also in the squid. Parental care is present in all classes of vertebrates, as well as in some invertebrates, for example Hymenoptera.

To turn now to man as animal, and especially as social animal. All the manifestations of social need described in Chapter VII apply to man as well as to birds.

That the social bond increases with the unfamiliarity or unfavorableness of the environment is shown by our proverb "Misery loves company." In the city we ignore strangers, in the wilderness we speak to them. A class-mate we barely knew in college becomes important when met in after life; an acquaintance from home becomes a friend in a foreign land. The increase of solidarity in a country at war is axiomatic.

The suggestibility of human beings is only too evident; our rushing after fashion, our lack of independence, our keeping up with the Joneses is a constant theme of reproach to us. We are sensitive to movements of our fellows; slight "intention-movements" inform us as to their next moves. The instinct to follow is strong. When in a strange environment we stay close by an experienced comrade; we feel safer if we follow the crowd instead of striking out by ourselves. On shipboard if one person appears to be seeing something, others hasten to the railing; in the street if some one looks at the sky, every one else does likewise. A crowd quickly gathers wherever there seems to be evidence of something unusual happening. No words are necessary; like other animals we respond to slight deviations in the usual behavior of our companions. Also, like many other animals, we resent marked deviations from customary behavior (Goethe 1940a).

We react instinctively when we see or hear sudden running of an adult which is obviously neither play nor has some evident goal such as a street car, or when we heard a person falling, or hear cries of distress. In the matter of fear, we, like other animals, are disturbed by the unfamiliar in sights or sounds. We judge of the dangerousness of an approaching automobile by the speed at which it is approaching.

As to social attack, the fanaticism of mobs against some supposed enemy is only too well known.

Although a distinguished writer tells us that animals do not want power, we know that the dominance urge is exceedingly strong throughout much of the vertebrate series. While it brings good in human life, it is also the cause of some of our greatest misfortunes. "In humans, as in animals, the first meeting is usually far more important in determining dominance status than any subsequent meeting" (Maslow 1937:410). With men as well as with hens, the "unpracticed despot is the worst of despots". We resent it when an underling makes himself conspicuous. As with Carpenter's gorillas, a person may dominate another in some respects and be dominated by him in others.

Like many birds and animals we have a protective feeling toward babies and children. Like those birds whose chief concern is the nest rather than the offspring, some women make a fetich of their houses to the detriment of their families' happiness. Social facilitation in eating, learning, courting and fighting occurs in human beings as well as in other animals.

Like many colony-nesting birds, we are strongly territorial as well as social. When our enemy submits, we cease fighting. As Craig (1921:275) writes, "Thus we see that in the male animal there is a fundamental trait which tends to prevent him, and in most cases does prevent him, from doing any injury to a non-resisting member of his species."

In an article on "Man's Culture and Man's Behavior", Malinowski (1941) discusses the "Biological Determinism of Culture", listing the "Permanent Vital Sequences Incorporated in All Cultures", all of which are shared by other vertebrates. He then shows how culture has grown out of these:

"A, *Basic needs:* 1, metabolism; 2, reproduction; 3, bodily comforts; 4, safety; 5, movement; 6, growth; 7, health.

B, *Cultural responses:* 1, commisariat; 2, kinship; 3, shelter; 4, protection; 5. activities; 6, training; 7, hygiene."

The motives of the scientific investigator are analyzed by Wheeler (1939:95) into 8 instincts that are "innate" and "purposive"; 4 of these are individual—curiosity, hunting, collecting or hoarding, workmanship; and 4 are social—emulation, communication, cravings for sympathy, and cooperation.

A suggestive book on sociality in animals, and particularly in man, was written by Trotter (1917) on "Instincts of the Herd in Peace and War". His thesis is that man's behavior is fundamentally influenced by his instincts as a social animal.

"The quite fundamental characteristic of the social mammal, as of the bee, is sensitiveness to the voice of his fellows," p. 108. "Specialization fitting the animal for social life is obviously in certain directions restrictive. . . . Among qualities of restrictive specialization are inability to live satisfactorily apart from the herd or some substitute for it, the liability to loneliness, a dependence on leadership, custom, and tradition, a credulity towards the dogmas of the herd and an unbelief towards external experience, a standard of conduct no longer determined by personal needs but influenced by a power outside the ego—a conscience, in fact, and a sense of sin—a weakness of personal initiative and a distrust of its promptings. Expansive specialization, on the other hand, gives the gregarious animal the sense of power and security in the herd, the capacity to respond to the call of the herd with a maximum output of energy and endurance, a deep-seated mental satisfaction in unity with the herd, and a solution in it of personal doubts and fears," pp. 109-110.

As to "Characters of the gregarious animal displayed by man",—"1. He is intolerent and fearful of solitude, physical or mental" . . . the "religious needs and feelings of man are a direct and necessary manifestation of the inheritance of instinct with which he is born," p. 114. "2. He is more sensitive to the voice of the herd than to any other influence." "3. He is subject to the passions of the pack in his mob violence and the passions of the herd in his panics." "4. He is remarkably susceptible to leadership." "5. His relations with his fellows are dependent upon the recognition of him as a member of the herd."

In conclusion, I will quote from a letter of Dr. Lorenz: "The study of animal behavior is the only and ultimate source of understanding ourselves."

E. SUMMARY

1. The basic needs of all animal life are nutrition, protection, and reproduction.
2. The broad outlines of adult Song Sparrow behavior are laid down by instinct, but many of the details are filled in through personal experience, particularly in regard to the object of the instinctive activities. As shown in Table XXVI, most of its activities show both innate and learned elements.
3. There are beginnings of primitive culture among birds and infra-human mammals, experience being handed down non-genetically from generation to generation, particularly in matters regarding protection from enemies.
4. Many instinctive behavior patterns run throughout the vertebrate series, man included, as for instance, group-attraction, suggestion, dominance, territory, pair-formation technique, parental care.
5. All the manifestations of social need as described in Chapter VII apply to human beings.

6. Man's culture is based on and grew out of his biological needs.

7. A great deal of man's behavior may be explained on the basis of his instincts as a social animal—his need for companionship and leadership, his lack of independence, his obedience to custom, his reliance on some power outside himself.

8. The study of animal behavior is the only and ultimate source of understanding ourselves.

APPENDIX I

Chief Vocalizations of the Song Sparrow

	Given by		
	Young	——Adult——	
		Male	Female
1. Food notes: *see-see, kerr, tit-tit-tit*, etc....................	x		
2. Location note: *eep* or *ick*..	x		
3. Scream	x	x	?
4. Cry of pain—felt or anticipated: *weech*....................	x	x	x
5. Threat note: *shee*, a growl...	x	x	x
6. Fear note: *tik*..	x	x	x
7. Fright: *tik-tik-tik*, at hawk or sudden appearance of cat or person..		x	x
8. Call note: *tsip*, between transients or mates...........	x	x	x
9. Alarm: *tchunk*, disturbance, self-assertion...............		x	x
10. Warble—prolonged, soft, varied.................................	x	x	
11. Advertising song—short, loud, stereotyped...............		x	
12. Flight song—a chatter, then a song...........................		x	
13. Female song—harsh, unmusical..................................			x
14. Caterwaul—harsh chatter. Significance unknown..		x	
15. Anxiety: *tchip*, over young in nest, excitement in territorial quarrels		x	x
16. Trill: *ee-ee-ee*, copulation note, greeting to mate....			x
17. Chatter: nest-building, greeting to mate.................			x
18. Nest-call: soft twitter, when hunting for a nest, female when building...		x	x
19. Strong anxiety: *ick*, over young in nest...................		x	x
20. Intimidation: *puh-puh-puh*, to person endangering young		x	x
21. Miscellaneous soft notes—used at nest with young		x	x
	8	16	15

Most of the notes have been described in the text. Two, however, need further comment.

10. Although I have asserted in print that adult male Song Sparrows never warble, my hand-raised males do use a kind of warble—3 to 3.5 seconds in length, rather soft, and more warbling in tone than the advertising song. Y often gives it in response to rustling of paper, or miscellaneous noises.

14. The "caterwaul" is a peculiar note. I have 19 records of it from Y: 8 in April 1939, 1940, 1941; 3 in May 1939, 1940; 2 in October 1939, 1941; 5 in February and one in May 1942. All but one were given in the evening, from 6 till 12 p.m., most often between 7:00 and 9:00; 3 times it was given immediately after lights had been turned on. The one time it was heard in the daytime occurred at noon Oct. 6, 1939 when D suddenly flew against Y's cage; Y immediately caterwauled, then went into an extreme puff-sing-wave demonstration. The caterwaul is a loud, harsh chattery series, lasting perhaps 6 seconds. Occasionally it is repeated once or twice. Y ordinarily gives it sitting on a perch, puffed

out, bill open, and wings vibrating a little. Once he gave it when standing in his almost empty bath tub. I very rarely heard it in the wild, sometimes in winter, once from 4M in the breeding season, and always in the daytime. I have no suggestion as to its significance.

APPENDIX II

Dominance, Singing, and the Challenge (Puff-Sing-Wave Posture) in the Hand-Raised Birds

The "challenge" consists in puffing out the feathers laterally, soft singing, and waving of one or both wings. The elements shown each time are designated by letters; *pw* means that the bird puffed and waved; *ps* that he puffed and sang. When *psw* was given more than once from one bird the number of times is shown.

FROM OCTOBER 1938 THROUGH JANUARY 1939
B AND R HATCHED JULY 24, Y JULY 25, 1938

Date	Boss	Caged	Free	Singing B	Singing Y	Challenge	Circumstances
Oct.							
3	B		B, R, Y	Short songs when fighting			
6	B		B, R, Y			R at Y sw	Y alighted near
9	B		B, R, Y		Short songs when fighting		
15	B		B, Y	Loud short songs			
23	B		B, Y		Short song when he lands in safety		
27	B		B, Y			Y psw	B landed near
31	B		B, Y	Loud warbling	Loud warbling		
Nov.							
1	B		B, Y			Y sw	B above Y
2	B		B, Y	Loud short songs	Silent	Y psw	B above Y
3	B		B, Y	Loud short songs in front room	Loud short songs in study when B is in front		
4	B		B, Y	?	Same behavior	Y psw	B suddenly landed near Y
5	B		B, Y	?	Same behavior		
6	B		B, Y	?	Loudly, harshly	Y pw	When released from cage in morning; fight
7	Y		B, Y	Nearly silent	Loudly, harshly	Y psw	B above; B flies
8	B		B, Y	Warbles	Warbles		
9	Y		B, Y	Warbles	Loud, short songs		
10	B		B, Y	Warbles	Loud songs in evening		
11	Y	Y	B	Warbles	Loud songs		
12	B	Y	B	Warbles	Very loud; no form developing yet	Y psw	B on top of cage

Date	Boss	Caged	Free	Singing		Challenge		Circumstances
				B	Y			
13	B	Y	B	?	Loud			
14	Y	Y	B		Very loud	Y	pw	B on top of cage trying to fight
15	Y	Y	B		Very loud	Y	psw	B on top of cage
16	Y	Y	B	Warbles	Much and loud			
17-22	Y	Y	B	Warbles	Much			
23	B	B	Y		Loud			
25-27	B	Y	B					House very cold
29- Dec. 7	B	B	Y	Silent	Silent			
8	B	B	Y	Silent	Warbles	Y	ps	Tried to get into cage
12-17	B	B	Y	Silent	Warbles	Y	psw 6X	Outside of cage, opposite B, nearly every day. Fight
19-22	B	B	Y	Few short songs	Warbles	Y	psw	Start to fight
23-27	B		B, Y	Warbles, some short songs	Warbles	B	psw 2X	Fight
(B taken upstairs from 7 P. M.-10 A. M.)								
28	Y		B, Y	Silent, warbles	Loud, short songs	Y	psw	When B returned
29	Y		B, Y	Warbles loudly in front room	Repeats songs up to 3 times			
30	Y		B, Y	Adult timing, loud, in front room. Tries to establish territory there	Suddenly changed to songs of more definite form, repeats some many times	Y	psw	When B comes to netting between study and front room. B flees
31	(Y upstairs)		B	Sings little, tries to get into front room	Adult songs			
Jan. 1	B	B	Y	Adult singing, loud	Warbles	B	psw 2X	When Y brought in little cage
2	B, Y	B	Y	Loud, short	Loud in front room	B, Y	psw	Y on top of cage
3	Y	Y	B	Warbles loudly in front room	Loudest singing nearly all day	Y	psw	
4	Y, B	Y	B	Proclaims territory in front room	Proclaims territory in study	Y	psw	B on top of cage
5	Y, B	Y	B	Nervous in study, proclaims territory in front; returns, loud, short songs	Warbling in cage			
6	B	Y	B	Loudly wherever he goes	Few loud songs, later very loud	Y	psw	B dashing to side of cage, fight. Y defeated
7	Y	Y	B	Loud in front	Loud in cage			
9	Y	Y	B	A great deal in front room	A great deal in cage	B Y	sw psw	B to cage, wing up Y greatly puffed. Y picks up stalks
10	B	Y	B	A great deal	A great deal			Fight; Y retreats
12	Y	Y	B	Tries to enlarge territory from front room	A great deal			Y gets out; great fight thru netting
16	B	Y	B	A great deal	Not much	Y B	psw psw	
17	B	Y	B	A great deal	A great deal	B, Y	psw	Y picks up paper and weed stalks, carries them about

Date	Boss	Caged	Free	Singing		Challenge	Circumstances
				B	Y		
18	Y	Y	B	Loudly in front, softly in study	Loudly in cage	Y psw	Rushes at B and routs him
20-21	Y	Y	B	Loudly in front, upward flights	Loudly in cage	Y psw 2X	B approaches cage; Y fights
30	Y	Y	B	Loudly in front, tries to enlarge territory despite blizzard outdoors	Loudly in cage		

There were 18 revolutions in the 72 days between Nov. 7 and Jan. 18. Counting from Oct. 3 through January, B dominated about two-thirds of the time; during the 84 days after Y's first revolution, about half the time.

FROM JULY 1939 TO MARCH 1940
D HATCHED JUNE 14, J AUG. 4, 1939

Date	Boss	Caged	Free	Singing		Challenge All psw	Circumstances
				Y	D		
July 1-13	Y	Y	D, F, S	Sings a little	Warbles a little	Y at D, F, S	When they alighted on cage
Sept. 14	Y		All	Song after a chase	Warbles rather loudly	Y at S	S indifferent
Oct. 6	Y		Y, D			Y at D	D suddenly flew near: Y picks up grass and carries it
Dec. 17	Y	J, Y	D	Silent	Warbles with bill open	D at J, Y Y at D	Y responds to D's psw by extreme posturing
19	Y	J, Y	D	Sings softly	Short songs		
22	D	J, Y	D	Silent	Loud, short songs. Much tchunking	D at Y	D on top of cage psw, loud singing, Y intimidated
23	D	J, Y	D	Silent	Adult songs. Awakening song		
24-28	D	J, Y	D	Silent	Sings much. Much tchunking		
29	Y	J, D	Y	Silent	Sings		Y got out and chased D
30	D	J, D	Y	Silent	Loud songs		Y came to cage, D routed him
Jan. 1	D	J, D	Y	Silent	Sings and warbles	D at Y	Fight; Y defeated
2-9	D	J, D	Y	Silent	Sings much		Y fights J
10	D	J, D	Y	Sings a little	Sings much		Y intimidates J
16	D	J, D	Y	Sings softly	Sings much	D at Y	Y fights J
17	Y	J, D	Y	Sings all 6 songs, softly, then loudly	Sings much then silent	D at Y Y at J 4X	Intimidates J, then D
18	Y	J, Y	D	Sings loudly	Soft songs	Y at D 6X	D on top of Y's cage, Y tears at string
19-20	Y	J, Y	D	Sings loudly	Soft songs	Y at D 2X	D on top of Y's cage

Date	Boss	Caged	Free	Singing		Challenge	Circumstances
				Y	D	All psw	
21	D	J, Y	D	Sings	Sings	D at Y	By Y's cage
23	D	J, D	Y	Sings softly	Sings loudly	Y at J	Y fights J, D tchunks
24	D	J, D	Y	Sings softly	Sings much	D at Y	While both are out; Y flees
25	D	J, D	Y	Silent	Sings loudly	Y at J	She got out. Y below her
26-31	D	J, D	Y	Sings much	Sings much		Intimidates J. Y and D seldom meet
Feb.							
1-5	(D at Ewers)			Little singing			Less despotic to J
5	Y	J, D	Y	Soft singing		D at Y	Y eats, sings softly; D crest up
6-7	Y	J, D	Y	Much, loud singing	Sings when in front room	Y at D 6X	D got out; Y chased him
8-26	(Y at Ewers)				Much singing		D fights J
27	Y	J, D	Y	Loud singing	Silent	Y at D 2X	Y fights J
28	Y	J, D	Y	Loud singing	Silent	Y at D Y at J	Y picks up straw
29	Y	J, D	Y	Loud singing	Silent		Y dashes at J
Mar.							
1-3	Y	J, D	Y	Loud singing	Soft songs	Y at J	Intimidates D and J; she fights
4-7	D	J, D	Y	Soft singing	Loud singing		Y fights J
9	Y	J, D	Y				
10-12	D	J, D	Y				
13	Y	J, D	Y				

There were 10 revolutions in the 63 days that the birds were together from Dec. 17 to Mar. 13; during this period Y dominated about one-third of the time.

REMARKS ON DOMINANCE, SINGING AND THE CHALLENGE

The challenge (puff-sing-wave or psw) was first shown by R at 74 days when Y alighted near him; this was incomplete, for the puffing was omitted. The next instance was given by Y at 94 days when B suddenly landed near him; this was complete. B did not give it until 160 days; the stimulus was the return of Y after a 15 hours' absence.

From Nov. 11 one bird or the other was kept in the large cage, 2′ x 3′ x 4′, except in late December. From Nov. 29 on, B tried to establish a territory for himself in the front room; his favorite place was by the large east window some 18 meters from Y in the cage by the west window in the study. For food and water B had to return and procure them near Y. Netting hung at the door of the study, so that the birds could not pass freely back and forth, but had to search for an opening.

The despot often threatened the underling with *shee* whenever the latter came too near; it was through this note that I knew who was boss, when the boss was caged. The underling often raised his crest when near the boss, and especially at hearing the threat note.

As to song and dominance, B was at first ahead of Y in development and dominated him. On Nov. 3, Y sang loud, short songs when in the front room well away from B, but was silent when in the study with him. On Nov. 7, the first revolution took place; B fell silent, while Y sang loudly in stage III (Chapter XI). Until Nov. 24 Y remained in stage III, while B *retrogressed to I and II.* After the cold spell in late November song and aggressiveness were at a low ebb; B was dominant, but Y challenged him with psw from Dec. 8 on. Upon B's return Dec. 28 after a 15 hours' absence, Y intimidated him, using loud, short songs. On the 31st *adult songs were established with Y.* B, in the meantime, was silent in the study, but sang loudly in the front room, even trying to get there during Y's absence on the 31st. On Jan. 1 *B's singing was adult* and he intimidated Y on his return, using the psw for the first time. The next day Y worked up his courage by loud singing in the front room (B being caged); he returned, B flew down, puffed like a ball, vibrating his right wing and warbling. At 3 P.M. both were singing loudly, B in the cage, Y in the front room. Y was chased into the study by us, sang on top of the cage, puffed up and vibrating his wings. B puffed up, but Y chased him. They defied each other, B with crest raised and bill open, then soon flew away. Y gave a bounce towards B and B retreated. Y sang his loudest on the cage, while B's crest stayed up. Y drove B when he came near the edge. B gave *tchip tchip* softly when he was chased.

Early in the morning of Jan. 5 B was very nervous, panting and trying to get out of the west window, while Y was restless in the cage. We "shooed" B into the front room; he at once started to sing loud, short songs, while Y fell silent. At 8:03 B returned, singing loud, threatening songs, and it was Y who was nervous, panting with his crest up.

During this month each bird showed a new activity. B endeavored to enlarge his territory in the front room by making repeated flights up from the window sill of the east window, on the 30th doing this in spite of a blizzard raging outside. On the 9th Y for the first time showed a substitute activity immediately following the psw; he picked up stalks and carried them about.

In July 1939 Y went through the psw at the young birds landing on top of his cage. They were indifferent, as was S on Sept. 14 and D Oct. 6. On Dec. 17 Y was feeling poorly and I shut him into the large cage for the first time since mid-July. An hour later D began to warble louder and louder by J's cage, then started to wave his wings at J, whereupon she retired. He then flew to Y's cage, warbling loudly, wings waving; Y went into a perfect ball, vibrating his wings and singing softly. D's crest went up; he looked like a flycatcher perched on the rim of the cage. Y rushed at him and he left. On the 19th D sang *short songs* on top of the typewriter some 2 meters from Y; Y was excited, uttering many *tchunks* and trying to get out. D warbled on the floor a meter from Y, while the latter rushed up and down, giving loud *tchips.*

On the 22nd D was singing loud, short songs, intimidating Y who flew back and forth in his cage with his crest up. D suddenly sang *very loud,* puffed up and wings waving on top of Y's cage; Y's crest went up. Ten minutes later D started to *tchunk,* then flew to the cage and repeated the challenge *with loud singing,* instead of the typical soft singing.

On Jan. 17, Y suddenly burst into song; he and D sang the same songs most of the time, D echoing Y. Y busied himself giving the psw at J, then turned his attention to D, whose crest went up. Both Y and D increased their confidence by intimidating J, then turned to intimidating the rival male.

In May Y started to intimidate his only bird companions, the Goldfinches, by dashing back and forth over the top of their cage, just as he had done to B and B to him. Once a Goldfinch suddenly flew down near him; he lifted a wing and waved it a little. Another time the Goldfinches were flying noisily back and forth in their cage; Y puffed and vibrated his wings.

The third year—1940-1941—the set-up included Y, who was kept in the large cage all the time, the subnormal male A, hatched in July 1940, and usually kept in a roomy cage; and from February on 2 hand-raised male Bobolinks hatched in July 1940, one kept in a sizeable cage south of Y's, the other free on top of Y's cage. The Bobolinks dominated Y to some extent by loud singing, wing spreading and hissing, as long as he was caged, but when he was let out, they were evidently afraid of him, the free Bobolink hastening into his cage. Y and the Bobolinks never fought each other; it may have been that Y's quick movements disturbed them. All three dominated A. (A never got beyond stage I in singing, and never showed the psw.) When A was out and flew to Y's cage, Y immediately went into the psw for a minute or two, then picked up seeds and leaves and carried them about or yanked at strings or attacked straws. Once when A approached, Y merely tugged at strings without going into the psw. When Y was once let into A's cage, Y pursued him and A fled, panting. Once when a Bobolink crouched down on top of the cage and hissed at Y, Y, who was right below, crouched and with bill pointed up, *raised a wing and vibrated it.*

The challenge has been a more prominent activity with Y than with B or D, as is witnessed by its early appearance and its frequent use. In the first 2 years Y was seen to give it at least 69 times, in contrast to 9 records for B and the same number for D. In the third year there are 24 instances of its use by Y against A. In the first year Y gave it 14 times as boss, and 17 as underling, but all the other instances were when he was boss, even though the second year from Dec. 17 to Mar. 13 he was dominated by D two-thirds of the time.

APPENDIX III

Behavior Upon the First Arrival of Females

It is unfortunate that I never saw the very first arrival of a female that stayed with the male.

One record early in the season was made on a resident pair; the male, 55M, had been hatched May 29, son of 5M and K2.

(1) Feb. 11, 1931. 55M and K54 are eating near each other much of the time. 9:20, 55M pounces on K54 and gives an abortive song. She makes some objection. 10:30, she chases him. 11:00, 55M in the trap; K54 excited in the vicinity.

Twice I saw the arrival of the female, but in neither case did she stay.

(2) Feb. 28, 1930. 8:52, I am watching 1M and 4M, who are both unmated and singing steadily; I notice an unbanded Song Sparrow eating near the boundary between the 2 territories. Both males approach. The bird gives a kind of chatter, 4M goes near, she threatens him, and he retreats. 1M sings, 4M *tchunks*. She utters *zhee zhee*. 1M sings; he and 4M puff at each other (threat-posture); the female leaves.

(3) July 16, 1930. 47M, unmated, is singing on the territory he took up the middle of June. An unbanded female comes straight from the south, lifts a wing and flutters; he approaches, she postures in copulatory attitude. He tries to mount, but she does not let him. This is repeated several times; then they settle down on an elm branch a foot apart. He sings constantly. I never saw her again.

In the following cases the mate had arrived the day of observation, but before my observation began. In the first two there was posturing, but no copulation, also fighting between the mates.

(4) Mar. 16, 1930. 9M has a mate. He sings on the ground a number of times, then he and this unbanded bird have a regular fight together, jumping up and down and bumping breasts. Shortly afterwards she flies with a chatter. 9M hurries near, *picks up a straw* and says *chip chip chip*. Later he sings various songs. She flies with a chatter and trills.

Ten minutes later 9M's mate chatters and trills vigorously. 9M follows her. She postures on a weed, standing in the extreme copulatory attitude, fluttering her wings. He does not try to mount. He is a young bird as revealed by his singing in February.

(5) Mar. 19, 1932. 70M has a mate, an unbanded summer resident. She postures 3 times. He appears to try to mount her; she pecks him vigorously and they fight. She gives no note.

In this case rivalry was shown between 2 males.

(6) Mar. 1, 1932. 50M and 107M are both interested in an unbanded summer resident female, the first of the season. 50M behaves like her mate, sitting about and *tik-tik-tiking*, but 107M wants her too. When she flies, both males follow her, then 50M drives off 107M. She does little but feed. 50M is busy driving 107M away.

(7) Mar. 22, 1929. 5M has a mate. They crossed the ditch but were driven back by a neighbor. She chattered and *tchunked* loud and long. . . . She gave a simple little song. He flies near, she pecks at him, then postures and trills. He climbs up the bank. She flutters her wings and follows. His back is turned. She flutters more and continues to follow.

The most dramatic of the records I have on first morning behavior of mates concerns 4M and K200, Mar. 7, 1935. I had heard the chatter of a female at 6:47 A.M., but was not able to get out to watch the birds until almost an hour later. 4M was 8-9 years old at this time, while his rival, 225M, was a bachelor, hatched in 1934. 4M's defensive behavior was very mild in comparison to his activities 6 years earlier. He gave 117 songs in the first hour I watched and 51 in the next half hour. 225M sang constantly, except when visiting. I will give the high lights of the action.

(8) 7:40. 4M's new mate, an unbanded summer resident, is on a post; he attacks her, chases her and sings D. She gives various notes, and trills.

She flies over to the brush pile (near 225M's land); 4M is after her and chases her back. She preens and shakes herself in the little elm. She is looking towards 225M's land—he is singing loudly. She flies to the brush pile; 4M goes after. 225M joins them; 4M *chases her home*.

7:50. He flies to the road to eat; she flies to a tree. He follows and attacks her; they fight; he sings G. She goes to the ground with a chatter; he follows.

7:54. She flies and chatters, then flies again. He follows, but she avoids him.

7:59. Both are feeding near together, 4M following the female. 225M approaches. She gives a queer note *greech*. 4M is *tchipping*. She gives the threat-note. 225M comes to call. 4M goes toward him, he retreats, while she mounts the little elm and watches. 4M chases 225M off. K200 feeds, 4M watches. She flies with a chatter and he follows.

8:03. 4M sings in a tree, she chatters several times and comes into the tree too. She flies, he dashes towards her, nearly hitting her. She drives him, he sings, she trills, then chatters, then *tchunks* in the rose hedge and *tchunks* again on a post, then on the ground. She flies up into his tree. He flies west and she follows; he returns and she does likewise. She flies to the ground below him, chattering.

8:14. 225M comes to visit; 4M meets him a little hunched. 225M sings constantly; approaches nearer and nearer to K200; 4M drives *her away from him*. She says *greech*. 225M again here; 4M drives him.

8:21. She chatters and *greeches* as she flies near 4M. He and 225M have a boundary feint, threatening each other.

8:28. 4M pounces on K200, she fights; he sings.

8:34. He pursues 225M who is flying puffed out. She is in the little elm; *greech;* 225M approaches and 4M drives him off.

8:37. 225M is back home singing. The pair are feeding in the weeds; she drives him and off he goes.

8:40. She flies, he follows, they fight. She trills.

8:48. She flew to 225M's weed patch, 4M is after her at once. 225M is here. 4M always keeps between her and him. Now the males fight. She flies over *into* the patch; 4M drives her home, pounces and sings.

8:53. She flies into a tree, then to the hedge with a chatter. Now lifts a wing, then both wings.

8:59. They are feeding on the ground. She drives him. Both males are near together; 4M drives 225M; both have spread tails. 225M is singing. 4M won't let him come near K200. 4M approaches her, she threatens him.

9:04. He sings B. She chatters. Both are in hedge. He flies to drive off 225M. She goes to the little elm, 225M comes there, 4M hastens and drives him off.

K200 was unusual in her mounting trees so much, for females usually stay close to the ground. I thought perhaps she would desert to 225M, but she did not. She proved to be a "cold", despotic mate, and there was not a close bond between her and 4M, in contrast to the other pairs I have studied.

APPENDIX IV

Some Samples of Coition in 1929

Mar. 21. K2 flutters her wings; 1M does not see her. An hour later she flutters her wings; he gives her a little peck as he jumps over her. She trills.

Mar. 22. She flutters her wings for a minute or so after a pounce; 1M flew up on the bank beside her; she repulses him with uplifted wings, but trills.

Mar. 29. She is getting material and flutters her wings; he is nearby; he mounts; they copulate; she trills. They repeat the process a minute later.

Mar. 30. She flies to the ground; he flies to her; she postures and they copulate twice in rapid succession.

Apr. 2. 8:51. Both fly to the weeds, she chattering; they copulate; she trills.

9:37. She is taking stuff to one of her favorite spots, chattering; he follows her. She postures, he mounts, but slips off. She trills.

Apr. 4. 7:30. She is picking up material, he flies over her; she crouches and flutters, trilling with bill open and losing her load. He leaves.

8:07. She is gathering material and he flies to her; she crouches and flutters. He appears to be going to mount, but instead gives her tail a tweak, then flies away. She trills.

Apr. 7. She chatters as she flies out from the nest she is building, alights near 1M and trills with fluttering wings; he approaches, but she gives the threat-note and turns away.

Apr. 8. 8:02. K2 postures with her bill full of nesting material; they copulate; she trills and with a chatter takes her load to the nest.

11:33. They copulate about 2 yards below the nest; she trills; then flies chattering to the feeding station. He follows and they copulate there 3 times in quick succession.

Apr. 10. The first egg was laid.

APPENDIX V

List of 13 Orders and 16 Passerine Families in Which Distraction Display (Injury-Feigning) Has Been Reported

*=common. **=very common.

See species index for scientific names.

Authorities frequently mentioned: F=Forbush 1925; G=Grimes 1936; J=Jourdain 1936-37. No attempt is made at a complete list of species, nor complete bibliography.

Order Suborder Family	Species
Struthioniformes	Ostrich (Knowlton 1909:64).
Colymbiformes	Pied-billed Grebe (Gabrielson 1914), Dabchick (J).
Anseriformes*	Many species: Mallard and 7 others (J), Wood Duck (Saunders, 1937), Lesser Scaup (Munro 1941).
Falconiformes	Merlin (J).
Galliformes*	European Partridge (J), Ptarmigan (J), Ruffed Grouse, Bobwhite, etc.
Gruiformes	Common Crane (J), Limpkin (G), King Rail (G).
Charadriiformes	

Charadrii**	Plovers, Turnstones, Surf-birds (Charadriidae); Snipe, Woodcock, Sandpipers (Scolopacidae); Avocets, Stilts (Recurvirostridae), Phalaropes (Phalaropodidae); Pratincoles (Glareolidae) (Jourdain and many others).
Lari	Jaegers (J); Sooty Tern.
Columbiformes**	Mourning Dove (Nice 1922-23), Ground Dove (G), Turtle Dove (J), etc.
Cuculiformes	Roadrunner, Yellow-billed Cuckoo (G).
Strigiformes	Short-eared Owl (J), Long-eared Owl (J), Great Horned Owl (J).
Caprimulgiformes**	Nighthawk (G), Chuck-will's-widow (G), Nightjar (J), etc.
Passeriformes	
Tyrannidae	Gray Flycatcher (Russell and Woodbury 1941).
Alaudidae	Prairie Horned Lark (F), Woodlark (J).
Campephagidae	Minivets (J).
Paridae	Chickadee (G), Tufted Titmouse (G).
Timaliidae	Quail-Thrushes, Pilot-bird (Chisholm 1936).
Pycnonotidae	Bulbuls (J), Zambesi Nicator (the Moreaus 1937). 1937).
Chamaeidae	Wren-Tit (Erickson 1938:297).
Turdidae	Song Thrush, European Blackbird, Ring-ouzel, Wheatear (J).
Sylviidae	At least 6 Old World Warblers mentioned by Jourdain.
Muscicapidae	Whistlers (Chisholm 1936), Willie-Wagtail and Yellow Robin (Roberts 1942).
Motacillidae	Meadow Pipit (J).
Meliphagidae	Honey-eaters (Chisholm 1936).
Compsothlypidae*	At least 18 species: see Grimes 1936, Forbush 1925, Nice 1926a, 1931b, Nice and Nice 1932, Cottam 1936.
Ploceidae	House Sparrow (Daanje 1941).
Icteridae	Southern Meadowlark (G).
Fringillidae (Emberizinae)	Buntings (J), Sparrows-Vesper, Savannah, Grasshopper (F), Pinewoods (G), Song; Towhee (F) (G).

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INDEX TO SUBJECTS

INDEX TO SPECIES

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