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Field Observations of East Greenland Birds

II. The Behavior of the Snow Bunting (*Plectrophenax nivalis subnivalis* (Brehm)) in Spring.

BY

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I. INTRODUCTORY

Howard's work on the phenomenon of territory in the natural history of birds (Howard, 1907-1915, 1920, 1929) led him to certain generalizations that have caused much discussion on this highly complicated matter, and in recent years a wealth of arguments *pro* and *contra* his conclusions have been brought forward. As Howard's observations had all been made on species of the north temperate zone, his ecological conclusions might have been based on special facts valid only in these regions, and it was thought that comparable work in other regions might throw new light on that aspect of this complex problem. So when my wife and I had the opportunity to spend a year in east Greenland, we decided to give this time to a careful study of some species of Passerine bird, with special attention to be given to spring fighting and other activities that might throw light on the problems of territory.

From July, 1932, until September, 1933, we stayed in the Angmagssalik district, which is situated on the east Greenland coast near the Arctic Circle.

In ornithological respects, this district is the best known region of east Greenland. For general descriptions of the country the reader may be referred to Holm & Petersen (1921), Helms (1926) and Tinbergen (1935). Data on the avifauna are published by Helms (1926, based on observations and collections of Johan Petersen, who lived in Angmagssalik from 1894 until 1915), Chapman (1932), Pedersen (1930, 1934) and Salomonsen (1935).

During most of the time from our arrival until February, 1933, we were the guests of the Dutch expedition of "The International Polar Year 1932-1933." Our base during that time was Tassiussaq, the trading station of the Danish government. From here we made several journeys into different regions of the district, in August, September, October and January, in order to find a favorable spot for our work in spring. In the beginning of February, 1933, we settled in the Eskimo settlement, Kûngmiut, situated at Angmagssalik fjord, about twenty-five miles from the outer coast.

Our observations were made at different stations in this region. From March until July a great part of each day, averaging about eight hours, was given to careful observation of the behavior of Snow Buntings. Our observations started some time before the birds woke up. At the end of March this occurred at about 3:30 A.M., from the end of April through May, June and July at about 1 A.M. During the end of

June and the beginning of July, our work on the Snow Bunting had to be partly interrupted by work on the Northern Phalarope; hence, our observations during that period are somewhat less complete than are the earlier ones.

Our work was centered on the Snow Bunting for several reasons. In the first place, it is a close relative of the European Buntings, several of which have been carefully studied by Howard and have served as the basis of his views on the territory problem. Second, the Snow Bunting had a certain reputation—based on the observations of Nicholson (1930)—of differing considerably in behavior from Howard's territorial birds. Furthermore, it is the most common Passerine species in Angmagssalik, and it is the first species to arrive in spring. It was not at all shy and could be watched from a short distance.

In outlining our program, we had to choose between two possibilities. We could either make a broad review, a survey, of the whole sequence of events during the entire reproductive cycle, or we could restrict ourselves to a study of a few detailed questions, in order to investigate these more thoroughly.

In our opinion, the present knowledge of these problems requires primarily observations without experimental specialization. In purely observational work, it is absolutely necessary not to disturb the bird; consequently, if we direct our attention to only a few specific problems, we lose much time. It is, therefore, a question of efficiency to maintain as broad a view as possible in order to prevent the unnecessary disregard of valuable facts. Moreover, in questions of territory a restriction as to details is at present not justified until a survey has been made.

For several reasons our observations show more or less important gaps. It was impossible to make all observations at the same place. Owing to changing snow and ice conditions, our original observation stations became temporarily inaccessible and we had to move about several times. This handicap made it impossible to get observations covering the whole reproductive period of a single pair, but on the other hand it had the advantage of enabling us to see the same phases of reproduction in different pairs, as at each new observation post, we chose individuals whose breeding cycle was some days behind that of the birds we had just abandoned. Nevertheless, our description will be incomplete in many respects, as we had only one season at our disposal.

The assistance of my wife was of great value to me, not only because she did most of the practical camp work, thus leaving me more time for observation, but because she served as an independent observer, having been trained, during several years in the Netherlands, to do this kind of work.

Though our primary aim was the study of territory, many observations on other elements in the behavior of the Snow Bunting were made as a natural consequence of our method. So far as it seemed desirable I have included them in the descriptive part. As will be seen, some of these supplementary observations were of sufficient interest to justify the discussion of the problems upon which they bear, though they may have no direct connection with our principal theme.

In the discussions, I have made ample use of the literature. I have not succeeded, of course, in being complete; the disorganized state of the literature on bird behavior renders this impossible. In most cases, however, I have sought to review the most important facts.

It will be seen that the facts from the literature are used for a special kind of comparison. Comparative treatment is given primarily for the study of the *causes* and *functions* of certain reactions, not for the study of homologies in ethological elements. Therefore, comparison has not only been made with closely related species, but with more distantly related forms as well.

I wish to express my sincerest thanks to Mr. S. van den Bergh, London, and to Mr. G. J. Tijmstra, The Hague, for the generous way they enabled me to spend this year in Greenland. My thanks are further due to the "Maatschappij Diligentia" (The Hague), the "Vereeniging Het Natuur-en Geneeskundig Congres" (Amsterdam), the "Bachiene-stichting," the "Fonds van Mr. H. Vollenhoven" and the "Leidsch Universiteitsfonds" (Leiden), for further financial aid; to Professor Dr. E. van Everdingen, Dr. G. van Dijk and Dr. T. van Lohuizen, organizers of the Dutch Polar Year Expedition, for allowing us to attach ourselves to the expedition and for help in several ways; to the Danish functionaries, Mr. G. Rassow (†), Mr. P. Rosing and Mr. W. Stilling Berg for their kind help during our stay, and last but not least to our host, Kârale (†) and his wife for their most generous hospitality and invaluable help on numerous occasions; further to Mr. Fr. Haverschmidt (Haarlem), Dr. G. J. van Oordt (Utrecht), Dr. P. Palmgren (Helsinki), and Dr. B. Stegmann (Leningrad) for generous help in acquiring literature; to Mr. J. J. Hickey (New York), Professor Dr. C. J. van der Klaauw (Leiden), Dr. Ernst Mayr (New York), Mrs. M. M. Nice (Chicago), Dr. G. K. Noble (New York), and Mr. Wm. Vogt (New York) for reading the manuscript and for valuable criticism; and to Mr. D. J. Kuenen (Leiden) for revising the English text.

II. DESCRIPTION OF BEHAVIOR DURING THE BREEDING CYCLE

It is necessary to distinguish several successive periods or phases in the life of the Snow Bunting during the reproductive season. The beginning of each of these is marked by a rather sudden change in behavior. The periods may be chronologically classified and characterized as follows:

FIRST PERIOD: MALES HAVE ARRIVED AND ARE LIVING IN FLOCKS, FEMALES STILL ABSENT

The dates of arrival of the Snow Buntings in Angmagssalik are very well known thanks to the careful observations of the first governor of Angmagssalik, Johan Petersen. His data were published by Helms (1926) and cover a great number of years. Petersen's notes show that the date of arrival varies considerably for the different years; sometimes the first bird is seen as late as April 8th; in 1914 a few birds arrived as early as February 10th. More often the first arrivals were seen in the second half of March. The average arrival date for seventeen years is March 21st. Sometimes Petersen's own dates fall somewhat later than those that the Eskimo natives reported to him. Since the Eskimos are very alert to the Snow Bunting, because it is the first bird to arrive in spring, their dates have been taken here to be sufficiently reliable to be used in finding the average date of arrival.

The great variation in the dates of arrival may be due to a considerable extent to weather conditions at the last stage of the migration route. Our host Kârale, who was a very careful observer and a reliable man, told us that the first flocks always arrive during a *neqajâq,* an easterly wind accompanied by a heavily clouded sky and rather thick snowfall. This was indeed the case in the spring of 1933, when the first three Snow Buntings were seen during a heavy easterly snow storm on March 22nd. Great numbers of new Snow Buntings arrived on April 20th, the day after a nocturnal *neqajâq.* This does not mean that no birds arrived at other times, but only that a *neqajâq* caused an increase in the number of new arrivals. The arrival of new birds always occurred during the early morning, up to about 6 or 7 A.M.; during the first three hours after midnight, flocks were often observed that did not alight but passed on.

The first arrivals, those seen at the end of March and the beginning of April, never stayed, but soon disappeared. It is impossible to state whether they settled in the district or further north. In the course of April and May all breeding birds arrived.

There was a great interval between the arrival of the males and that of the females. While the first arrivals were always males, and the majority of the resident males settled on the breeding grounds during April, the first female was not seen until April 20th, with the greater part arriving during May. The arrival of the females, therefore, occurred about a month later than that of the males.

Dates of first arrival are known from several other localities in Greenland. For the region around Danmarks Havn (76° 46′ north latitude) in east Greenland Manniche (1910) reports that both in 1906 and 1907 the first males were seen on April 5th, only a few days later than the arrival in Angmagssalik in the same year (1906: some days before April 8th, 1907: "April 1st," Helms [1926]). For Liverpoolland (71° N.) Alwin Pedersen (1934) gives March 26th; for Clavering Island (74° N.) April 1st; for Hochstetters Foreland (75° N.) April 10th. Bertelsen (1932) has carefully collected data on the arrival of the Snow Buntings on the west coast of Greenland from 60°-77° N. On the west coast the Snow Buntings appear to arrive much later than on the east coast; Bertelsen gives for 60°, March 31st; for 64°, April 4th; for 67°, March 30th; for 71°, April 8th; for 74°, April 12th; for 77°, April 29th. The west coast birds winter in North America, a bird banded in Michigan during February, 1932, was recovered in Julianahaab (61°) in April of the same year; moreover, Bertelsen observed west-east migration in spring across Davis Strait. The different behavior of the western and the eastern populations is very interesting considering the fact that climate and vegetation of the southern part of west Greenland doubtless are far more favorable for the Snow Bunting than those of the east coast. One is forced to the conclusion that the different climates of the winter quarters are determining factors for the difference in time of migration.

Several observers report the earlier arrival of the males in relation to that of the females. Dr. P. Palmgren writes me from Helsinki that he has recorded this also in Lapland. From the region around Danmarks Havn, Manniche mentions that "the males arrived first." Petersen (in Helms) and Alwin Pedersen do not mention the earlier arrival of the males. Bertelsen says "the arrival of the females occurs two to three weeks later" than that of the males [translation mine, N.T.]. In the older reports, which are compiled by Pleske (1928), no data about separate arrival of the sexes are given.

This difference in the time of arrival is found in many other birds and especially in those species where one sex plays a leading part in courtship, in sexually dimorphic species as well as in those species where a sexual dimorphism occurs only in behavior and no or little morphological sexual dimorphism occurs. It seems to be the rule, in birds that mate after arrival on the breeding grounds, that the sex showing the most elaborate courtship is the one that arrives first on the breeding ground. In species with reversed sexual dimorphism, the female is the first to settle, as was pointed out in my study on the Northern Phalarope (Tinbergen 1935). In species with mutual courtship it is possible that the sexes do not arrive together but that the male arrives first; this is probably the rule for the unmated birds in the Great Crested Grebe (Huxley 1924).

During the first few weeks not a single male was seen in complete breeding plumage. There still was much brown on the head, neck, and throat, and the scapulars, back feathers, upper wing-coverts and upper tail-coverts had brown margins. There was a marked individual variability in the extent of brown-margined and white-margined feathers of the back.

One is inclined to consider the birds that showed most white and black and less brown older than the other ones, but probably the originally brown margins of the feathers become whiter in the course of early spring, before they are worn off.

Not only were there many individual differences in the extent of brown and white in the margins of the individual feathers, but there also occurred great differences in the extent of the black on the back. In some males the black continued toward the tail, and a broad black connection between back and tail existed; other birds had a large white rump. This wide variety has already been described by le Roi (in Koenig 1911, with figures of such black and white males), and for winter plumages by Natorp (1931).

The first males completed their summer dress by the middle of April; the brown and white margins had disappeared and the plumage showed only a brilliant white and black. The bill and legs were also black. In the course of the next four weeks the rest of the birds gradually lost the light feather-margins. Most males still had spotted backs at the beginning of the second period of their reproductive cycle.

The ability of Snow Buntings to find the necessary food in the desolate, thickly snow-covered country was amazing. They all concentrated in the Eskimo settlements and on the numerous ruins of Eskimo winter houses. In these places they fed principally on the seeds of grasses, the plants which only here covered the ground with a large, closed vegetation. In summer, the sites of these ruins were always

FIG. 1. *Male eating grass seeds.*

plainly visible from a distance as clear green patches; in winter the gales swept the more exposed parts clean, while filling up every depression with snow. The surface of the grass-covered walls, therefore, was always nearly bare of snow, as can be seen in Plate I, fig. 1.

Thus the Snow Buntings, feeding on the seeds of these grasses, and perhaps on small *Acarina* and *Collembola,* were illustrating the well-known rule, that in polar regions the sea either directly or indirectly favors the land communities (Elton 1927). Primitive man and dog in Angmagssalik are absolutely dependent on the sea, which alone makes existence possible for them, by providing food. Their feces cause a high development of some grasses, which provide favorable living conditions for the Snow Bunting during early spring.

During the first weeks the males lived in flocks. When foraging they kept rather close together, and took wing together at the least disturbance. During flight as well as when foraging they uttered two call notes, first the well-known trembling note, second a long monosyllabic *peee.* Exactly the same notes are heard when one observes a flock of foraging Snow Buntings in their winter quarters. Both doubtless act as a means of communication, as a *Stimmfühlung* (Heinroth), each bird reacting to a calling companion by remaining in the vicinity of the latter. Shortly before the birds took wing the frequency of call notes suddenly increased, only to decrease again when all members had joined to form a homogeneous flock. When the birds were traveling over some distance, the frequency of call notes diminished shortly after they had started, but when the birds traveled over short distances, as foraging troops do, each short flight is indicated by a continuously high frequency of call notes, because the short flight does not permit the formation of a well ordered flock. The increase in frequency is apparently sufficient to inform every individual about the intentions of its companions; a special note during flight was not observed.

More than once we witnessed natural experiments on the functions of the monosyllabic *peee* note, one of which may be described here. On April 20th, six Snow Buntings were foraging on some house ruins near

Qangârtiq. At our approach all but one of them took wing. The one that remained looked after the other birds and then uttered a loud and long-drawn *peee* note. At the same moment the five birds, which were about 50 m. away, turned and alighted at their starting point, to resume foraging.

It appears, and it has often been observed in the winter quarters, that the Snow Bunting lives in flocks outside the breeding season. It is not known to have winter territories like some other territorial songbirds, the best known of which are the Song Sparrow (Nice 1933), the Mockingbird (Michener and Michener 1935), the English Robin (Burkitt 1924-26), the Loggerhead Shrike (Miller 1931) and the Wren Tit (Erickson 1938). In this respect the Snow Bunting shows more resemblance to songbirds like the Reed Bunting, the Yellow Bunting, the Siskin, the Greenfinch, etc. A further discussion of this phenomenon will not be attempted here.

The first sign of a coming change in the behavior of the birds was a growing noisiness. At first this consisted only of a higher frequency of repetition of social sounds, but soon some birds started to sing softly. These individuals still behaved as a part of the flock, but coinciding with the beginning of their song, they grew more excitable, quarreling with their companions now and then. These quarrels consisted only of walking in a threatening attitude (head lowered between the shoulders, bill pointing in the direction of the enemy) or an occasional fluttering of wings. Not until later did this develop into a more or less prolonged fight. As far as we could ascertain, a bird having shown these first signs of excitability soon isolated itself and did not remain in the flock for more than two days.

SECOND PERIOD: MALE HAS SETTLED ON A TERRITORY; FEMALES STILL ABSENT

On the 21st of April we discovered the first solitary male. He was feeding on some pieces of lichen-covered rock, which were the only parts showing through the covering of snow. From patient watching it appeared that he confined himself to a certain area with a diameter of about 600 m., foraging on the different small parts of bare ground. He turned up small crusts of lichen with his bill and seemed to discover edible things underneath.

FIG. 2. *Male turning up lichens.*

We turned up many lichens ourselves to find out what he might be eating, but generally we found nothing. The only animals we could discover were *Collembola.* The bird, however, apparently always found something, as we were sure it did not eat any part of the lichens themselves. Killing such birds would, of course, have interfered with our work. The quantities of food found by the birds must have been minute. Comparing the food store of the bird's new habitat with that of the feeding grounds of the flocks, an extreme relative paucity of the former was apparent. This was in general accordance with the fact that such a solitary male spent part of the day in foraging on the common feeding grounds.

From this date on, every male we observed on its territory spent a great part of the morning in singing. During the first few days we heard only a rather soft song, which was uttered during foraging, and at long intervals. A few days later, he stopped foraging every now and then, jumped onto a stone, sang a few phrases, stopped, and started foraging again. Still later he selected some large rocks to sit on and sing, and uttered his now more frequent song in longer spells. Soon he had his special singing rock or rocks on which, soon after awakening, he often sang continuously for more than one hour.

FIG. 3. *Male preening on song-stone.*

FIG. 4. *Male singing on song-stone.*

As has already been remarked, most males, if not all, did not confine foraging to their territories during April and the first half of May. In the early morning they kept within their territories evidently finding something edible there. By midday many territories were deserted and at the same time the flocks near the Eskimo settlements grew larger, indicating that a considerable part of the food was certainly collected outside the territories. After the middle of May, foraging was done more and more exclusively within the territory. Special attention was paid to this question during the period of the rearing of the young, and it then appeared that food was often collected outside the territories (see p. 36 sqq).

A feature that struck us when we used the song as a field character of the individual birds (there is an enormous amount of individual variation in song) was the existence of very restricted, local dialects. Some male Snow Buntings, residing close to each other, had characteristic songs, which were very different from all others we knew, but were undistinguishable, or nearly so, *inter se.* They constituted a small population living in an area some hundreds of meters in diameter: a nucleus of a dialect. Such nuclei were found at several places; in some few cases nuclei that were situated more than 3 km. apart closely resembled each other in certain characteristics of their song dialects. The fact that for some time we were often unable to discriminate between the song of two neighbors, stood in striking contrast to the great general variability of the songs and it will serve to give an idea how obvious were the dialectical nuclei.

There appear to be three possible explanations. The first is that a male that settles on a given spot has an inclination to adopt the dialect of its neighbor. As I have ample evidence that the song of a male does not change to any discernible degree after he gives his first song in spring, this first possibility seems to me rather improbable.

One may ask how I know anything certain about the first song of males in spring. Of most males we had under observation, we actually heard the very first phrase of song, because we always were at our observation posts before the birds woke up, and any new territories were occupied after that time. When one is acquainted with the habits, songs and whereabouts of a small number of individuals during a few days only, the appearance of a new male in a new place is instantly perceived. The first song, uttered by a bird while still living in the flock, cannot have any influence on the formation of these dialects, as these flocks consist of individuals belonging to a number of different dialectical nuclei.

A second possibility is that a male inherits its father's song dialect, and the return of the young males to their birth places would thus result in the formation of dialects.

Still another explanation is possible: the young males may learn, when still in the nest, the song of the father. When they return to their birth place the next spring, this must have the same effect as the second assumption. Between those two latter alternatives it is difficult to decide; but so much seems certain, that the formation of these song dialects is not possible without the young males returning to the vicinity of the territory in which they were born. This is in general accordance with many results of bird banding.

I have observed similar cases of song dialects, restricted to some few territories each, in the European Blackbird (Tinbergen 1939a).

Characteristic of every male in full song was the taking of a commanding position, which allowed a wide view over its territory and the adjacent country. We were sure we could always predict which places would be preferred as singing rocks by a male in any territory. This behavior is characteristic for many songbirds in spring, and certainly serves to obtain a good lookout. This latter conclusion is justified only when it is observed that the birds actually settle on these posts, as soon as they are aware of something of vital importance to them without being able to locate it, *e.g.* a strange male. This was indeed the case with the Snow Bunting. Upon hearing the call notes of strange Snow Buntings, a territory-holding male invariably flew to one of his lookout posts in case it did not at once see and attack the calling bird. Likewise, we could induce a territory-holding male to occupy its lookout post by imitating the call note of the species (see p. 14). Convincing cases of this action in another species are given by the Micheners in their detailed study of the habits of the Mockingbird (Michener and Michener 1935).

We often observed the awakening of the birds. It appeared that 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.

The same is reported by Haviland (1926) for several species of birds in northern Siberia. Palmgren, on the contrary, reports from Lapland that most Passeres regularly take a rest from approximately 6 P.M. until 8 P.M., and that activity is resumed some hours before midnight (Palmgren 1935).

The males slept within their territories, using the same hole for several nights successively, but now and then moving to a new site.

The weather had a marked influence on the singing of the isolated males. The following observations may illustrate this statement.

On April 29th at 4 A.M. a heavy snowfall in absolutely calm weather put an abrupt end to the singing of all Snow Buntings in the region. This could not have been caused by any difficulty in getting food, for on the snow-bare rocks, where foraging was done exclusively, the fresh snow thawed away as soon as it had fallen. The observations were carried on for three hours after the snowfall started, but the birds remained extremely inactive.

Next night a fresh layer of snow fell, and when observation began at 1:30 A.M., all rocky parts which were bare of snow the day before, were now covered to a depth of about 10 cm. Under overhanging rocks some bare spots remained. It had stopped snowing but it was still calm and heavily clouded. It was 8 A.M. before we saw the sun. From about 2:30 A.M. the Snow Buntings were singing loudly, many new territories were evidently occupied, and newly arrived groups roamed through the region. Foraging must have been more difficult than the day before; it was freezing a little, while the day before it was thawing; at 2:30 A.M. it certainly was much darker than the day before at 7 A.M., yet the birds were very active that day and dull the day before. Food abundance, temperature or light conditions alone or in combination cannot account for this, and the most plausible explanation seemed to me that the perception of a heavy snowfall influenced the bird's behavior in quite another way, independent of the first-mentioned possible factors.

This is supported by several observations made during light falls of snow. An interesting example was offered by our entries on May 12th: "Observation started at 2 A.M., at J's territory. The weather is absolutely calm, at first it is dry, though heavily clouded, and warm. The Buntings are singing and fighting. Soon it starts raining, which has no appreciable effect on the Buntings' behavior. After less than half an hour raining suddenly turns into snowing; this has the most remarkable effect, that all birds essentially reduce their song, while several of them stop it altogether, e.g. our bird J. After less than half an hour of heavy snowfall, it stops snowing and at the same time J and several others resume singing."

Later in the season we noticed several times that *heavy* rainfall had a depressing effect on all sexual activities.

These few notes do not pretend to have the value of an analysis of this interesting problem, but in spite of the absence of exact data, which would have interfered with our program, these notes are of relative importance because of the present state of the problem.

In Danmarks Havn, Manniche has observed that the mated males, living on the nesting sites in fine weather, "...in snowstorms and bad weather...would again join the flocks wandering around..." (Manniche 1910, p. 196). This we never observed in birds which were already mated; unmated males regularly returned to the flocks during the hours of sexual inactivity. Pickwell (1931), in his study of the reproduction of the Prairie Horned Lark, also mentions the return of the males to flock-behavior during heavy snowfall.

At this time of the year, the Snow Bunting's country is still so thickly covered with snow that the territories of most males are desolate white hills or slopes with a few exposed boulders, and quite unlike the territories as they are during the breeding time. This reveals a remarkable capacity of the male Snow Bunting. When the young males leave the country in their first autumn (most of them depart during September and October), the country is not covered with snow in any appreciable degree. It is impossible, therefore, that they know their territories by personal recognition, because in spring they are quite different from what the birds possibly could remember.

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 the 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

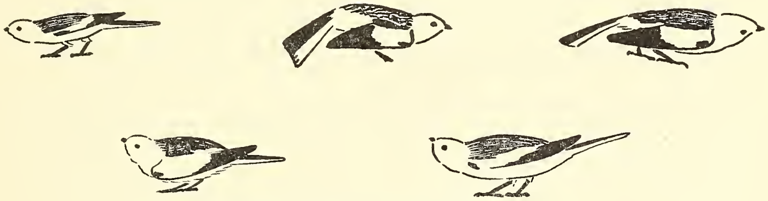
FIG. 1: SNOW BUNTING COUNTRY SHORTLY AFTER ARRIVAL OF THE MALES. ARROWS INDICATE GRASS-COVERED ESKIMO-HOUSE RUINS. QANGARTIK, ANGMAGSSALIK, APRIL, 1933.

FIG. 2: MALE (RIGHT) AND FEMALE SNOW BUNTING AT ENTRANCE OF NESTING-HOLE; MALE CARRYING FOOD FOR YOUNG, FEMALE BEGGING. TORSSUKÁTAQ, ANGMAGSSALIK, JUNE, 1933.

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.

The circumstance that the male restricted part of his movements to a limited area does not in itself justify the word territory. As Nice (1933) quite correctly points out, a territory not only implies that the bird restricts its movements to a certain area but also that it does not tolerate other birds in it; in other words, that it defends it. This was observed in the Snow Bunting.

A male Snow Bunting, once settled in isolation, reacts in a very peculiar way to every other Snow Bunting he notices in his territory. When he discovers an approaching Snow Bunting he turns his whole body, head foremost, in the direction of the newcomer, lowers his head between the shoulders, as was described on p. 8, and utters a sound we had not heard before, which may be written as *p*EEE, resembling more or less the well-known "sawing" note of the Coal-Tit. As all birds seen during the first few weeks were males, we first saw this reaction exhibited toward males alone. Young birds, with small white wing-patches, were not treated differently. Several times we even noted reactions to birds in nearly complete winter dress.



Figs. 5-9. *Male threatening.*

Other species were never reacted to in this way. Lapland Longspurs, Greenland Wheatears and Redpolls often lived in Snow Bunting territories but I never noted any hostilities.

Nicholson (1930) writes that "they often had Wheatears for neighbours and appeared to get on well enough with them; on July 6th a cock was seen to follow about a cock Wheatear engaged in a tacking demonstration against us" (p. 297). But this lack of hostility in Nicholson's birds was seen in a season when, according to the same author "territory was always lax," for birds of their own species were tolerated often enough.

The distance at which a territory holder can see an approaching Snow Bunting is considerable; several times we could observe an unmistakable reaction at about 400 m. distance. Often the route of a passing bird, crossing several territories successively, could be traced by localizing the *p*EEE reactions of the respective territory holders.

The owners of territories reacted quickly to sounds as well as to visual stimuli. On April 20th we observed a solitary male, occupying a territory. He sang with lowered voice while foraging and every now and then jumped on a large stone and sang with full force. Every time I imitated the social *peee*-call, described on p. 7, he stopped singing and stretched himself into a vertical position and looked around; when the sound was repeated he came flying in my direction, fluttering from stone to stone. When he started back to his headquarters, I could induce him to turn around by again imitating the *peee*-call. Both reactions were not observed when either a much lower or a much longer whistle was given. To my regret I was not able to imitate other calls of the Snow Bunting.

It seemed to us that the power of localization of the sound was rather poor; but later in the season it appeared that the sounds of the fledged young were localized by the parents much better than by us. It might therefore be possible that the localization-power depends on the nature of the sound, my imitation of the call notes being rather poor.

Beebe (1925), when experimenting with a chick of the Variegated Tinamou, found that it could localize very well the person imitating the call note of the adult male, and, in fact, showed much better ability than the men present. Engelmann (1928), to the contrary, found the localization-power in the common fowl very poor compared with that of man, of a cat and of dogs. This, however, might be due, apart from specific differences, to the nature of the sound used in the experiment.

In the majority of the observed cases a strange male, when received in the described way, did not alight in the neighborhood of the threatening bird, but flew on. If it did alight, the owner flew toward it, singing and posturing in a most peculiar way during flight. It rose steeply with frequent wing-strokes, then stopped wing-action, sailed in the direction


FIG. 10. *Song-flight.*


FIG. 11. *Song-flight.*


FIG. 12. *Song-flight.*

of the stranger, body curved upward, loudly singing, and keeping its slightly trembling wings in an approximately horizontal position.

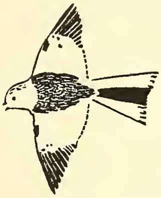


Fig. 13. *Song-flight.*

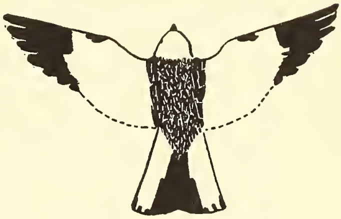


Fig. 14. *Song-flight.*

The intruding bird then did one of two things. In most cases it fled at once, and the incident was over. Sometimes, however, it did not flee, but responded in much the same way as its opponent, by threatening, or by performing a ceremonial flight itself. This response was shown by birds that had a territory contiguous to the other. As the extent and the form of the territories repeatedly changed during the first few weeks, owing to the arrival of new males, such mutual threatening could frequently be observed and often a struggle ensued. The actual attack was often preceded by a special sound, a shrill trembling *cherr*. When fighting, the birds used both feet and bill and often rose straight into the air, constantly trying to get each other down. Although the wings were, of course, continuously used during the aërial combats, we never could see that they were used as a weapon, where one bird would try to beat the other in the manner of the pigeons, for instance; we are sure, therefore, that real wing-fighting does not occur in the Snow Bunting, in accordance with what is known of other Passeres. Often they clung together while in the air, and fell on the snow. This did not in the least hinder them in continuing the fight, and often they rolled down the steep white slopes, a tangle of brilliant black and white feathers: head, feet and flapping wings appearing in the most grotesque positions. When they let go, one or the other of them fled, or else they both remained,

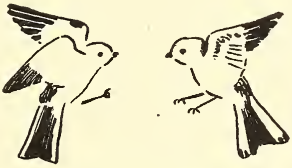


Fig. 15. *Males fighting.*

posturing against each other in about the same spot. In the first case, the victorious male often started in pursuit at once, and then a most fascinating scene could be observed. The fleeing bird only withdrew for a short distance, as he soon reached the boundary of his own territory; he then turned and became the attacker in his turn. Usually the other bird also turned and thus the parts were changed. This reversed pursuit only lasted a few seconds, and then, by reaching the territorial boundary of the other bird, the rôles changed again. Along this line a curious pendulum-like duel ensued, which would continue for many minutes, once for nearly an hour without pause! It was a marvelous sight to see the gay-colored birds hovering picturesquely over the snowy slopes, like great butterflies. Pickwell (1931) describes exactly the same action of the Prairie Horned Lark.

Instead of thus continuing the fight in the form of such a pendulum-flight, the birds often alighted and remained facing each other, nervously walking up and down, often reassuming the threatening attitude. Every now and then, these threatening birds performed characteristic movements, which looked exactly as if they picked up something from the snow. We were rather astonished to see this repeated picking-up, always on the bare snow, and were most eager to see what they were getting. Was it animal or vegetable matter, or was it snow? Careful observation showed that it was neither food nor snow, but that in reality they did not pick at all; they did not reach the ground and only performed a movement closely resembling the picking-up of something.

Similar movements, derived from activities belonging to non-sexual patterns, and displayed during fights, have been observed in many other animals. Elsewhere (Tinbergen 1939b) I have called them "substitute activities" and discussed their origin and function.

We could often observe that the song of an intruding male made a territory-holding male aware of his presence, and a singing male also elicited a much *stronger* response than a silent male, although it also was perceived. This could be determined in territories that were situated on or near favorable feeding grounds and therefore were continuously invaded by foraging flocks. The intruders were often so numerous that the owner of the territory had to tolerate them after some fruitless attacks, though he certainly remained aware of their presence. Every form of vocalization of a male, however, caused an attack, and in this respect the song of a male was more effective than mere call notes. On May 23rd I counted the relative numbers of attacks on silent males, on calling males, and on singing males on the territory of one of the pairs under observation during two hours.

Silent males present	10-15 individuals continuously
A silent male attacked	4 times
Calling male present	numerous times
Calling male attacked	12 times
Singing male present	15 times
Singing male attacked	15 times

In studying the territories of the males, we carefully recorded the position of every fight among the particular males under observation, and from the local distribution of the fights we drew our conclusions as to the boundaries of the territories. When a male occasionally continued the pursuit of an intruder beyond these boundaries, it was not taken as an indication of the size of the territory, for such pursuits never resulted in a fight, but always in the withdrawal of the pursuing bird to within its boundaries. In other words, when engaged in a pursuit a male occasionally went beyond the defended area.

As was mentioned before, a male holding a territory was often alarmed by call notes of other birds, before he had seen them. He then either started a ceremonial flight, or settled on one of the protruding stones in his neighborhood, standing very upright and looking in all directions for the stranger.

Sometimes a male, though foraging on an occupied territory, remained unnoticed by the owner for some time. This was especially the case when several birds intruded on one territory at the same time. We observed in such cases that an intruder, although he was not attacked himself, crouched every time the owner of the territory performed a ceremonial flight, keeping quite flat and motionless, only moving his head slightly to follow the singing bird with the eyes. This was the first proof we got of the warning function of the display of a bird holding a territory.

When a bird, soon after having settled on a territory, came into full song, he showed a new form of behavior. Now and then, mostly while singing, he would utter a long, high note, which resembled more or less the screaming of a Swift, though it was much softer, and which I therefore will call the "Swift" call. It was often performed two or three times in rapid succession and was often accompanied by trembling of

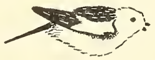


FIG. 16. *Male uttering "Swift-call".*

the wings and panting. Both Swift call and wing trembling sometimes occurred separately. As will be seen later, this behavior must be considered as an outlet for unsatisfied sexual impulse. It is uncertain, however, if such a bird was at this point capable of fertile coition.

Some males, though not all of them, suddenly showed interest in little holes and cracks in the rocks several times during one morning. They visited several of them at short intervals, disappearing into them for a few seconds. These were always occasional visits, occurring at random in many different crevices in the territory, and we seldom noticed any evidence of possible habit formation connected with special holes.

With the arrival of new males, which settled in the region, the territories of the earlier ones necessarily were much reduced in size. As the original territories were defended at the boundaries with much vigor, these changes only occurred after much fighting and quarreling. The strangers, however, were mostly unwilling to move from the once chosen piece of ground, and defended their rights with remarkable obstinacy. Owing to this we often witnessed prolonged fights, some birds struggling continuously for hours. Most newcomers succeeded in establishing themselves on the chosen territories; but once we observed a male which, after two days of continuous fighting with three settled males, finally disappeared.

THIRD PERIOD: FEMALES ARE PRESENT, BUT STILL UNMATED

The earlier males, which had already occupied territories at the end of April, remained unmated for a considerable period, some of them even for three weeks. Their daily routine, as described in the previous chapter, did not undergo essential changes. The arrival of the first females, at the end of April, did not bring a change either, as long as they lived in the flock. From this time on we observed mixed flocks of males and females. The flocks now were no longer exclusively foraging in the Eskimo-settlements, but roamed throughout the region. It occurred rather often that a solitary female, which had left the flock temporarily, passed over an occupied territory. In these cases we carefully watched the response of the owner of the territory, and were quite astonished to see him responding in quite the same way as against an intruding male; the male, perceiving the flying female from a considerable distance, assumed the threatening attitude, lowering the head between the shoulders and uttering the *p*EEE call. When we observed this for the first time, we thought it due to the great distance, which prevented the male's recognizing the sex of the new bird. But we soon discovered that this attitude was assumed as a reaction to every approaching Snow Bunting, whether it was far away or in the immediate vicinity.

The first reaction of the male always consisted of the threatening attitude, remaining thus for a considerable time, often until the approaching bird was within a few meters' distance. Only after this would a male show a specific response, which was exhibited exclusively in the presence of and with reference to the female.

The female often did not flee after the threatening of the male, but alighted in his neighborhood, hereby plainly demonstrating the great attracting influence of the male. When this occurred, the male exhibited new behavior. He assumed an erect, strangely stretched attitude, spreading his tail widely and spreading the conspicuously colored wings backward and downward. In this attitude he directed the piebald surface of back and tail toward the female and then ran quickly away from her. Having run for some meters, he abruptly turned, came back without any display, and then repeated the performance. This specialized display apparently served to demonstrate the conspicuous color patterns of the plumage. The Snow Bunting thus offers a rather unexpected case of the general rule that in courtship conspicuous structures are displayed before the female.

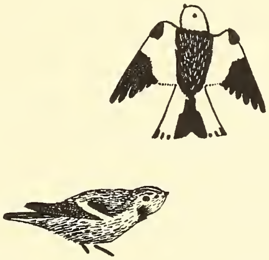


Fig. 17. *Display of male before newly arrived female.*

The behavior of the female was not very sensational; she either preened or picked in the vegetation, often with those hasty, more or less incomplete and intermittent movements typical of substitute activities serving as an outlet for inhibited activity (see p. 16).

As remarked above, the territories occupied by the males shortly after establishment were without exception larger than their final size. At the end of April it was a common sight to see a singing male make a sudden start toward a stranger some 200 to 400 m. away, and the diameter of the territory in some instances surely was about 600 m. Territories of 300 to 400 m. in diameter were of common occurrence. These large territories grew smaller and smaller in the course of May, as the result of the arrival of many new males that occupied territories within the original ones. These new settlers immediately caught our attention by their loud and continuous singing. The original occupant was rather silent during the first few hours, and furiously attacked the newcomer; in most cases, however, with little success. After some time he started singing again, and the attacks grew less frequent. It appeared in these cases that he had changed the place of his song center and had taken a new one near the newly settled frontier. This behavior of male Snow Buntings at the arrival of a new male agrees in detail with Nice's account of the same events in the life of male Song Sparrows (Nice 1933). Pickwell mentions the changing of the habits of the first male after establishment of a new neighbor: "The region of a breeding territory most frequently occupied were those boundaries which joined the territories of a neighboring Lark." (Pickwell 1931, p. 134).

The diameter of a territory actually diminished to about 50 to 100m. in most of the observed cases. We were convinced that the smaller territories were better defended than the larger ones. Intrusions into a smaller territory were instantly perceived and the intruder chased. In the larger territories a stranger was sometimes tolerated and boundaries were rather vague, except at some special places where one and the same neighbor was repeatedly attacked. We therefore agree with Huxley (1934), when he concludes that by an increase in the fighting intensity, correlated with a decrease in the territory's diameter, the territory-system actually results in limiting the number of individuals inhabiting a certain area, because the smaller the territory is, the stronger is the resistance to further reduction of its size. Eventually a limit is reached, at which the fighting intensity is sufficient to keep all new males from establishing within this territory. This will be discussed in more detail below.

FOURTH PERIOD: MALE HAS SECURED A MATE; FEMALE STILL IN PRE-OESTRUM

Soon after the arrival of the first females one of the observed males became mated. We witnessed the actual arrival of a female in several cases. The male always received her by threatening and subsequent display, and the female remained. They soon started foraging together, and before long the male tried to copulate. He walked or flew to the female in a slightly unusual way. We could not be sure whether this way of approaching always differed much from his ordinary mode of walking, but we usually thought we noticed some difference, though difficult to describe. Having nearly reached the female he took to his wings, and tried to alight on her back, but before he could do so, she took flight, immediately followed by the male. The two birds then started in wild pursuit of each other. "And, like the house flies that leave the ceiling and, meeting in the air, pass above and below and round one another so rapidly that the eye fails to follow their movements, these two buntings twist and turn with amazing rapidity." These words of Howard, applying to the Reed Bunting, fit the Snow Bunting equally well. The male tried, and sometimes succeeded, in getting hold of the female, which tried to escape and fought with great perseverance with the same male whose attractiveness she could not resist a few minutes before. Such "sexual flights," as Howard (1929) called them, always resulted in the male giving up the pursuit, and then both birds settled, or rather fell, on the snow, the male showing extreme excitement by several movements. First, he ran over the snow, turning his back to the female, as was described above, and repeatedly uttering the Swift call; this Swift call, when uttered by a paired male, was characteristic of the situation of attempted but unaccomplished coition, and we therefore took it as indicating sexual desire in the unmated male (see p. 17). Further, he panted with open bill, and often performed substitute feeding. The female often seemed tired, but never gave signs of extreme excitement. These sexual flights occurred several times every morning with each pair. Every attempt of the male to perform coition was invariably followed by a sexual flight, for the female never allowed him to mount. Weeks may pass, after the female has taken a mate, before she is willing to copulate. This phase of the sexual cycle of the female is called by Howard preoestrum, because of the similarity to the preoestrum in mammals (see Marshall 1929), where this term designates the first phase of the female's sexual cycle, during which coition is not yet desired.

In general we observed, in accordance with Howard's observation on the Reed Bunting, that the females that mated early in the season came in full oestrum a longer time after mating than those arriving later, and there was a greater difference in time of mating of the females than in the dates of the first eggs.

The performance of the sexual flight indicated, in most of the observed instances, that the birds had mated, and that the female would stay with the male she had chosen. In two cases, however, a female was observed to disappear after she had been mated for some days, leaving the male unmated for a considerable period. In another case we could observe a female that, after having been with a male for one day, left him and stayed some hours with a neighboring male, and then, after two days' flying alternately from the first to the second male and *vice versa,* finally stayed with the first one. With both males she took part in several sexual flights, and on both territories she drove off other females, a phenomenon that will be discussed below.

Our entries concerning this female will be given here in some detail; the observations refer to the males "Peter" and "John" who occupied the territories shown on the accompanying map (Fig. 18).

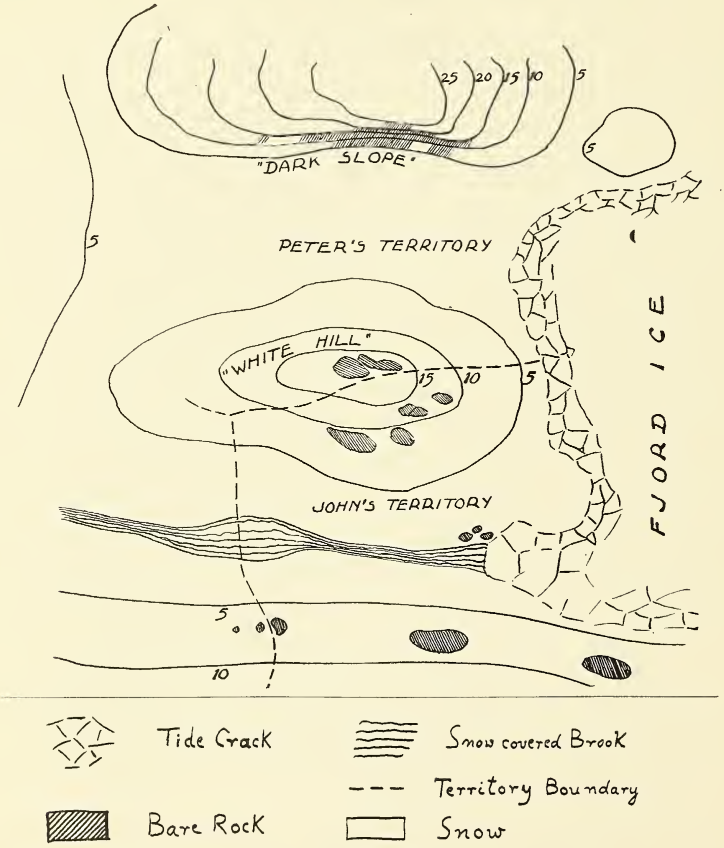


FIG. 18. *Territories of the males Peter and John; heights in meters.*

P is the first to get mated, and has a female in the early morning of May 11th. This female is easily recognizable by some peculiarities in the plumage. *J* is still unmated on the 11th, and spends a great part of the morning in singing, preferring for that purpose a certain little outcrop of rock, (a). On the morning of the 12th, *J* is obviously restless, flying to and fro, singing often on the White Hill and on the stones at the mouth of the brook. Every now and then he flies to the top of the White Hill, singing and uttering *p*EEE call, especially when approaching the boundary. *P,* who during the foregoing days has been seen visiting the White Hill only on rare occasions, is now frequenting the White Hill. *P's* female, instead of remaining on the Dark Slope, is now visiting White Hill, now departing for some minutes far outside the territory. Her flights outside *P's* territory are always in the direction of *J's* territory. When she is on the Dark Slope, she inspects several crevices, sometimes accompanying the male, sometimes joined by him, and sometimes inspecting the holes alone. She attacks strange females on three occasions. She often alights at or beyond the boundary between the two territories, and starts foraging on *J's* territory. *P,* generally after some hesitation, accompanies her, and is invariably attacked by *J,* who drives him off. The female then joins *P,* and thus returns to *P's* territory.

On May 13th there is still greater commotion. From 2 A.M. until 2:30 A.M. my wife observes at Dark Slope, to find that *P* is absent, and that two males, one of which arrived yesterday, the other today, have taken a part of *P's* territory, each at one side; both are continuously singing. Nevertheless *P* is at *J's* boundary, alone, and flies about nervously, calling *pjrrrr* (a call note frequently uttered by the members of a pair) every now and then.

J now has a mate. He is seen to perform a sexual flight with her, after which the male displays. The female follows him closely, when walking as well as when flying. *J,* which both of us have heard singing at about 2 A.M., is completely silent now. This sudden stopping of song is typical for a male that is newly mated (see below). Now and then *P* trespasses across the boundary and flies toward the new pair; he is always attacked by *J* and driven off. The female enters a hole in *J's* territory; when she appears again, I am close enough to recognize her as *P's* female. *J* drives off *P* and flies to stone (a), the female joins him. Sexual flight of female and *J.* They enter the territory of a third male (*B*) and the males start fighting; the female disappears. Soon afterward *J* goes off to persecute a strange male and female flying in the direction of *P's* territory. He returns alone, his mate is evidently gone! Most interesting is the fact that he starts singing again as soon as he turns at his boundary to alight on his stones. Loss of the female instantly evokes song! He flies back to White Hill and chases a pair; then a female appears on White Hill, followed by a male. Again *J* attacks the male, the strangers now remain on the spot, it is *P* and the female! The female evidently had returned to *P* while *J* was combating *B.* The fight between *J* and *P* comes to an abrupt end by the female starting for Dark Slope. *P* follows. *J* returns, alone, singing. Five minutes afterward exactly the same events occur: shortly afterward again; *P* now suddenly returns to Dark Slope to attack a male, the female stays with *J.* Again *P* returns, is chased by *J,* withdraws to White Hill, is joined by the female. The female then, followed by *P* returns to *J's* territory; *P* is again attacked by *J,* stops fighting and flies to Dark Slope to attack a stranger. The female remains on *J's* territory. A sexual flight ensues. The female, while in sexual flight, leaves *J's* territory, and the sexual flight is continued over White

Hill, to Dark Slope. *P* attacks *J*, but the latter remains and does not return to his territory until 60 seconds later, sings.

It would demand too much from the reader's good will to carry this on. In the course of this morning of the 13th of May, the female grew more attached to *P* again, and her visits to *J's* territory grew scarcer. She eventually mated with *P* and reared young with him.

A quite conspicuous feature of the behavior of the newly mated male was the abrupt stopping of his song. During the first few hours after the arrival of a female that stayed with him no male sang a single note. As soon as a female left an unmated male, which had become silent upon her arrival, the male immediately started to sing again. The song of a mated male was always quite occasional, with one exception, which will be considered farther below.

A male that had only recently mated reacted to many sudden movements of the female, especially to her taking flight and to her alighting in his neighborhood, by assuming the flat threatening attitude and uttering the *p*EEE call. After a few days this reaction disappeared.

A mated male seldom courted another female than his own (we have noted two exceptions to this rule), though before his mating no female could enter his territory without being courted in some degree. The typical response of a settled pair toward an alighting female was an unconcerned attitude of the male, vigorous attack by the female. Whether a male really knows his mate individually, I am not prepared to say with absolute certainty, though I am convinced he does, for I have notes on many cases where a male did not court a strange female, though he presumably had no knowledge of where his own mate was at the moment, and a male that had temporarily lost his mate has never been seen to take a wrong mate. This ability of finding his own mate (even from considerable distance) was most impressive in the case of males that had their territories constantly invaded by several other birds, sometimes as many as twenty or more.

I am inclined to combine the observations on the gradual obliteration of the *p*EEE call with those pointing to individual knowledge of the mate and to explain the disappearance of the male's *p*EEE reaction toward his own mate by an inhibiting influence of the acquired knowledge of the partner's individual characters.

The birds of a betrothed pair spent the whole day or nearly so in the territory. Most of the time they could be observed foraging, keeping closely together, the male sometimes following the female, and sometimes, more often in fact, the female following the male. It occurred only rarely that the birds separated, but these cases were of special interest to us, because only then was it possible to observe the behavior of the female in connection with the boundaries of the male's territory, without being influenced by the male's behavior. As will be seen later, it invariably occurred in those cases where the birds remained separated for a sufficiently long time that the female crossed the boundaries wherever she met them!

A few times every morning, the birds stopped foraging altogether and suddenly showed interest in little crevices and entered several in quick succession. However, they never handled any nesting material. When entering a hole the male often uttered a sound that to us was indistinguishable from the sound that was heard from a threatening bird. We did our best to detect a possible difference, because we did not expected to hear the same call in such widely different situations, but we must confess we did not succeed. Sometimes the male alone showed interest in holes, sometimes the female, but more often both inspected holes together, as if nothing else in the world concerned them.

Often the male of a pair was obliged to leave his mate because of an intruder that had to be driven off. As a general rule the female did not follow her mate on such fighting excursions. During foraging, however, there were periods when a female promptly followed the male each time he flew a little distance to explore a new feeding ground. At such times, she again did not follow her mate when the latter made a start in order to fight. This reveals once more the astonishing capacities of observation of these birds: they instantly know *why* their mate takes a sudden start and react accordingly. Lorenz (1931) mentions a similar case in his Jackdaws. In the case of the Snow Bunting this discrimination is not made possible by special calls, but most probably by the way of starting, which is different in both cases and evident even to a human observer. When starting for a fight, the bird generally goes at a much greater pace than in other cases.

Owing to the dull brown plumage of the female it was extremely difficult for us to keep a temporarily solitary female in sight, as long as she was on snowless places. For the male Bunting she seemed to be equally difficult to detect; for it often occurred that he was unable to find her on his return to the spot where he had left her. His behavior in such circumstances was of great interest. First he would call and repeat several times the call note *pjrrrr* with which both birds often communicated while foraging together; then, getting no answer (the female often remained silent for quite a long period, one minute or more) he hopped onto a protruding stone or tuft and started singing. This was the more surprising, as most males, when once mated, seldom uttered any song. While singing, the call note was repeatedly given, and the bird appeared to be constantly on the alert, turning its head all the time. A sudden movement or a short flight on the part of the female, which would display the white wing-mark, or an answering call note of the female, brought a change in the male's behavior at the very same instant. He stopped singing and calling and at once flew to his mate, alighted at her side, and resumed foraging. Such observations were made many times on several pairs. They show: first, the male's remarkable memory for the spot where he had left the female, secondly, direct acoustical orientation; thirdly, direct visual orientation.

Between the two birds of a pair there existed a definite social order, one bird being the despot and the other being submissive to him or her, similar to the peck-order observed by several authors in different species of social birds (Whitman 1919, Schjelderup-Ebbe 1922, Masure and Allee 1934, Allee 1936, Murchison 1935). This order was demonstrated when one of the birds found some tidbit while foraging. His movements betrayed such an event, even to human eyes, and often his companion, if this was the despot, would at once come and drive him away from it. In these short quarrels both birds or only one of them showed the threatening attitude, though giving no perceptible sound. We expected the male always to be the tyrant, but one pair showed a reversed order: the female was observed to drive her mate off in all cases. This was observed on several consecutive days.

A considerable change was caused by the mating of the male territory holders, with respect to the fighting activity. Not only did the fighting of the males become more frequent, but the females often fought, too. Both cases will be considered separately.

The increase of the fighting of the males was due to several different causes. First, the female on the territory of a mated male attracted unmated neighboring males, which trespassed across their boundaries in spite of the presence of the female's own mate, and courted her, or even forced her to join in a sexual flight. We never saw a female in such a case attack the strange male, nor, on the other hand, ever noticed any sexual response by her. The intruding male invariably was attacked by the owner of the territory, and a fight ensued. After several weeks of close observation of unmated males, it struck us as most exceptional that a solitary male voluntarily crossed his own boundaries to penetrate into an occupied territory, which he had so carefully avoided before! We therefore considered the first occurrence of such a border incident as a rare exception, but soon learned that they occurred regularly as soon as an unmated male discovered a female on his neighbor's territory.

A still more common cause of disturbance was the crossing of the boundaries by mated females. Above it was described how a female often went outside the territory and, because of the dense population, consequently trespassed on strange territory. If she was alone, either the strange male came to court her, or, if the latter was already mated, his mate came to fight, for females attack females. The resulting commotion attracted the mate of the first female, and a fight between the two males arose. Such fights occurred, not only on the borders between the territories, but often on the spots that were undisputed property of the second male. This was due, no doubt, to the intrusion of the first female. The behavior of her mate, after he had discovered that she had attracted the attention of the strangers, was of interest. He usually flew to the female, but stopped at the frontier. Here he lingered, uttered his call note many times in short succession, even sang some phrases, and gave signs of two conflicting impulses, by steadily making substitute movements. Soon, however, he crossed the boundary and joined the other birds.

These facts illustrate, first that the presence of the females caused an increased fighting activity, and second that the females induced the males to fight outside their territory.

Mated females do not tolerate other females in their neighborhood. Fights between two females were of common occurrence. When two pairs met on their common boundary, a fight often resulted, and these fights of pair against pair really consisted of two fights: one of male against male, the other of female against female. Although we witnessed hundreds of fights of male Snow Buntings *inter se* and females *inter se,* we only once saw a female attacking a male, and this attack consisted of a short pursuit of a retreating male after a prolonged fight between two pairs. We never saw a male attacking a female.

The following entries may serve as an illustration:

"May 21st. At 11 A.M. the *H* birds are foraging on their territory. A strange female alights in the male's neighborhood; he does not show a hostile reaction, nor court her. The *H* female immediately attacks the strange female.

"May 25th. The solitary male *D* gets a female today at 3:30 A.M. She is courted by him and a sexual flight results; she stays, and is still present at 6 A.M. This female attacks every female that alights in her neighborhood. Once the male shows interest in a strange female that remains unseen by *D's* mate for some seconds. *D* male flies to the visiting female, looks at her without any sign of aggressiveness and I expect him to court, but just then *D* female approaches and drives the stranger off.

"May 29th. The *D* pair is foraging on the territory. The female crosses the northern boundary several times and intrudes onto the ground of an unmated male (*B*). *D* male follows her, though reluctantly and is invariably attacked by the solitary male. The female changes her position several times as soon as the fight begins; *D* male follows her, but as long as the female remains on *B's* territory, the latter continues his attacks on *D* male. Fighting stops as soon as *D* female returns to the territory."

Several times a female Snow Bunting was seen reacting to an alighting Lapland Longspur by flying toward him in a straight course, which was a sure indication of hostile intentions, but it never came to a real attack, for the Snow Bunting always lost all interest when coming within a few meters' distance of the Lapland Longspur. We take it, therefore, that the Lapland Longspur was taken for a female Snow Bunting. These errors were of rare occurrence, however; in the vast majority of cases the Lapland Longspurs, either males or females, were totally ignored.

Still another cause for the increase of the fighting activity after mating was the fact that one member of a pair could induce the other bird to fight, merely by showing aggressive behavior himself. Thus an increasingly aggressive behavior on the part of the male was often followed by the same change in the female, but while the male attacked males, the induced female again fought against females! This was often observed in pairs whose territories were continuously invaded by foraging flocks. Such a state of affairs was, as remarked before, not uncommon in the Eskimo settlements where food was abundant. These pairs were not constantly fighting, but attacked the other birds at irregular intervals. The male or the female might be the initiator, but always an attack of one bird was followed by an attack of its mate, each attacking its own sex.

Numerous instances were noted on May 21st in the afternoon, when pair *H* was studied. Their territory was invaded by some 20 foraging Snow Buntings scattered over the whole area. The *H* birds were weakly defending, and occasionally attacked some other birds, rarely succeeding in driving them off. That day I wrote down the following remark in my diary: "They cannot be said to try to keep their territory clean, they only are aggressive every now and then, tolerating the strangers most of the time. It is quite remarkable that fighting of one of the pair excites the mate to fight too, that is to say, urges him to take his own enemy; each choosing its own sex."

FIFTH PERIOD: COITION OCCURS

The beginning of this new period was marked by a change in the behavior of the female. She had until now shown interest in holes, but never had picked up nesting materials. On a certain day, the female suddenly took some moss in her bill, carried it for a few seconds or even less, and then dropped it again. On this same day she did not flee when

PLATE II.

FIG. 1: FEMALE SNOW BUNTING BRINGING ADULT LEPIDOPTERA FOR YOUNG; TO THE RIGHT ENTRANCE OF NEST-CREVICE. TORSSUKÁTAQ, ANGMAGSSALIK, JUNE, 1933.

FIG. 2: NESTLING SNOW BUNTING ABOUT TO LEAVE THE HOLE. TORSSUKÁTAQ, ANGMAGSSALIK, JUNE, 1933.

the male, as on previous days, approached her, but adopted an attitude which was never seen before: she kept her back quite flat and horizontal, pointed her bill upward and lifted the tail. The male mounted and coition was accomplished.

The carrying of nesting material therefore indicated, in all instances studied, the beginning of the female's oestrous period. Exactly the same occurs, according to Howard (1929), in the Reed Bunting.

As was mentioned before, there often elapsed a considerable period between the first settling of a male on the territory, and the day of the first copulation. To give an idea, the dates of the male *P* are given, as far as they are known to us. *P* was one of the first to take a territory.

Male arrives on territory	April 23rd
Swift call uttered for the first time	April 25th
Male settles on a protruding stone while singing	April 29th
Persistent song on song-stone	May 1st
Male enters holes	May 2nd
Female joins him	May 11th
Coition not yet occurred by	May 18th

(Owing to changing ice conditions observation had to be stopped.)

It seemed to us that the initiative to copulation was most often taken by the male; the female, however, was sometimes observed to adopt the attitude that indicated her readiness before the male had given any sign. Of course, some movements of the male might escape our attention, though not that of the female. But as the movements by which the female takes the initiative to coition are much slighter than the movements we see in the male in the same case, we feel we may more readily have overlooked invitations made by the female than those made by the male. It seems to us impossible to conclude that the male initiates more often than the female. This difference in the manner in which desire for coition is expressed, together with the long preoestrous period in the female, which doubtless exists in many species, have given rise to the wrong view, that the male ordinarily is the more eager. Difference in intensity of movements can only be used as a measure for differences in intensity of drives when individuals of the same hereditary constitution are compared but not when comparing individuals of different innate disposition, *e.g.,* males with females.

Howard says that in the Chiffchaff "there is much evidence to show that coition depends solely upon a certain condition in the female." (1908, p. 17). In the Snow Bunting this is not the case, for the male, too, may refuse.

When the male did not take notice of the invitation of the female, nothing occurred, and the female soon assumed an ordinary attitude and resumed foraging. When, on the contrary, the female did not take notice of an invitation of the male, that is, when she did not adopt the attitude of readiness, she fled, and a sexual flight originated. Sexual flights indeed occurred during the oestrum of the female, too, though they were rare. Sometimes a sexual flight during this period ended in coition; in most cases, however, it did not, and especially in these cases extreme posturing of the male was observed, the latter walking away while displaying his back, uttering the Swift call at the same time. This type of posturing did not differ from the posturing of the unmated males when reacting to a newly arrived female. This seemed to indicate that the male was ready for copulation at least shortly after having settled on a territory, and that sexual flight originated as an attempt of the male to copulate. Posturing of either male or female also occurred after unsuccessful copulations. Incomplete coitions seemed to occur rather often, owing to a bad adjustment of the activities of the birds. This could be observed rather frequently, and we could predict the occurrence of subsequent posturing. In these cases, too, the male showed off very elaborately and conspicuously whereas the female, when posturing, only assumed the flat attitude.

After this first day the birds regularly performed coition, most frequently during the early morning, between about 2 and 6 A.M., and not more than 2 to 5 times a day.

FIG. 19. *Display of male and female after coition.*

FIG. 20. *Display of male after coition.*

Shortly after the first copulations the female started building, that is, she not only collected pieces of moss, but she really carried mouthfuls of it to a hole. What she did with it when she entered the hole, we were unable to see. Nesting activities were most persistent immediately after coition.

In the beginning she did not confine herself to one hole, even for half an hour, but took materials into two or three different holes successively. On the second day, a female often built for a quarter of an hour or longer at one nest, then left it and stopped building for the rest of the day. Next day, the nest of the previous day was apparently forgotten, at least a new nest was begun. The fact that more than one nest was built within one territory may be interpreted in different ways. We are inclined to conclude that evidently one territory contains more than one suitable nesting hole, and that the building of several half-finished nests is only one of many instances we know of of unfinished actions that are so typical for maturing instinctive behavior (*cf.* Lorenz 1935).

It is, however, possible that the first nests remained incomplete because they were begun at unsuitable places. This latter conclusion seems to be rather far-fetched, for two reasons. First, the same phenomenon of making several unfinished nests in succession is seen in many species of ground-nesting birds, where the demands are far less specialized than in the case of the Snow Bunting (*e.g.* the Lapwing, the Curlew, the Avocet) second, we found a hole with a former year's Snow Bunting nest, containing remains of eggs, in a territory occupied by a pair that built its nest in another hole in the same territory. One territory therefore contained more than one suitable nesting place. We may add that, after having seen many occupied nesting holes, we are sure that one territory may even contain dozens of suitable nesting-holes.

When collecting material for the nest, the female often wandered far. The male regularly accompanied her on these excursions, though not collecting material himself. Only once we noticed a male collecting a mouthful of moss; he carried it to the hole, and passed it to the female, after having waited for her outside the hole. The female then worked it into the nest.

When the female crossed the territory's boundary, the male showed the usual hesitating behavior and refused to follow her. When entering strange territory, the female was often attacked by a strange female. If, in such cases, a strange male joined the fighting females, the first male also joined with a resultant fight between the males.

In one out of four cases observed the nest was built by the female outside the male's territory. This male did not accompany her in the beginning, though it was the male's ordinary behavior to accompany the building female to the very entrance of the nest every time she brought materials. Soon, however, he joined her, and before the first egg was laid, he attacked the original owner of the ground in the immediate vicinity of the nest and thus became owner of it. The original possessor gave it up reluctantly, after having fought for two days.

The base of the nests lay in a hollow, which must have been scratched out by the bird itself, though I never saw it done. Manniche says: "The birds made a relatively large cup-shaped hole in the surface." (Manniche 1910, p. 196).

The nests we saw had a foundation of moss and earth, then a layer of *Carex* leaves, and finally the cup was lined with feathers. All birds, whose nesting activities we closely observed, brought the necessary feathers from a considerable distance up to 500 and 600 meters beyond their boundaries. They all went to the same place—a dead Gull behind the tent of an Eskimo family. The nests we found far from the settlements were also lined with feathers; where the birds got them we do not know, but as a Peregrine Falcon and a Gyrfalcon were nesting within a 5 miles' distance of our observation stations, it was probable that remains of their meals were present throughout the region.

Several of the peculiarities of nesting which have been described here have already been mentioned by Manniche: "...when the female is searching far and wide for materials for the nest, she is always followed by the male...but he takes no active part either in the nest building or in the brooding of the eggs." (p. 197). The lining, according to Manniche, consists of hair of Fox and Musk Ox and feathers of Ptarmigan, Skua and Snowy Owl. For further information about the construction of the nest see Pleske (1928).

The crevice in which the nest is built is so narrow that we could rarely reach the eggs with our hands. Nicholson reports the same ("...and the crevice was rarely wide enough to admit an arm," Nicholson 1930, p. 299); also Pleske (1928) and Malmgren (1863). Most nests, therefore, were certainly safe from the Arctic Fox, though a few holes were wide enough for him to slip in; apparently, however, the Foxes do not rob many nests, but confine themselves to the fledglings.

The nest-building activity of the female increased every day until the first egg was laid. The lining of the nest with feathers was still carried on for two or three days after this.

Sixth Period: Female Laying

Owing to several causes, we could only in two cases ascertain the interval between the first copulation and the laying of the first egg. It lasted thirteen days in the first case, eight days in the second case. We had, of course, no certainty about the effectiveness of the first copulations observed.

Most clutches were completed by the middle of June; in two cases we actually observed the laying of the first egg: June 5th and 11th respectively. The first young we saw hatched June 18th; this, therefore, represents an earlier clutch.

In Danmarks Havn, Manniche found eggs from June 6th until July 18th. In the Godthaab region egg-laying seemed to start at about the same time, for Nicholson states that fledglings first appeared in numbers on June 26th. Other dates, for different regions of the Eurasian tundra, are compiled by Pleske (1928).

The eggs were always laid during the early morning, generally at about 3 or 4 A.M. Before that moment, the two birds of a pair were always foraging together, and the only new element in the behavior of the female was a slight increase in her restlessness: a female that was about to lay an egg, no matter how many she laid already, left her mate more often than she had done during the preceding periods, only to fly a short distance and start foraging again. The male followed her nearly every time. At a certain moment the female went to the nest—which in both cases proved to be the same nest that she had been working at during the last two days—and disappeared in the hole. As disturbing her would have spoiled our observations, we did not know exactly what she did during her stay within the nest cavity. She remained inside for 20 to 50 minutes. All the time the male remained in the neighborhood, sitting on some prominent stone and occasionally singing, a quite conspicuous phenomenon, for during the 4th and the 5th period song had been of rather rare occurrence. The *pjrrr* sound, too, was often uttered on these occasions.

When the female eventually left the hole, she alighted on some stone quite near the entrance and started preening, giving special care to the feathers around the genital aperture. After thus having made her toilet, she joined the male and they started foraging together. The nest was left alone during the rest of the day.

Foraging was done almost entirely within the territory during this period. The male, for his part, still never left the territory, except when the female ignored the boundaries and intruded upon strange territory. The same fights resulted with which we now were quite familiar.

Fighting of males against males was observed and of females against females, but fighting seemed gradually to become less frequent, perhaps in part due to the female getting some knowledge of the male's boundaries, but certainly in part, too, to a decrease in the fighting drive of the male, for intrusions by other males were more often tolerated than before.

After the female had laid her first egg, she no longer allowed the male to copulate.

The male not only sang while the female was laying, but his song was also often heard at other times of the morning. In the beginning of June, when most females were laying, we noticed a general increase of song in the whole region.

The eggs were laid at intervals of twenty-four hours. A full clutch contained about 6 eggs; we noticed four clutches of 6, two of 5, and one of 3 eggs; the latter was a second clutch of a female that had successfully brooded a first clutch of 6.

Nicholson noted one clutch of 7, two of 6, one of 5 and three of 4 eggs (Godthaab region). Manniche (p. 197), states that "the number in a clutch was most frequently 5 or 6, seldom 4. In a certain case I found a Snow Bunting incubating 3 eggs." Pleske (p. 135), for different regions of the Eurasian tundra mentions " . . . . the normal number of 6 eggs."

Seventh Period: Female Incubating

Incubation is carried out entirely by the female and begins from one to three days after completion of the clutch. During the first day after the last egg has been laid, the female does not appear to incubate at all; during the second day some time is spent sitting on the eggs; on the third day the eggs are constantly incubated. This was observed with three females.

The male now shows a striking change of behavior. He sings nearly as persistently as during the second and third period, is much more alert than during the preceding two periods, and attacks strange males with great perseverance. Though it did not occur to us before that his alertness should have waned during the fourth through the sixth period, it certainly must have done so, for the sudden increase at the beginning of the seventh period struck us as similar to the behavior of unmated males. This uncertainty in our judgment shows once more the value of counting exactly all distinguishable elements of behavior and thus getting reliable data for comparison. But by doing so, one is forced to focus attention on some few problems and sacrifice the possibility of making a survey of the whole sequence of activities. At present, the latter task has still been accomplished rather unsatisfactorily for most birds, and yet such general life histories are most urgently needed.

Besides much singing, the male also uttered the Swift call, which we took for an expression of desire for coition. Once we observed a male, which certainly had a female with eggs (though we were unable to find the nest) and which, after the female had begun to incubate, showed renewed song, etc., and after a few days mated with a new female. This second female had just finished her first brood, which had been a very early one. This must be considered as a rather accidental circumstance and it may occur in a few cases that such a male gets a new female before his sexual potency wanes. This particular male stopped singing again as soon as he was mated, and resumed singing on the very day the second female laid her first egg. He now courted every female Snow Bunting that came into his neighborhood and even tried to force a female to coition on several occasions. In this he never succeeded. Had there been a third female available, we feel sure that he would have mated for a third time.

This case is the only proof we have of the existence of double-broodedness in the Snow Bunting. All other Snow Buntings we watched had only one brood.

In the foregoing we have seen, that the male sings especially when his female is absent, further that his song increases when his mate refuses copulation, and lastly that his song approximates its original strength when the female begins incubating. At the same time, the Swift call is heard again, and one male was actually observed to mate with a new female during this period. We therefore take it that the renewed singing activity indicates that sexual potency still exists. The male Snow Bunting appears to be ready for copulation before the female reaches the oestrous phase, and remains sexually potent some time after the female's oestrum has finished.

EIGHTH PERIOD: THE REARING OF THE NESTLINGS

The hatching of the young is followed by a sudden change in the behavior of both male and female. Both feed the young, though during the first few days the female brings far more food than the male. The same is stated by Manniche and by Nicholson.

During the first days, the female often brooded the young for some minutes immediately after each feeding. As far as we could see, the young got only animal food: small *Lepidoptera* and *Diptera* dominated.

While the young were being fed, they uttered a long, high note, which became louder as they grew older, and which called attention to the nests from a great distance. Nicholson says about this call: "The loud metallic chittering of nestlings carried quite 150 yards." (p. 299).

As Heinroth has pointed out, the innate noisiness of nestlings is often correlated with the relative safety of the young from predatory enemies. Most hole-breeding birds, most large strong birds and most colony-breeding birds have noisy young, while the young of open-breeding, solitary and small birds are as a rule silent. There are, however, groups in which the hole-breeding species are as silent as the open-breeding species (Pigeons). Most convincing are those cases where different species of one and the same genus or of closely related genera show this difference in inborn noisiness parallel to the nature of the nest site. Heinroth points to the difference betwen the Rook and the Carrion Crow. A similar case is offered by the Snow Bunting, when compared with its open-breeding relatives, the Reed Bunting and the Yellow Bunting. Whereas the Snow Bunting has noisy young, the latter species have rather silent young. It may be repeated here that the holes of the Snow Buntings in by far the majority of cases are absolutely inaccessible for the only predator which concerns us here: the Arctic Fox. How things are in regions where the Ermine occurs, we don't know.

For a fuller discussion the reader may be referred to Heinroth, 1928, I, pp. 75 and 135.

Several times we observed that this sound strongly influenced the old birds' behavior, urging them to enter the hole and to deliver the food under conditions that otherwise prevented them from doing this. This occurred several times when we approached the nest too closely in our endeavors to determine the nature of the food, or to obtain photographs of the old birds at the nesting hole. The old birds then sometimes hesitated, but as soon as the young called, they slipped into the hole. In all pairs we observed, the male was the first to stop feeding at our approach, whereas the female went on feeding until the danger was much nearer. The greater shyness of the male in the nest's vicinity might be connected with his brighter plumage.

The food for the young was not collected on the territory alone. Birds from different nests would often be seen foraging together on favorable spots, the males tolerating each other in close proximity. Whether a spot was favorable or not depended, of course, on the season and on the weather. For instance, in the middle of July, in rainy weather many Snow Buntings fed their young for days continuously with small *Lepidoptera,* which they gathered in dense vegetation of *Betula, Vaccinium* and *Salix.* On sunny days they fed the young mosquitoes that they caught on the stones along the fresh-water pools. Food-seeking rarely was limited to the territory, and during considerable periods nothing in the behavior of the foraging birds indicated the existence of territory.

Nicholson reports that he observed the parents collecting food on strange territories, sometimes as many as 200 feet from the nest. The foregoing description of the rôle of territory in the mating history of the Snow Bunting shows that conclusions as to the value of territory in the life of a species must not be based on observation made in too short a period of the bird's life cycle. The reputation of the Snow Bunting as being a non-territorial bird is based on observations made in the period when sexual fighting was at its lowest.

All the males that were collecting food for the nestlings still occupied their old territories themselves and here drove off every other male Snow Bunting. We never noticed any tendency in such a male to enlarge his domain by taking parts of neutral ground.

The influence of the weather on the foraging excursions of the parent bird was demonstrated most clearly in the case of a pair that bred on the little island where we camped. This island was about 80 x 30 m. and was inhabited by one pair of Snow Buntings. On sunny days the island could yield insects in sufficient numbers to allow the adults to collect all the food for the young on the island alone. As soon as the weather grew less favorable, especially when it was raining, the birds regularly flew to the mainland to forage. As the food they collected on the island was mostly mosquitoes, and as we saw that those trips to the other side of the fjord were made on days when mosquitoes did not appear in appreciable numbers, it is certain that there are territories that can only produce sufficient food for the offspring under favorable conditions and that fail on many days during the time of rearing of the young.

Now on the mainland, too, foraging was done outside the territory to a great extent. Whereas it might be supposed that the island Buntings were forced by the circumstances to content themselves with a territory under the minimum size, the mainland Buntings could, by fighting, prevent their territories from growing too small. We conclude, therefore, that the minimum size of a Snow Bunting's territory must not necessarily be determined by its food store.

To return to these common foraging places, they were sometimes situated within an occupied territory, and sometimes they were evidently neutral ground. In the first case, the owner did not always attack every strange male that was seeking food on its territory, but now and then he suddenly drove some of the strangers off. We noticed the same phenomenon as during the second period (see p. 17) : as soon as one of the strange males would sing, he was invariably attacked. A singing male, therefore, is, in the *Umwelt* of a territory-holding male, something quite different from a silent male. This phenomenon was still more striking now than during the second and third period. This was due to the fact that the males during those earlier periods were so extremely alert that a silent male was often seen by them and consequently attacked before it was seen by us. During those earlier periods, therefore, it was much more difficult for us to notice cases where a silent male was not attacked.

That the foraging males were often tolerated is, most probably, not only the result of their being silent, but also the result of a gradual waning of the aggressiveness of the owner of the territory: continuous intrusion of foraging males caused the owner of the territory gradually to become less excited by them.

The fact that males often foraged close together without showing any hostility has also been described by Nicholson, who got the impression that territory was of minor importance in this species ("territory was always lax...", Nicholson 1930, p. 297).

One of our entries about the gradual waning runs as follows: "July 6, 1933. During the last few days, the male *W* has been frequenting the territories of the males *F* and *G* in search of food. The latter ones are tolerating him now, which is surprising, as he was vigorously attacked at first. But *W* did not give up, and returned at regular intervals and thus succeeded in establishing a situation similar to that observed by us in Scoresby Sound last summer, and that reported by Nicholson."

There were cases of common feeding ground, where we could not detect a bird that could be the owner. It is quite possible that the original owner had withdrawn from it entirely, but then we would expect to see him defending a territory adjacent to it. Now sometimes there was no adjacent territory, and then the foraging birds evidently fed on nobody's land. This was especially the case on slopes bearing dense vegetation of *Salix, Betula* and *Vaccinium,* where insect life was relatively abundant on rainy days. Owing to the dense vegetation this type of terrain probably did not fit the requirements of a Snow Bunting for a nesting place: the majority of the holes in such situations were either covered by plants or were soaking wet.

When the young grew up, some of them appeared at the entrance of the crevice now and then. They grew more noisy every day, and we could everywhere hear the cries of several broods.

To their repertoire of call notes, which up until now had been very monotonous, a new note was suddenly added: a short, shrill, far-reaching monosyllabic squeak that was repeated at rather long intervals of about 20 to 40 seconds. At about the same stage, as a rule perhaps on the same day, the excrements of the young, which until now had been regularly delivered in a thin membrane and had been carried away by the old birds, no longer had the enveloping membrane and consequently the nest quickly became dirty.

Miller (1931) reports the same for *Lanius ludovicianus* (L.): "concomitant with the beginning of hopping or flying, the feces lose the mucous sac and resemble the feces of the adult. This change may occur within a few minutes after leaving the nest." (p. 190).

As we soon learned, this was with the Snow Bunting an indication that the young were about to leave the crevice.

On several occasions, a female was observed begging food from a male, and, when getting it, seen to bring it to her young. We saw one female that often asked and actually got food from strange males who were foraging themselves. This happened both when she was foraging along the border of a pool on neutral ground, and on strange territory.

One of these males was foraging for his own young, another male was caring for himself. This female never showed sexual behavior on such occasions, but immediately flew to her nest and delivered the food to her young. The male did not behave sexually either. As will be remembered, the delivering of food does not play a rôle in pairing behavior.

Another case was observed, when we once so closely approached a nest with young, that the male coming with food would not enter the hole. The female showed no signs of anxiety and kept on feeding. When she met the male with his bill full of food, she begged for it and got it, and then brought it to the young (see Plate I, Fig. 2).

NINTH PERIOD: YOUNG HAVE LEFT THE NEST

The change in the constitution of the feces of the young, *viz.*, the loss of the membrane, and the change in their vocabulary, was followed within one day by their leaving the nest. They were not able to fly, but walked about with amazing rapidity. They remained in the neighborhood of the nesting hole only during the first few hours, and soon spread in different directions. This indicated that they did not in the least appreciate each other's companionship, which is in striking contrast with their behavior a few weeks later, for as soon as the young become independent, they collect in large flocks.

The same phenomenon of avoiding each other's companionship immediately after leaving the nest was pointed out by Heinroth (1928) in Chats (*Saxicola*), Wheatears (*Oenanthe*), and Thrushes (*Turdus*). Its function is obvious: it decreases the chance of the destruction of the whole brood when a predator discovers one of them.

The new call, appearing at the same time as the change in the feces' structure, the function of which was quite problematical as long as the young were in the nest, now showed its value. In the course of a few hours each young had taken a position at least 10 meters from the nest, cleverly hiding itself under vegetation, and it would have been impossible for the adults to find them but for their calls. This new call was uttered at rather long intervals, and there was a striking contrast between the noisiness of the young when still in the nest (in the last period they were seldom silent at all) and the inconspicuous intermittent squeaking of the fledged young. Only when the old bird was actually feeding was the erstwhile nestling's call heard.

A similar sudden change in calls of the young seems to exist in several other Passeres. Heinroth (1928) mentions it for *Lanius c. collurio* (L.) and for *Emberiza sch. schoeniclus* (L.), Howard (1907, 1913) for *Acrocephalus schoenobaenus* (L.), and for *Sylvia borin* (Bodd.). On the other hand *Emberiza c. calandra* (L.), appears to remain very silent after having left the nest (Heinroth 1928, Ryves & Ryves 1934). The same is reported by Pickwell (1931) for the Prairie Horned Lark.

When observing the old birds bringing food to the young we saw three ways of orientation: first, the old bird remembered quite well the exact place where it had fed a certain young the last time, and alighted just there the next time, even in those cases where the young in the meantime had moved to another place; second, in all those cases when it evidently searched for the hidden young, it was directed to it by a single call, and appeared to localize the sound much better than we could (*cf.* p. 14); third, in similar cases the adults looked around and were also able to discover the young by sight, which revealed a keen visual orientation, as the young conceal themselves very well. The facts of the first category show that the birds must have an excellent detailed knowledge of the locality.

The old birds each took care of a part of the brood; during several consecutive days the same young were fed by the same old bird, as we could observe by means of banded individuals.

As the young were soon moving farther and farther from the nest, we were anxious to see what would happen when they reached the boundaries of the territory. They eventually reached and crossed them, thus intruding on strange territory. The owner of such a territory, in which strange young birds were intruding, was never observed to react to their presence. The parents of the young continued feeding them as if nothing had happened. They were attacked now and then, but persisted in visiting their young and therefore were tolerated to some degree.

Although the young scattered in all directions and did not limit their movements to the territory, the latter was still defended by their father. We actually observed how a male, just after having fed one of six young that had all deserted the original territory, suddenly flew back to the vicinity of the old nest and attacked and drove off a strange male.

Here a few words about the reactions of the parents to predatory animals may be given. On July 5th an adult Peregrine Falcon swooped down on a Lapland Longspur just before us; he missed and disappeared, flying in wide circles low over the mountain slope. Numerous Snow Buntings there all uttered a special call, a monosyllabic, soft *weee,* but not one Snow Bunting took wing; they all remained on the ground, a quite striking phenomenon. This same sound was heard every time we ourselves approached a nest or a fledged young too closely, but in these cases the birds showed no disinclination to fly, and often fluttered in circles around our heads. The latter behavior was also observed at the presence of an Arctic Fox on July 5th; besides the *weee* calls we then heard some hasty fragments of song. Roaming Eskimo dogs were reacted to in exactly the same way.

On the 12th of May an adult male Merlin visited our observation ground and we had an excellent opportunity to see the reactions of the male Snow Buntings, most of which were still unmated and had settled on a territory. As soon as the Merlin appeared over the crest of a hill, the Snow Buntings, which had been busily singing and fighting until now, became silent, kept to the ground, and now and then uttered the soft *weee*. This lasted until the Merlin was out of sight; after that the birds gradually resumed their song.

These observations showed that different predators caused correspondingly different reactions; though we could not detect any variation in the *weee* calls in different situations, the disclination to leave the ground when a Falcon was within sight, as opposed to the behavior to other predators was apparent. I suppose, therefore, that for the Snow Buntings the *weee* calls in the different situations sounded differently, for otherwise I cannot account for the promptness in exhibiting the right reaction by all the individuals. Yet, it cannot be excluded with absolute certainty that not only the sound, but also the behavior of the warning birds influenced the others' reactions. In this case, though, the reactions could scarcely be so prompt.

Different calls and reactions in different predator-situations are found in many species. For further information see Heinroth 1924, Verwey 1930, Pickwell 1931, Makkink 1936, and Tinbergen 1939a. In some species the different alarm calls correspond to different degrees of danger only (*e.g.* in the European Blackbird, Tinbergen 1939a), in other cases they are reactions to entirely different kinds of danger, and they evoke entirely different responses in the other individuals (Jungle Fowl, Heinroth 1924; European Avocet, Makkink 1936).

The first sign of the beginning of independence in the young was observed three to four days after they had left the nest. They began to show interest in flying insects and sometimes hunted them by fluttering clumsily after them. A young bird, which left the nest on June 28th, tried to catch a flying mosquito on July 2nd, and was fed by its father until July 10th. On the 9th it uttered for the first time the trembling note of the adults, which is regularly used by birds living in the flock, and which serves social purposes. At the same time it still used both youth calls. On the 11th this young bird, as well as its brothers, had apparently left, for the adult male was observed foraging and softly singing, but not feeding any young. Here, too, is an instance of a new call appearing in the repertoire shortly *before* it will serve as a means of communication.

It appeared to us that very few birds had a second brood. Our host, Kârale, had told us that second broods occurred, though seldom. We were fortunate enough to witness one quite interesting case, which was mentioned above (p. 34-35). A female of a pair with six young showed sexual behavior in reference to her own male, shortly before the young left the nest. When begging for food (which itself probably had nothing to do with sexual conduct), she assumed the flat attitude by which oestrous females expressed their willingness for coition. The male did not respond sexually. Begging for food was not uncommon among females (*cf.* p. 38-39).

The case of this female developed in a most interesting way. For several days she did her part in caring for the young, which had left the nest on June 28th, and did not respond to a strange male on whose territory the young had settled. This male, though he was himself mated, was constantly singing and uttering the Swift call (see p. 34). One day, July 3rd, he suddenly showed extraordinary interest in this female. She did not pay any attention to him, and was still foraging for the young and regularly feeding them from 2 until 3 A.M.. When she entered the territory of another male that was also singing, this male, too, was strongly stimulated by her. At 3 A.M. the situation suddenly changed. The first male was nearly silent, the female had joined him, and had abandoned the young, which were heard calling at their old places. She now showed great interest in several holes and entered them. About an hour later a copulation was seen. From the very same moment the female joined the male, she was never seen feeding the young, and some days afterward we found two of her young dead at about the spot we had located them for the last time. The first male of the female was still feeding the young he had been caring for all the time. This was, at the same time, again quite positive proof of the rigid division of labor between male and female: when one of them stops taking care of the young, they are apparently lost. The great distance over which the young travel before they are independent doubtless favors this process of splitting-up of the family into two groups.

It was certainly interesting that the female joined the new male several days after she had first shown the beginning of a new cycle by posturing for her own male. It seems that remating during her pre-oestrous phase was inhibited by the presense of her first young, and that she only remated when she had reached the oestrous stage, for she copulated with the new male shortly after having joined him.

During the following days, several copulations of the female with the new male were seen. There was a tendency in the pair to frequent the female's old territory, the result of which were several attacks by the owner, the female's former mate, on her new one. By July 10th the female had completed a clutch of three eggs in a hole on the territory of the new mate.

III. DISCUSSION

A. Occasional Bigamy

As a rule, the Snow Bunting is undoubtedly monogamous. The fact that cases of bigamy or polygamy occur in usually monogamous species has been pointed out by Verwey (1930), who mentions several cases of bigamous males in the following species: European Sparrow Hawk (Jourdain 1926, Greeves 1926), the Marsh Harrier and the Hen Harrier (Jourdain 1926, Hens 1926), the Spotted Flycatcher (Sunkel 1926) and the Chaffinch (Knauel 1925). (See also Groebbels 1937, p. 107.

Though it would take us too far afield to review the complete literature on this subject, I may point to a few observations that serve to give us some insight into the way such anomalous bonds arise.

Our male Snow Bunting did not mate with two females simultaneously, but only took a second mate after his first mate no longer allowed copulation, and he was only ready to take a third mate (as indicated by renewed song and Swift call activity) after his second mate had also passed into the non-copulatory stage. Now the same has also been observed in other birds. Freitag (1936) reports on a male European Starling that mated with three females successively, taking a new one only after the previous mate had started incubating. Dewar (1936) mentions seven known cases of bigamy in the Mute Swan, two of which are known in some detail and which allow us to see that in both cases there was a considerable difference in time between the two clutches: about four weeks in one case (Portielje 1936), about three weeks in the case observed by Dewar himself. Portielje writes: "The promiscuous behavior, exactly as in the case mentioned by Tiemann, only appeared after the female had started incubation . . . . . ." (p. 150) [translation mine, N.T.]. As the relations between one male and two females in the Mute Swan may exist during more than one year, the sequence of events in a second or later season may be different, but nothing is known of this.

A male Willow Warbler observed by Trahair Hartley (1934) had two mates, each of which raised her own clutch. The first brood was fledged on June 18th or 19th, the second on June 27th or 28th. A similar case is reported by Gooch (1935) in the Great Tit. The second female laid eight days after the first female. The Bishopbird, *Euplectes h. hordeacea* (L.), also shows this form of polygamy. Lack (1935b) writes about this species: ". . . . the male courts only one female at a time, but, having built a nest for her, is ready for a new female" (p. 824).

In all these cases bigamy is favored by the circumstance that the male remains sexually potent during a longer period than his mate, and a new mate is taken only when the original sex partner ceases to respond sexually. Therefore, Allen's conclusion (1934) that male birds as well as females have a short oestrous period cannot be generalized too much.

In other species the situation may be different. In a close relative of the Snow Bunting, the Corn Bunting, the Ryves (1934 a,b) have found regular polygamy, and their tables of the hatching dates of the different broods of one and the same male reveal that in a number of cases two or more females laid at about the same time. Especially convincing cases are: male No. 3, whose first female laid on July 5th, while his second mate laid on July 7th, and his third on July 9th; male No. 8 whose first mate laid on June 17th, the second on June 18th. This allows us to conclude that a male of this species may often live with two or more oestrous females at the same moment. In the Lapwing, Verwey (1928) observed a male that was mated with two females, copulating with both on the same day. Two female Chiffchaffs that were simultaneously mated with one male laid on about the same day (Hurrell 1934).

Other cases of polygamy arise in quite another way. A female may lose her mate when incubation has already started and then unite with the neighboring male. This has been observed in the Song Sparrow by Nice: "Four cases of bigamy have come to my notice . . . . . . In two cases I know positively the extra bird lost her mate while she was incubating eggs; in the other two I assume this was the case." (Nice 1937, p. 88). This one instance may be sufficient to illustrate this type of bigamy; many instances of it may be found scattered throughout the literature.

B. Change of Mates for Second Brood

Thanks to the extensive banding of birds, it is now known in a series of cases in several species, that birds may change their mates for a second brood. In a few species there is sufficient evidence to reach a conclusion as to whether change of mates between two broods is a rule or not. Change of mates as a rule was found in the House Wren by Baldwin (1927); frequent change of mates, though not so regular as in *Troglodytes,* occurs in the Bluebird and the Brown Thrasher (Nice 1930). In the Song Sparrow both partners as a rule remain together during a whole season; but it is an exception if this occurs during more than one season (Nice 1933).

In other species such precise knowledge is still lacking, though the occurrence of a change in one season is known. I know of such observations in the following species: the European Blue Heron (Verwey 1930), the English Robin (Burkitt 1925, Baron 1935), the Great Tit (Schenk 1929), the European Starling (Kluyver 1935), and several species of Pigeons (Whitman 1919, Craig 1908).

In one respect our observation on the taking of a new mate for a second brood by the female Snow Bunting is of special interest. We know that this female showed sexual behavior toward her own mate before leaving him. While still attending nestlings she was once observed to adopt the characteristic attitude described on p. 29 which indicated readiness to pair. The male did not respond. We may take it, therefore, that she took a new mate, because her own mate did not respond to her advances. This is a confirmation of Heinroth's conclusion (1921) that change of mates may be the result of one of the mates coming into a new oestrum before the other, and then taking an oestrous partner. Craig (1908) came to the same conclusion for Pigeons: "If it happens at this time that the male, for example, lacks energy to perform the ceremonies and rouse himself for the duties of a second brood, the female entices him for a long time, but finally, if he fails to respond, she deserts him and seeks another mate" (p. 97). Verwey's observations (1930) on the Blue Heron point in the same direction.

In our case the male Snow Bunting apparently was not able to feed young and to pair with a female at the same time. Whether this is the rule in this and other species is an open question. It is known, however, that in many species the male is able to come into a new cycle, while still feeding young. The result is that the two broods then overlap (*ineinandergeschachtelte Bruten*). This has been observed several times in the European Blackbird (Berndt 1931, Heyder 1931, Schuster 1933, Tinbergen 1939a), in the Great Tit (Musselwhite 1930, Steinfatt 1933), in the European Nightjar (Heinroth 1909, Lack 1930, 1932, Stülcken and Brüll 1938), in several species of Pigeons (Whitman 1919), in the Ring-necked Plover (Koehler and Zagarus 1937), in the European

Waterhen, and in the Song Sparrow (Nice 1933, 1937), in all of which species it occurs regularly. In the Blackbird, the Nightjar and the Song Sparrow the female begins a new nest while the male takes care of the young of the previous brood. The same has been observed in the Reed Warbler, *Acrocephalus a. arundinaceus* (L.), (Noll-Tobler 1924). Overlapping broods have further been observed in the Mistle Thrush (Taylor 1938), the Redstart, *Phoenicurus ph. phoenicurus* (L.), (Koefoed 1935), the English Robin (Osmaston 1934), the Goldcrest (Palmgren 1933) and the Shrike, *Lanius excubitor* (L.), (Musselwhite 1934).

In *Charadrius hiaticula* (L.), the division of labor between the two sexes while taking care of two overlapping broods is again different (Koehler and Zagarus 1937): both birds share in incubating the new clutch, and both take care of the young of the previous brood. At regular intervals the bird that is leading the young relieves the brooding bird and the rôles are exchanged.

In species where feeding of halfgrown young and renewed sexual activity do not exclude each other, and where, therefore, overlapping of successive broods is possible, the cause for change of mates, as pointed out above, is often absent and change of mates may be of much rarer occurrence. It is generally recognized that continued association of the partners is in many cases due to their being both attached to the breeding area (*Ortstreue*). This is the case in the Song Sparrow, about which species Nice remarks: "Faithfulness during a whole season is the rule between Song Sparrow mates, partly, I believe, because they are so attached to their territories, and partly because broods usually overlap, so that there is seldom any occasion for a break in the close association of the birds." (Nice 1937, p. 85).

Another cause for the continued association of the partners may be individual attachment, as is the case in many *Anatidæ* (Heinroth 1910, Lorenz 1935). In the Herring Gull I observed that after disturbance of the brood breeding is begun anew, which is always an affair of the same two partners. Here, too, individual attachment prevents change of mates (unpublished observations).

Although this review certainly is very fragmentary, it will at least show that the same goal, *viz.*, the rearing of as many young as possible in as short a period as possible, is reached in various ways in the different species. As in so many problems, the gradually increasing number of facts primarily serves to upset too sweeping generalizations of the past. A great deal of detailed information is needed before new rules can be established.

C. The Discrimination of the Other Sex

THE MALE'S FIRST REACTION

It was described above (p. 18 sqq.) how the male Snow Bunting shows the same reaction to the approach of a male as to that of a female. A second reaction, different toward males and females, occurs after that. This phenomenon, an identical reaction to approaching males and females, was also observed by us in the Northern Phalarope and I discussed it in my paper on this bird (Tinbergen 1935). It seems to be of widespread occurrence, not only among birds (*Ciconia,* Heinroth 1924; Pigeons, Whitman 1919, Heinroth 1928), but among fishes, too (Fighting Fish, Lissmann 1932; Stickleback, Ter Pelkwijk and Tinbergen 1937), and it has even been reported for the Cuttlefish, *Sepia officinalis* (L.), (L. Tinbergen 1939). It will be well worth while to make an attempt at an explanation.

The fact that the *p*EEE reaction of a territorial male Snow Bunting is only evoked when another bird is approaching proves that this male reacts to a stimulus from the approaching bird. Considering the fact that the reaction is evoked by both males and females, the obvious interpretation would be that the sense organ that is used in this case does not allow a sharper discrimination. The sense organ in question must be the eye, as silent birds are reacted to as frequently as calling birds. Now the Snow Bunting doubtless has keen eyes, like most songbirds. Proof of this could be seen in the field in numerous instances of reactions to soaring Gulls, other Snow Buntings, or birds of prey, as the ability to discover such birds at great distances certainly exceeds ours. Visual acuity of the Snow Bunting certainly exceeds that of man. When we, therefore, see an evident lack of discrimination between males and females in cases where the observer did not feel the least doubt, the cause must not be sought in inadequacy of the optical apparatus. This shows that the first interpretation is wrong, and the problem concerns central nervous processes.

There remain two possibilities: either the bird really discriminates between male and female, and reacts to both by slightly different reactions that merely *seem* identical to us, owing to our inadequate power of discrimination; or male and female and all kinds of similar objects evoke the same response, a sense impression containing very few recognition marks being sufficient to cause the first reaction. The latter supposition requires some explanation.

It has been proved in a number of cases that an animal does not react to the complete receptual field, but only to certain elements in it. Other elements may have no influence, although they can be received by the animal's sense organs equally well. A few instances may illustrate this.

The carnivorous fresh-water beetle, *Dytiscus marginalis* (L.), has highly stereotyped prey-seizing movements. When stimulated by certain odors, like the smell of meat, of fishes, or of frog-larvæ, it will dive to the bottom. There, when receiving renewed chemotactual or mere tactual stimuli, it will seize the prey with its well adapted fore-legs. Experiments with optical preys (*e.g.,* frog-larvæ in a glass-tube) show that this series of reactions cannot be evoked by any optical stimulus. Nevertheless, anatomical examination together with experiments proves that the beetle has well developed eyes and is able to see well; several other reactions, like finding shelter, avoiding obstacles, are directed optically (Tinbergen 1936c, and unpublished observations of G. P. Baerends and J. Zaayer). This shows that certain reactions may be influenced by part of an animal's sense organs only. We have to assume that a neural coupling between the other sense organs and these reactions does not function.

Furthermore, parts of the receptual field of one sense organ may be functionless in regard to a certain reaction. As an illustration, experimental evidence about the releasing of the gaping reaction of young Thrushes may be cited.

Nestlings of the European Blackbird and of the Song Thrush open their eyes at about ten days of age. The gaping reaction, which during the blind phase could be elicited by tactile stimuli only (tap on nest rim), now responds to optical stimuli from the parent birds. The situations that evoke an optimal response are extremely varied and the birds react to every object, provided it is moving, is larger than three mm in diameter, and is above the nestlings' horizon. Immobile objects, or ones smaller than three mm in diameter, or objects below the horizontal plane of the nestlings' eyes are never reacted to, though they are observed and fixed by the young, or even followed with eye and head movements (Tinbergen & Kuenen 1939).

These and other observations show that parts of the visual field received by the nestlings' eyes have no influence on the reaction.

A most striking example has been described by Lorenz (1931) in connection with the Jackdaw. The individuals of a Jackdaw colony are able to discriminate among all members of the colony, knowing each of them individually. Many reactions are shown only toward certain individuals. This must depend on discrimination of very minute visual details, and only a highly trained human observer can approach the birds' level of discrimination. At the same time, however, a special reaction (the *Schnarreaktion*), causing a social attack on a dangerous predator carrying away a Jackdaw, is dependent on a situation in which only a few characters of the Jackdaw have influence: any animal carrying something black causes the social attack. That "something black" (the Jackdaw), which in the first-mentioned reactions is articulated into numerous subtle details, enabling an individual to treat other individuals differentially, contains, in the other case, only very few recognition marks; a black tricot or a few black feathers, carried either by a predator or by Lorenz himself, or even by a Jackdaw, evoked the attack just as well as a complete Jackdaw.

The conclusion to be drawn from these and other analyses is that there exist many reactions which have a fixed neural coupling with special parts (recognition marks) of the receptual field. This coupling, called "releasive mechanism"

(*Auslösendes Schema*) by von Uexküll and Lorenz, can be studied with experimental methods.

It is obvious that a reaction, dependent on a releasing mechanism with only very few recognition marks, like the social attack in the Jackdaw, will be evoked by very different situations, provided these situations all offer those few marks. It would certainly be premature to conclude from this fact that the animal is unable to distinguish between the different situations. Another reaction may be more specific and thus may reveal a surprisingly sharp power of discrimination.

Returning to the Snow Bunting, the question can be formulated as follows: does the *p*EEE reaction consist of two closely similar reactions, each with a highly specific releasive mechanism, one responding to a female, the other to a male? Or is it one reaction, coupled with a very poor releasive mechanism, containing so few recognition marks that males and females equally evoke the *p*EEE? In experiment, the distinction would not be difficult to detect. In the first case the introduction of a situation, intermediate between the two first observed situations, would fail to call forth either of the reactions; in the other case, an intermediate situation would be as effective as the other two situations. In our case, a bird, intermediate between male and female, would either evoke a quite new response, no response at all or the *p*EEE reaction. Experimental data of this kind (which could easily be acquired by the use of mounted birds) are not at my disposal, and I feel unable to settle the question in the case of the Snow Bunting. But in some fishes, where a similar first reaction is found, experimental results are available that prove the second assumption to be true. The experiments of Lissmann (1932) with male Fighting Fishes (*Betta*) show that their first reactions to males and females of the same species were also shown to many intermediate objects. Dependent on the further behavior of those objects, the male Fighting Fish, after his first reaction, then either fights them, courts them, or ignores them.

In coöperation with Ter Pelkwijk, I analyzed the first reaction which is shown by a male Stickleback in sexual condition toward males, females and animals of other species. This reaction, too, is a response to a situation with very few recognition marks (Ter Pelkwijk and Tinbergen 1937).

In birds, no experiments of this kind are known to me. The experiments on sexual discrimination, made by Noble and Vogt (1935), Allen (1934) and Chapman (1935), though interesting enough, are confined to the question of whether birds are able to distinguish between the sexes at all, and do not permit any conclusion as to the causes of separate reactions.

The only fact pointing to our second assumption was found in the female Northern Phalarope, where the first reaction was not only shown toward males and females, but occasionally toward an approaching Lapland Longspur, Purple Sandpiper and Ringed Plover. For a further discussion I may refer to my paper on the Northern Phalarope (Tinbergen 1935).

A description of the sensory situation that releases the first reaction, which was possible in some degree in *Betta,* is still impossible in the Snow Bunting, but some characteristics of it may be suggested. It seemed to us that the reaction was especially shown toward a flying bird. Further, we never saw a male Snow Bunting reacting in the described way to an approaching Lapland Longspur or a Greenland Wheatear, though these two species were not uncommon in the country, and several of them nested quite near and even in Snow Buntings' territories. This indicates that the mechanism that calls forth the first reaction is not so simple as we might at first expect, for it must contain marks that are not present in the Lapland Longspur and in the Greenland Wheatear. Perhaps the white wing-marks form part of it. A further, experimental, study might be possible, as is demonstrated especially by the results of Lorenz with free-flying tame birds of undomesticated species (Lorenz 1931, 1935), and of Noble and Vogt (1935), Allen (1934), Chapman (1935) and Vogt (1938), with wild birds to whom stuffed specimens were offered under proper conditions.

The first reaction may be short and may be followed immediately by the next reaction, such as is the case in the Snow Bunting, or it may last for a much longer time, as in the Ruffed Grouse (Allen 1934) and in the Common Tern (Tinbergen 1938). In other cases it may be absent, and the reactions to males and females different from the beginning. This seems to occur in many Ducks, and certainly occurs in those *Lepidoptera* where the males are attracted from afar by the scent of the virgin females.

Such different first reactions appear to occur only in those species where the differences between the sexes are extremely obvious. These differences may be morphological, as in the sexually dimorphic Ducks, and in the Golden Pheasant (Noble and Vogt 1935); they may be olfactory as in some *Lepidoptera* (*cf.* von Frisch 1926), or acoustical as in many *Orthoptera;* in other forms perhaps they may consist in different behavior though I am not aware of any instance. A differential first reaction on the part of the female seems to be much more common than it is in the male, but as only the male's first reaction is discussed here, I will not enter into this matter.

The Ruffed Grouse and the Common Tern form a special case. Here the existence of a much longer identical reaction is favored by the fact that approaching males and females behave identically for such a long time, whereas in the Snow Bunting their behavior, when alighting near the overturing male, is quite different. In the case of *Bonasa* this behavior of the partner is induced by the aggressive behavior of the male, which causes males and females to develop an inferiorism; in *Sterna* 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.

The hypothesis of a first reaction released by a very poor unspecific releasive mechanism possibly cannot cover all the facts and may require supplementation, as the following facts will show.

In the Three-spined Stickleback, as mentioned before, the male shows an identical first reaction to both males and females. In experiment the reaction could be evoked by various decoys. So far, these facts fit in our hypothesis.

New observations on the first reaction of the male Stickleback, however, reveal slight differences in intensity of the response to males and females. In this case, therefore, the mechanism of the first reaction, though it is very unspecific, must contain some recognition mark that is responsible for these slight differences.

This phenomenon can be explained in at least two ways. First it is possible that the differences between elements with releasive value and those without releasive value are of *degree* only and that we ought to speak of weaker and stronger elements. If some weak recognition mark would belong to the male and not to the female, this slight difference would account for the differential behavior toward males and females.

Another possibility is that the inborn mechanism of the first reaction is changed by conditioning, and that the differential behavior may be due to this conditioning process. At present it is impossible to come to a decision in this matter. The assumption of a vague, unspecific mechanism underlying the first reaction will have to be supplemented in order to cover all the facts known.

Owing to the extreme scarcity of available facts concerning these problems, it is a very difficult task to study the finer details of this mating mechanism and to find causes and functions of special forms of it. Though I recognize how unsatisfactory the foregoing comparative treatise is, nevertheless an attempt was made in order to focus attention on this complex of questions.

The Male's Mating Behavior as a Reaction Chain

A study of the further course of the male's display reveals new problems. The male's first reaction is followed by others that are dependent on the nature of its associate. If the latter is a male, it is at once attacked; if it is a female, it is courted. Such a bifurcation of the initiator's behavior occurs sooner or later in most of the species where a single first reaction is found. It depends on new sense impressions from the associate. A new stimulus situation is necessary to induce the second reaction, which is governed by a different mechanism. This is shown very clearly in those cases where the first reaction is caused by an object which, although it contains sufficient recognition marks to release the first reaction, offers too few characters inherent in the highly specific mechanism of the next reaction. In such case the behavior suddenly breaks off. Instances are: a female Phalarope that had reacted to an approaching Purple Sandpiper and, at the end of its first reaction, had suddenly ceased to pay attention to the stranger (Tinbergen 1935); a male Lapwing, watched by Selous (1902), that reacted by making a scrape before three Stock-Doves, and after this first reaction suddenly stopped "with a little start."

Owing to the necessity for a succession of different sense impressions in order to induce the whole series of activities, it is certainly wrong to speak of "the schema (mechanism) for the sex-partner," as different characters of the same sex partner appear in different mechanisms. For this reason, also, the use of von Uexküll's term "companion" (*Kumpan*) causes difficulties. It would be consistent only to speak of the mechanism of a behavior element, *e.g.,* of the here-mentioned first reaction.

The mechanisms for the new reactions are, as a rule, much more sharply defined and contain more recognition marks than the mechanism of the first reaction. They are, therefore, much more specific ("improbable," Lorenz). As the new reactions are different to males and females, we have, from this moment, an objective proof of sex discrimination.

The discriminative treatment of the two sexes by the initiator is not the same in all species. In fact, the differences are so obvious that Lorenz (1935) could describe three types of mating, based on the different types of sex recognition.

These types, which he recognizes among birds, are to be found in other vertebrates as well, and Lorenz points out that *Cairina* and some other ducks show the same type as certain lizards, known from the studies of Noble (1934) and Noble and Bradley (1933); that the mating mechanism of pigeons, of the Raven and of other birds are very similar to those of certain labyrinth fishes; and that mutual display of many birds has an analogue in cichlid fishes, such as *Aequidens pulcher* (Gill.) and *Hemichromus bimaculatus* (Gill.).

Although for a full treatment of these three types the reader must be referred to Lorenz's original paper, the main characteristics of them are recapitulated here.

In the "lizard-type," a sexually active male reacts to every individual of his species by displaying the bright part of his skin, his epigamic characters. This display culminates in an attempt at coition in all cases where the other individual fails to show a similar display. Display of the second male is the only response that prevents a false mating; special stimulative behavior (*Auslösehandlungen*) does not exist or is very poorly developed.

In the labyrinth fishes the display of the male develops into fighting except when the partner shows female behavior. All other circumstances cause an attack. The female shows stimulative behavior, which is very different from the male's behavior. Further, the male display is exhibited as a social reaction by the female; it serves as a threat when the social relationship of despotism is disputed between two individuals. The female's and the male's threatening behavior in non-sexual conflicts is thus the same as the male sexual display. The female's and the male's submissive behavior in non-sexual encounters is identical with the female sexual display. Coinciding with this, every individual is able to show male behavior, or female behavior, dependent on the behavior of the other individuals, a condition which renders the state of things extremely complicated. Male display (threatening behavior) of one individual induces female behavior (submissive behavior) in the other individual. The result is that false matings may occur, where the weaker of two males shows submissive behavior or where the stronger of two females shows dominant behavior. Allen (1934) calls the two kinds of moods superiorism and inferiorism.

In the third type of mating, that of the cichlid fishes, both sexes show display, and an inferiorism is not necessary for mating. Lorenz identifies this type with the mutual courtship of the English authors, *e.g.,* Huxley (1914, 1923), but as the cichlid type not only includes those forms where female and male display are alike or very similar, but also those forms where they are very different, it is clear that the group of birds with mutual display form only a small part of the group of birds with cichlid courtship. In this type, therefore, both male and female show releasing behavior (*Auslösehandlungen*), though not necessarily alike.

If one tries to bring a known form under one of these three types, one meets several difficulties. This is due to the fact that Lorenz did not give an exhaustive classification, but only points to the remarkable fact that convergences exist among many representatives of very different groups, as a result of which these types are found in different classes of vertebrates, and even in invertebrates (*Sepia*). The result of this has been that his description of each type contains characters, and therefore criteria, of different order, 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.

By using this criterion alone, a comparative review of mating types so far known reveals three large categories. The "lizard type" comprises those forms where the male alone has releasers, and where, consequently, non-displaying males are treated like females. The "labyrinth fish type" has releasers in the female; all individuals that do not show the female releasers are attacked (treated like a male). The third group, the "cichlid type" has releasers in both male and female.

Now, by a careful examination of mating mechanisms of different species, it is seen that there are species that belong to the cichlid type, but that are very similar to the type of the labyrinth fishes. One instance is the Herring Gull. The male Herring Gull, when unmated, is apt to attack any other Herring Gull. The female has a releasing movement, which alone inhibits his fighting impulse and induces courtship. Nevertheless, the male Herring Gull has releasers, too, though of minor importance: a displaying male Herring Gull is much more vigorously attacked than a non-displaying male (unpublished observations). Very similar is the behavior of the Three-spined Stickleback. The males of this species, when in sexual condition, attack every other Stickleback, unless it shows the characteristic movements of a female in laying mood. Non-displaying females, therefore, are attacked like males. The attacks are, however, of different vigor toward the different categories of non-laying individuals. Individuals that bear the secondary sexual characters of the male, the red belly, are more often and more strongly attacked than all other individuals (Ter Pelkwijk and Tinbergen 1937). This shows that the male, too, bears a releaser, though one of minor importance in this matter. The fighting behavior is not absolutely dependent on the presence of the male releaser in the opponent; its presence is of relative importance only.

On the other hand, it seems that some species show equally small deviations from the lizard type. This type, it may be remarked in passing, does not include all lizards, as is pointed out by Kramer (1937). Noble and Bradley (1933), upon whose study Lorenz's lizard type is based, report for one of their species, *Sceloporus undulatus* (Latr.), that the males sometimes showed different reactions to males and females. They think that this is a result of conditioning.

It seems, therefore, that lizard type and labyrinth fish type represent the extremes of a large series of cases, at the one end of which are the species with releasers only in the male, at the other end those with releasers only in the female. It is clear that releaser here means *a feature that evokes reactions on the part of the male at the formation of pairs,* not in the other activities of the pair. Moreover, it will be understood that those releasers may be either structural (morphological) or behavioral. The cichlid type, therefore, is a heterogeneous mixture of all kinds of intermediate forms.

To what extent the drawing up of these two types with intermediate forms will be sufficient as a basis for further classification, I am not prepared to decide. Those forms where individual attachment before a bethrothal period plays an important part (such as *Anatidæ*) present special difficulties.

Sex Discrimination

The fact that the male shows the same first reaction to every newcomer independent of its sex may cause difficulties in settling the question of sex discrimination. Different interpretations have been given in recent literature, dependent, in my opinion, on differences in emphasis rather than in the underlying facts. A reconsideration of the question, therefore, appears to be worth while.

It would be wrong to conclude from the fact that male and female evoke the same first reaction in the male that he is not able to distinguish between the two sexes. For, as was discussed above, the first reaction is soon followed by subsequent reactions that vary with the different sexes. In general it is certainly right to conclude that an animal does discriminate between two things, when it reacts differently to them, but it is too early to conclude to the contrary when it shows the same reactions to them; in the latter case the existence of discrimination is problematic. But when other reactions of the same animal are different toward the very objects that were treated in the same way at first, this is positive proof that the animal is able to distinguish between them.

Allen (1934) in his interesting paper on the Ruffed Grouse, where he gives the results of a long study of this bird in captivity, puts forward the conclusion, that "birds are not sex conscious, that is, they do not discriminate between the sexes as such" (p. 198). This conclusion was based on the following facts: males could be induced to show female behavior by threatening behavior of other males and, conversely, females could be induced by submissive behavior of another female to become dominant and play a masculine rôle; in this way homosexual pairs could be formed, and once a reversed mating occurred; further, a preoestrous male drove off every other Grouse irrespective of its sex; finally, an oestrous male tried to mount males as well as females.

That Allen is here generalizing in too bold a way from observations largely of only one species has already been stressed by Lorenz (1935).

A second objection to this thesis is that the facts on *Bonasa,* given by Allen himself, fit only in part into his conclusion. It was demonstrated above that with the Snow Bunting the existence of different reactions toward males and females proved the capacity of sex discrimination. Whereas it would seem that the Snow Bunting, when judged from the first reaction only, is unable to discriminate between the sexes, other reactions show that discrimination is made. Something comparable is found in the Ruffed Grouse. According to Allen, the spring behavior of *Bonasa* has two stages, one that could be called preoestrum, in which the male fights females as well as other males, and a subsequent oestrum, during which he is willing to copulate. I understand, though Allen's statement is not quite conclusive at this point, that an oestrous male also receives every approaching *Bonasa* with his intimidation display, independent of the sex of the other bird. Characteristic of the oestrous period of the male is the showing of the mating display and the fact that he tries to mate not only with females but with (submissive) males as well. From these facts the conclusion is drawn, that a male *Bonasa* (and birds in general!) does not discriminate between sexes.

This is true insofar only as the different colorations of male and female and other morphological characters (which are used as a means of discrimination by man) evidently have no influence. By simple experiment, however, Allen showed that males in oestrum copulated with stuffed birds only when these were mounted in rather special attitudes: "One had merely to place in his cage each morning a stuffed Grouse or a Grouse skin or a dead Grouse—the exact pose was unimportant so long as it was more or less flattened, or at least not mounted in an attitude of display, and the sex of the stuffed bird was equally unimportant" (p. 192). This, however, shows that sex discrimination *is* present, and that it depends on the behavior of the other bird, not on morphological characters. Allen's experiments consisted of giving to a bird another bird, with morphological characters of one sex and the (induced) behavior characters of the other sex, and as the bird always reacted to the behavior characters, he apparently "did not discriminate."

In general, in birds as well as in other animals, special movements are of no less importance than morphological characters in sex recognition, and it certainly is an anthropomorphic attitude to presume that only the morphological differences are of any value.

The evidence that at first sight seems to give strength to Allen's conclusion, *viz.* that males of different species of birds may try to copulate with stuffed males, and further that homosexual pairs have been observed in several species of birds (*cf.* Heinroth 1928, Allen 1934, Craig 1914, Whitman 1919, Lorenz 1935) all fits into the conclusion that special movements rather than other characters are recognition marks. Stuffed birds all show a characteristic "movement" of a female bird that is willing to copulate: keeping motionless, and in homosexual pairs one of the birds always shows female the other male behavior. The fact as such that a bird occasionally may behave exactly like an individual of the other sex is certainly interesting enough, but it does not concern us here.

Even this great importance of behavior as a sex character for a bird is not universal: Noble and Vogt (1935) showed that there are birds, especially those with great morphological sexual dimorphism (the Redwing, the Northern Yellow-throat and the Golden Pheasant), that use morphological characters rather than behavior peculiarities. The same holds good, according to Chapman (1935) for Gould's Manakin, and, according to Cinat-Tomson (1926) for the Shell Parrakeet.

In the Ruffed Grouse, the mechanism based on behavior characters would certainly suffice to prevent false matings in nature. It seems to me that many homosexual matings among Allen's birds were due to the fact that the inferior males were unable to flee. It is my experience, like Allen's, that among males of a territorial species, kept together in a confined space, a severe despotism develops in the season of the staking out of territories, one of the males often actually killing all the others. *In nature, the weaker males do not develop an inferiorism,* as they all take care to avoid occupied territory, and occupy a territory of their own, where they are not inferior, but despots in their own turn. A male on its own territory is undefeatable.

D. Fighting, Territory, and Song

INTRODUCTORY

Opinions are very conflicting about the whole complex of problems grouped around fighting, territory, and song. This originated in Howard's reconsideration of Darwin's views on the function of spring fighting of male birds (Howard 1920). Darwin's conclusions cover two fields: first, he thinks that the motive of the fighting males is to secure a female; this, it should be emphasized, is a psychological conclusion. We are now accustomed, on good grounds, to think that the motive of the fighting is not to be sought in a certain insight of its end-effect, but that the physiological status of the bird's body, together with certain external stimuli, causes it to show an inborn, instinctive behavior pattern. Insight into the immediate effect, if present at all, is certainly insufficient to determine the behavior.

Darwin's other conclusion applied to the function of the fighting, judged by its effect. He thought he had sufficient proof to conclude that the females chose the victorious (which were at the same time the more brightly colored) males, whereby the weaker males would be excluded from reproduction.

It is well to recognize that the abandonment of the psychological conclusion does not necessarily mean that the interpretation of the function is wrong. Howard, finding that many male birds are seen fighting even before any female has arrived in the region, recognized that it was impossible to conclude that the female was the cause of the fighting, and abandoned Darwin's psychological conclusion. At the same time, seeing that fighting was limited to territory, Howard concluded that the function of spring fighting was to secure a suitable territory. According to Howard, the territory is the only cause of the spring fighting, as well as its function. Fighting and song are centered by Howard around the territory.

Howard, after arguing that territory exists in many species of birds and accounts for all spring fighting, carefully considers the possible biological significance, the function, of territory. He has an open mind for the different possibilities, and does not attempt to find one and the same function of it in all different species. He considers the general function of territory to be the prevention of overcrowding. The limiting factor, which makes overcrowding harmful, may be different for each species: scarcity of nesting sites (cliff-breeding sea-birds), or scarcity of food for the young (Warblers, Buntings). The most discussed possible function of territory is that it guarantees sufficient food for the young.

At several points Howard's views caused a reaction among those ornithologists who followed Howard's own method of carefully watching few or even only one species during a prolonged period. The first substantial criticism of the territory theory, by the Lacks (1933), held that the existence of a territory is not so universal as Howard would have it, but that many species have no territories at all, including colonial birds. A further objection was that the food function of territory had not yet been proved, and even that a territory system has no influence whatever on the density of the population. As will be argued below, several of these criticisms are due to a misunderstanding of Howard's concept of territory, which again is understandable, as Howard does not give any definition of that concept. The discussions that followed this first criticism were concerned principally with the supposed food function of territory.

I rather think that the discussions have drifted away from the original problem. Darwin and Howard were concerned with the spring fighting of birds, and tried to find an explanation for it. Spring territories, therefore, are connected with the problem, and it must be realized that all other kinds of territories form a problem apart. A reconsideration of the problem, therefore, which is one of causes and functions of special reactions, has to take these reactions as a starting point.

In the course of the discussions a great many detailed questions have arisen, and the treatment of all those questions in the literature reveals a great lack of suitable facts. The primary aim of our study, therefore, was to collect facts that would bear on the territory problem. The facts we collected, however fragmentary they are, appear to be of sufficient importance to serve as a basis for the more general discussion given in the following pages. In order to avoid superfluous repetitions, I may refer to a short discussion of our facts in a previous paper (Tinbergen, 1936b).

If we take the reaction as a starting point, it must be defined carefully. Darwin speaks of spring fighting; for several reasons I prefer to include all fighting linked with mating. This will be called *sexual fighting* and in this definition I will include *all fighting occurring shortly before and during the formation of sexual bonds.*[1] Excluded, therefore, are fights to settle a social hierarchy, fights against predators and against direct food competitors. As a special case of fighting against predators the defence of nest and young are to be mentioned. This is to be distinguished from sexual fighting as it has another external releasing situation, another seasonal periodicity, and another connection with the occupied area. The difference has already been stressed by the Lacks (1933).

The area to which certain reactions against the predator "man" are confined is called anxiety area by Venables (1934), who made a study of these reactions in the Dartford Warbler. He reports that the anxiety areas of neighboring pairs often overlap, and takes this as an instance of the overlapping of territories. As the boundaries of a territory are determined by the spatial limits of quite another reaction, *viz.* sexual fighting (in this species: spring fighting of males against males of the same species), overlapping of anxiety areas does not permit any conclusion about the territories. Here we feel the lack of a suitable definition of territory. For this question the reader may be referred to the next chapter.

Moreover the anxiety area is a heterogeneous conception in that its boundaries may be different for different predators. In many species, dogs are attacked within a much greater anxiety area than men. In the Snow Bunting, the difference between

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[1] Often sexual fighting continues after the formation of a sexual bond. Further, the expression sexual bond is used here in a very wide sense; one coition of a Ruff is, in our sense, a sexual bond.

dog (and fox) and man was enormous; while our presence caused disturbance in one or two pairs at the same time, an Arctic Fox was surrounded by quite a flock of screeching birds.

Sexual fighting does not occur in birds alone, but is widely distributed, in invertebrates as well as vertebrates. Comparison on as broad a base as possible will appear to be of great value, especially when considering the function of the reaction.

THE CAUSES OF SEXUAL FIGHTING

No doubt the causes of sexual fighting are, like those of all other reactions, partly internal factors. To study these internal factors, and the external factors that influence them, in the field, is only possible to a very limited degree. We have, however, some indirect evidence that tends to link up sexual fighting with other reactions. First, the seasonal cycle of sexual fighting often runs parallel to that of other sexual activities: courtship, song and coition. Secondly, the daily cycle of sexual fighting also parallels that of other sexual activities. Whether this daily periodicity depends more on internal than on external stimuli is unknown. These observations suggest, however, that the factors determining the periodicity of sexual fighting are, at least partly, the same as those causing the cycles in the whole complex of other sexual activities. A dependence of sexual fighting on the testes was demonstrated in Pigeons by Carpenter (1933). Miyazaki (1934) reports that artificial increase of daylight caused testis progression, song, and fighting in *Zosterops palpebrosa japonica* (Temm. and Schl.).

Together with these internal causes of sexual fighting, external stimuli are at work. These are so important that except under abnormal conditions no fighting is observed without an opponent. Those exceptional conditions, under which fighting may be released by a minimum of external stimuli, arise by keeping a male in full sexual condition away from all adequate opponents. Such a bird soon fights many inadequate objects. Convincing cases are reported by Braun (1915). In observation areas such as ours there was no opportunity for such an extreme lowering of the reaction threshold.

The external stimuli that release the reaction are easily studied in the field by carefully noting a great many cases where fighting is and is not released. It has to be considered, however, that the threshold of the reaction is continuously moving up and down owing to the changes in conditions. The daily cycle, seasonal cycle, and weather conditions may all influence the reaction's intensity. Too, the bird's former reactions may have some after-effect: courtship probably has an inhibiting influence, fighting a stimulating one. It is obvious, therefore, that a great many observations are required. Even then an absolute judgment about the releasing value of the external situations is impossible; but it is possible to find, with approximate accuracy, an optimum situation.

In the Snow Bunting, some of the factors in the external situation are easily recognizable. As male and female both fight, they will both be considered but, of course, separately. In both cases we have to consider two questions: what is the situation to which sexual fighting is spatially restricted, and against which birds is sexual fighting directed?

The Male

In general the fighting of the male is restricted to the territory. As soon as the male goes outside its territory, it does not fight the very same opponents he furiously attacked the moment before when on his own ground. It is scarcely necessary to point out that this connection between sexual fighting and territory exists in many species of birds. It is of more importance to consider that the specific characters determining the selection of a territory are so extremely different for different species. The Blue Heron takes a branch on which a nest may be built; a Kestrel takes a nest which has already been built. In many colonial breeders, sexual fighting is strictly bound to territory. It may be a rather large piece of ground, as in the Herring Gull, or it may be scarcely large enough to bear a nest, as in Gannets, Sandwich Terns and others; in all cases sexual fighting is restricted, absolutely or for the greater part, to a territory.

In some species of birds sexual fighting is independent of any territory. This is the case in many ducks, where sexual fighting, coinciding with the formation of sexual bonds, occurs in autumn, and is entirely independent of a spatially restricted area. In the Avocet (*Recurvirostra avosetta* L.), sexual fighting certainly is not restricted to territory. Makkink (1936), in his thorough study of this bird, says: "Observation teaches us that fighting very often occurs in situations in which territory cannot be the point. First, long before the birds are in the colony haunts, the encounters are of a very common occurrence. Second, fighting is as common in the water as on the land, independent of a nest. Third, every bird, when it possesses a nest or young ones, may be observed fighting in any part of the colony, at a smaller or greater distance from its own nest" (p. 28). Although in this case sexual fighting is not discriminated from other kinds of fighting, a connection of sexual fighting with territory appears to be absent or at least very loose. No evidence is given as to how far sexual fighting is spatially restricted in regard to the mate although it is stressed that it may occur without a mate being present.

In other vertebrates examples of both territorial fighters and non-territorial fighters are known. The Three-spined Stickleback belongs to the first type (Wunder 1930, Leiner 1929, 1930, Ter Pelkwijk and Tinbergen 1937). In the Bitterling, a species that lays its eggs in the gills of fresh-water mussels (*Anodonta*), sexual fighting is closely connected with the presence of such a mussel. Males and females, when kept under experimental conditions without *Anodonta* will never come into full sexual condition. One mussel is sufficient to cause the sexual cycle to run its complete course. Fighting of the males is not linked with territory, but is restricted to the vicinity of the mussel, which is constantly moving about. The fish follows it, and thus his "territory" moves about, too (Wunder 1933, Boeseman a.o. 1938).

The reproductive behavior of several ungulates, of which the Moose is best known to me and therefore taken as an example, does not show a connection between sexual fighting and territory. Fighting of the bulls is restricted to the vicinity of the herd of females, and when the herd wanders, the bull and its boundaries wander with it. The same is true of *Cervus elaphus* L.

These few examples may suffice to show that sexual fighting often has no connection with a territory. Now in some species, where a connection with territory exists, sexual fighting need not always be restricted. The male Snow Bunting, though restricting its fighting to territory in most cases, may fight outside under special circumstances. I have described (p. 27) how a newly mated male often followed its mate over the boundary and there fought its neighbor. Unmated males were seen to visit their neighbor's newly arrived female, to court her, and in this situation they may fight the neighbor on the latter's territory (p. 26). This shows that the presence of the female is a factor in the external situation which in some cases may be sufficient to cause sexual fighting without the factor of territory. In this, the Snow Bunting stands not alone. Howard himself says about the male Garden Warbler that it sometimes fights outside its territory as soon as it is mated, and that this occurs when its mate occasionally comes outside the territory (Howard 1913). Dewar (1920) reports the interesting fact that a male Blackbird changed the boundaries of its territory as a result of the changed movements of the female. A piece of ground outside the original territory was chosen by the female for a nesting site, and the male consequently added it to its territory. Mayr (1935) gives an account of fighting connected with the female in Pigeons. Nice (1936) watched a female Song Sparrow building a nest in a neighbor's territory. After prolonged fights her mate succeeded in conquering this piece of ground.

Now the second part of the question may be considered. A careful study of the objects of sexual fighting together with a study of the objects of other aggressive behavior in any species is still lacking, although there are many fragmentary observations to be found in the literature.

Many authors report territorial males attacking individuals of other species, but in nearly all cases it is impossible to see whether the author speaks of sexual fighting or of fighting against predators, and also if the other species is set upon as often as the attacker's own species, or if it is an occasional occurrence. 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. As a rule these false reactions are recognizable by their occasional occurrence.

For these reasons the fighting reaction has to be studied during the whole course of the breeding season in order to get sufficient data about both the spatial restriction and the adequate object. The available reports about sexual fighting regularly directed against strange species are to be accepted with reserve so long as these conditions are not fulfilled. Howard's conclusions that in many species not only sexual competitors but also territorial food competitors belonging to strange species are attacked seem too bold and certainly need careful re-examination. In those birds with which I am acquainted, sexual fighting is restricted to birds of the same species. See, however, Lack's observations on the Bishop Bird (Lack 1935b), also Venables (1938).

Not all individuals of the same species are attacked, however. In the Snow Bunting, as in many other species, fighting is directed only toward other males. It was reported above (p. 17) that calling males were attacked more often than silent males and that singing males were attacked even more. This could be confirmed over and over again in all territories that were invaded by foraging flocks. Confirming evidence is found on p. 40. Males that are foraging for their young, and consequently silent, are generally tolerated by other males on the latter's territories.

The strongest stimulus, finally, is a male that refuses to be driven off the territory and withstands the attacks of the territory owner. In such cases the most furious fights ensue.

THE FEMALE

Howard concludes from his observations that the fighting of the female is also connected with territory. In the Snow Bunting, this is true in part only. Certainly, in this species, the female's fighting has a certain connection with the territory, but this must be explained in another way. The female Snow Bunting never shows any knowledge of the *exact* boundaries of the male's territory, nor do her movements show a connection with it. Further, the female is much more ready than the male to fight outside the territory, and, in fact, does not show the hesitation that is characteristic for the male in the same situation. The female, however, has a strong inclination to remain in the male's vicinity, and the fact that she restricts her movements to the territory at all must primarily be explained by her remaining in close proximity to the male, and not by her own linkage with the territory. Howard says of the female Willow Warbler that she has to learn the boundaries of the male's territory (Howard 1911). In the Snow Bunting there are cases in which the female appears not to have learned the male's boundaries, as she makes her nest outside the territory. Exactly the same is reported by Brock (1910) for the Willow Warbler; he emphasizes that in this species the female does not know the male's boundaries. I refer also to Dewar's observation on the Blackbird and to Nice's description of the same events in the Song Sparrow, which were mentioned above.

In all of these cases it is impossible to determine whether the female actually did not know the male's exact boundaries or merely neglected them. They suffice, however, to show that the female often does not show such a rigid connection with the territory as the male.

Next we will consider the objects against which the fighting of the female is directed. Howard uses the general occurrence of fights between pairs as an important argument against Darwin's thesis that the attacked individuals are sexual competitors. Fights between pairs cannot be understood, he argues, if we take them to have the function of the defense of a mate. They are at once understood if they are considered to serve as a defense of the territory, for, as territorial competitors, females are as dangerous as males. Now in the Snow Bunting, the fights of pair against pair appear to consist *always* of double fights; one of male against male, and another of female against female. Our observations of numerous fights only revealed one single exception to this rule, as mentioned on p. 27. I am convinced that there is a similar state of affairs in many territorial birds, if the fights were carefully studied. Indications of this are seen in the many instances where males fight males and females fight females. Instances may be found again in Howard's Warblers. The female Whitethroat, according to Howard, comes to witness the fights of the males, but "I never remember her seeing her actually attack an intruding male, but when a second female intrudes she does not hesitate to do so, the attack being very vigorous . . ." (1906, p. 6). In the Reed Warbler the male attacks intruding pairs: "If it was a pair that was intruding, the attack was generally aimed at the male, but the female from the adjoining territory, while collecting food for her young, was also attacked" (1910, p. 8). That Chaffinches fight against birds of their own sex only, is also reported by Howard (1920). According to Kluyver (1933), the same is also true of the European Starling. In the Herring Gull exceptions to this rule are also rare. In the Wren-Tit, to the contrary, both males and females generally attack both sexes (Erickson 1938).

From these observations it is possible to make an extremely rough sketch of the external situation that stimulates sexual fighting. In the male Snow Bunting it may be described as: a male Snow Bunting in sexual condition (singing) intruding on the territory or coming in too close proximity to the mate. That it really concerns males in sexual, and not in general, those in reproductive condition, is shown by the fact that foraging males, which are silent, are attacked not nearly so vigorously as singing males, although the former are certainly showing reproductive behavior.

For the female Snow Bunting the situation that releases sexual fighting is: another female Snow Bunting, coming too near the male.

The fact that almost no reactions to the other sex or to other species (Lapland Longspurs) were observed indicates that the recognition of the object of sexual fighting is based on a rather specific, highly articulated mechanism.

The Functions of Sexual Fighting

Before discussing the functions of an animal's activities it is necessary to consider exactly what we mean by "function." The recognition of the existence of some function (biological significance, value) always presumes some goal. The function of a process *as such* is nothing, as long as we do not know toward which goal it has to function. Now the goal toward which we take life processes to be functioning is always the conservation and promotion of the species, in a qualitative as well in a quantitative sense. With this axiom the subjective element of our study of function is put aside, and on its basis an objective analytical study of function is possible. The only objective basis for any conclusion about the function of a process is the study of the effects of the process. Now every process has several effects, and not all of them have to be considered as functions of it. Those effects that appear to influence the species' status either quantitatively or qualitatively are considered functions of life processes. An instance may serve as an illustration. The incubation of an egg has several effects. One is that the constituent materials of the egg, dead and alive, expand slightly. Another is that the living tissues are kept alive and develop in an optimal way. As we cannot see any influence of the first effect on the state of the species, we reckon this effect to have no function; the second effect, on the contrary, prevents death, actually promotes growth, and therefore has a function. This trivial example is merely to illustrate the way in which the concept of function will be used here.

Every biological process is materially composed of a highly complex system of causal relations. The result is that a change is never the result of one single causal factor, but of a complex of several factors. This means that it is impossible to find an absolute function of one factor. Its function is always relative, and exclusion of this one factor must not necessarily stop the process it was causing. Other factors may continue to function.

However natural this may be, in questions of functions of behavior it is too often neglected, with the result that irrelevant arguments are used. The question, for instance, of whether territorial behavior tends to prevent overcrowding, is often answered negatively, on the sole ground that defense of the territories of the first arrivals does not *absolutely* prevent the establishment of new males that conquer part of the first arrivals' territories. To function in the direction of the prevention of overcrowding it is only necessary that sexual fighting results *in a certain number of the cases* in driving a male off. As this certainly is the case, sexual fighting tends to prevent overcrowding. Further treatment of this question will be found below.

The function of reactions therefore is always relative, tending toward some goal and not always absolutely acquiring that goal.

The problem of the functions of sexual fighting can be divided into three separate questions. First, since the fighting is directed toward special individuals, which category do they form? Further, fighting is always spatially restricted, being confined to the vicinity of some one thing, and thus defense of that thing ensues. The next question, therefore, will be: what things or situations are defended? When these two questions have been answered, that is to say, when we know what is defended against whom, then the question as to the function of this defense has to be answered.

A review of the facts mentioned before, showing the objects or situations that are defended in different cases, will enable us to find some common property of all objects, and along this line the essential properties of these objects may be found. It is unnecessary to point out that these properties are not to be confused with the sign stimuli that caused the bird's responses. Now we have seen that the Warblers and the Buntings defend a territory, and a female *Rhodeus* defends a mussel, *Alces, Cervus* and ducks defend females. Looking now for properties that are common to all objects here mentioned, our conclusion will be: *The fighting before and during the formation of sexual bonds serves (without the animal "knowing" it) to secure objects or situations that are indispensable for reproduction.* It is impossible to give a closer description without excluding many known facts.

The question, against whom these objects or situations are defended, may be answered in the same manner. *The common character of the attacked individuals is always: sexual rivalry.* Other individuals of the same sex and species, and in full sex condition, are the optimally adequate objects of the sexual fighting reaction. *Sexual fighting therefore serves to defend mate, territory, or other things that are indispensable for reproduction, against sexual competitors.*

The fact that so often sexual fighting serves to defend a potential or real mate against a sexual rival has been recognized by several ornithologists. Nice (1933, p. 98) says: "It may be that the food aspect of territory has been overemphasized, and that sex jealousy in many cases plays a definite part." Nicholson (1929, p. 57) wants to "draw a line" between "performances incited by ownership of territory and those inspired by sexual emotion," but says that he is unable to do so. Mayr (1935, p. 36), considering the "connection between jealousy and territorialism," says: "There is a good deal of evidence that (at least in some species of birds) acts of intolerance or even fights are equally or more induced by sexual jealousy than by the desire for territory." The facts for the Snow Bunting, described above, strongly support these suggestions.

Summarizing, sexual fighting in birds serves to defend a territory or a sex partner, or both, against sexual competitors. The function of the territory will be studied in the next chapter; the function of the defense of a sex partner may be discussed here. The intolerance against individuals of the same sex, resulting in the defense of the sex partner against sexual rivals, certainly tends to prevent the partner from pairing with a second mate. Like all causal factors that we are isolating from a whole complex of factors, it need not always be absolutely sufficient to prevent bigamy; it only helps establish monogamy. When both sexes fight, monogamy is, of course, promoted even more.

The question of the value of monogamy may be asked. The answer was given by Heinroth long ago when he said (1910), that monogamy was necessary in many species for a successful rearing of the young. This again, does not mean that all clutches of abnormally bigamous individuals found in normally monogamous species are certain to die, but only that they have a smaller chance of survival. In the Snow Bunting, we saw that desertion by the female even when the young were fledged resulted in the death of the young she had taken care of up to that time.

The Functions of Territory

One of the functions of sexual fighting is the defense of a territory. This territory is a very different thing in various species of birds, depending on specific preferences. According to its innate disposition the bird selects its habitat and the part of it that is to be defended. About the factors which determine this habitat selection in any species of bird little is known. Lack and Venables have made a start with the study of these specific, selected habitats (Lack 1933, 1935a, Lack and Venables 1937).

The word territory is used in many different senses; a definition is seldom given. Howard himself does not define his conception of territory, though it is clear from his descriptions which kind of territory he means, at least in his "Territory in Bird Life" (1920). As Mayr (1935) quite correctly points out, Howard is more vague in his later publications. Mayr is the only author who has given a practicable definition, making as sharp a distinction as possible between true territory and other instances of occupied space. He gives the following definition: "Territory is an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous" (p. 31). In general, this description applies very well to Howard's conception of territory. As I pointed out in a former paper (Tinbergen 1936b) I prefer a more direct definition and propose to define territory as an area that is defended by a fighting bird against individuals of the same species and sex shortly before and during the formation of a sexual bond. Using the definition of sexual fighting that was already given, my definition of territory would be: *Whenever sexual fighting is confined to a restricted area, this area is a territory.* Like Mayr, I consider it wrong to include any reference to the function of territory, as the function may be, and in fact is, so different for different species.

By this definition our discussion is restricted to a particular form of what is commonly called territory. As has been stressed by Meise (1930) and by Mayr (1935) several other types of occupied space can be distinguished, all of which are territory. *To avoid confusion, I propose to call the type of territory defined above sexual territory.*

Now I should like to point out the fact that in many birds, regarded as non-territorial by Howard's critics, a territory in this sense is found. This applies especially to the colonial birds. Jackdaws (Lorenz 1931), Herring Gulls[1] (Tinbergen 1936a, Goethe 1937), and Rooks (Yeates 1934) are territorial, colonial birds. The arguments used by the Lacks to prove the absence of territory in the Guillemot are entirely insufficient; in order to know if territory exists, close observation at the very beginning of the mating season is necessary.

In most birds of prey a sexual territory exists. Lack's criticism of Howard is here right only to the extent that a bird of prey does not defend its total occupied space (hunting ground) against members of the same species, but only a small area around the nest (Kestrel, L. Tinbergen 1935; Hobby, Schuyl, Tinbergen and Tinbergen 1936). This is no reason to deny the occurrence of territory. As the Lacks themselves doubt the food value of territory, it is only logical to exclude the food argument in the definition of territory.

These few examples will be sufficient to show that sexual territory in its different specific aspects is of wide occurrence.

What is the function of territory for different species? Many discussions have arisen from Howard's suggestion that in some species

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[1] In the Herring Gull, sexual fighting begins before the formation of a pair and is, in the beginning, independent of territory; defense of a territory begins as soon as a pair is formed.

the territory has the function of preserving food for the young. His argument was twofold. First, he considered that territory could prevent overcrowding; second, he tried to find the factors for each species that would make overcrowding harmful. It is necessary to consider the two questions separately.

Some of the critics do not believe that the territory system prevents overcrowding. Based on facts developed by Howard and others, their conclusion is that every newcomer trying to take a territory on already occupied ground succeeds in establishing itself, in spite of the attacks of the resident bird.

It must be said, however, that the available observations supporting this conclusion are very few. Furthermore, it is much easier to observe ten cases where a newly arrived male succeeds in settling down, than one case where it is expelled, because it is only in the first cases that conspicuous, long-lasting fights draw the attention of the observer. The critics do not consider the numerous birds that may trespass, and are at once attacked and expelled. In the Snow Bunting, as was described before, we often observed how newly arrived males roamed over the country, settling on occupied territories every now and then, and being chased from one spot to another. One male that had taken a territory between other territories was vigorously attacked by the settled males and eventually driven off. The observations of Erickson (1938) on the Wren-Tit demonstrate that in this species attempts to settle in an occupied territory often fail. She writes: "Since the individual holding a territory is almost without exception successful in its defense, only an unusually dominating individual can get a foothold in an occupied area. In each of the three years of field work, three or four individuals have failed to do so" (p. 315).

Further, we observed that the pugnacity of the males grew stronger and stronger, as their territories grew smaller. I therefore agree with Huxley (1934) in assuming that aggressiveness increases as the size of the territory decreases. Of course, it is impossible to speak of a definite limit of the territory's size, as individual birds vary a great deal and the fighting urge is affected by environmental factors of varying intensity, but our point is that *aggressiveness may increase until that level is reached where it is strong enough to conquer all newcomers.* That such a stage is really reached is proved by the behavior of captive birds kept in a room that is smaller than the minimum size of the territory of the species. Four captive male Blackbirds, which I kept living in a cage 2x1x1 m., developed a severe despotism, as captive birds are apt to do in the spring, one of the males actually killing all the others.

In experiments with other males, I succeeded, by taking the despot away, in making one of the oppressed birds to become despot in the course of half a day. If this bird was taken away, the next bird became despot. Exactly the same can be demonstrated *ad libitum* in the Three-spined Stickleback, a rigidly territorial fish, whose territorial habits have been studied by several authors (Wunder 1930, Leiner 1929, 1930, Ter Pelkwijk and Tinbergen 1937).

The first question, therefore, whether territory has the function of the prevention of overcrowding must undoubtedly be answered in the affirmative. Our only restriction is that the word prevent must not be taken in an absolute sense. As was pointed out before, a function of a biological process may not be expected to be absolute, for every process functions in coöperation with other processes.

The next question, that of the first deleterious effect of overcrowding, is much more intricate. As in the question of the function of sexual fighting, some insight may be gained by carefully comparing the different situations that are defended, in order to find the essential characters of a territory. If we do so, for instance, with the Kestrel, it is not difficult to detect that the sexual territory of this bird is the area around a suitable nest. The fights of Kestrels in spring always occur in the immediate vicinity of a Carrion Crow's nest or of a nesting hole. Often fights ensue between Kestrels and Carrion Crows that are competitors for the nest (L. Tinbergen 1935).

In the Snow Bunting, a territory probably contains numerous suitable nesting sites. We have carefully examined the possible significance of the territory and have found the following facts: the nest is built by the female, not always on the territory, but sometimes outside of it. Food is not taken exclusively from the territory, in fact during unfavorable weather the territory seems to yield too little. Some foraging areas are neutral ground. The occurrence of neutral foraging grounds has been observed in the Reed Warbler by Howard and in the Little Grebe by Trahair Hartley (1933); foraging in a neighbor's territory without resulting fights is observed with the Willow Wren, Nightjar and Chaffinch (Lacks 1933). Further facts are cited by the Lacks showing that with territorial species food often is not taken exclusively from the territory. In the Snow Bunting, foraging males are frequently tolerated on strange territory by the very same males that vigorously attack any singing male that intrudes. In my opinion all these observations do not disprove the food value of the territory that was claimed by Howard.

The Lacks begin their criticism of Howard's food thesis with the following words: "First, many species nest in colonies and yet seem to experience little difficulty in obtaining food, although some of them are closely related to territorial birds of apparently similar feeding habits." No bird watcher, however, Howard included, has ever claimed a food value for the territories of the Guillemots or Herring Gulls. Several other arguments against a food value even in those species where the territory is more than "a mere nesting site" seem to me to be irrelevant. The Lacks, and Mayr too, lay stress on the fact that territorial defense is not strongest at the time of feeding of the young, whereas, according to Mayr: "The intolerance of the male should be constantly increasing during the course of the breeding season, since the amount of food that is being needed is growing with the growth of its family" (p. 35). The answer is that defense of a territory is most efficient if it occurs in the period of the establishment of territories, and not at a time when no more males arrive. The only serious objection seems to be the fact that the defense of a territory is not or is only rarely directed against food competitors of other species.

It is certainly true that we know very little of the food habits of the birds in question, and of the species that are regularly attacked by any one species, but nevertheless what meagre knowledge we have, gives us the right to doubt the assertion that fighting against food competitors is the rule. That it occurs is shown by Lack's study of *Euplectes* (Lack 1935b).

The critics of the food-value theory ask too much of it. There may be different kinds of food value, and Howard himself has been very careful in expressing the value he postulated. In a short note, he has again stressed the principal point (Howard 1935) and it seems that his arguments still hold good. Howard says that we know that young birds need an enormous quantity of food, and further that they need, in their first days, regular brooding at very short intervals, for experiments have proved that a relatively short exposure causes them to collapse and that young birds that do not beg for food are not fed. This *proves* that with some species it is necessary for the parents to make but short foraging excursions. It is, therefore, *proved* that a foraging area around the nest is a necessity with some species. It seems to me, therefore, that it is idle to argue against a food value of the territory in general, and that 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. If this function is recognized, it is clear that it is irrelevant to claim that some of the food, or even much of the food, is taken outside the territory, especially if this occurs when the young are half-grown.

Of course, the problem remains of the functions of territories where this food value does not exist and an analysis of many kinds of territories is badly needed. I have not attempted to collect the scattered facts to be found in the literature, but I may point to the studies of Moreau (1935), Venables and Lack (1934, 1936) and Palmgren (1932a, 1932b, 1933).

SONG

The problems about causes and functions of song are quite as much confused as are those about territory. The opinions in this field are conflicting, and especially those ornithologists who have a wide experience in this matter show a disinclination to assume a general and at the same time precise function of the phenomenon. This attitude is justified to a certain extent by the enormous diversity of bird calls that are commonly labeled as song. As an illustration of this diversity a few instances may be mentioned: the spring song of the Baltimore Oriole; the song of a Purple Sandpiper or any other wader; the song of a Tit, which may be only slightly different from the social call notes; the song of a male European Starling while enticing the female for coition (Kluyver 1933); that of a Hawfinch, which according to Nicholson (1929) pairs while living in the flock; the warbling communal song of roosting Redwing Thrushes, which is so well known a sound in winter throughout northwestern Europe; the warbling song of some incubating birds (*e.g.* the European Jay); that of young male songbirds, such as Song Sparrows (Nice 1933); the winter song of birds that have winter territories, such as the English Robin (Burkitt 1924-26) and the Mockingbird (Michener and Michener 1935); 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.

The principal cause of this complexity of what is commonly called song is the lack of an objective definition of the word. This again is the consequence of borrowing it from daily-life language. When the progress of the study demands a stricter outlining of concepts, such terms fail, though they may have done pretty well during the previous phase of research. As a first step of analysis, therefore, some subdivision of song into different categories has to be made, and the different phenomena must be studied separately. As in other cases of the study of behavior or of morphological structures, the most highly specialized forms offer the easiest subjects for causal analysis. As the song of the Snow Bunting happens to be such a specialized reaction, my discussion will naturally apply to this kind of song especially. The arguments of the following account, therefore, are not intended to hold true for all those other phenomena which are possibly quite different.

In order to arrive at a clearer definition of this type of song, a closer study will be advisable of some examples that are generally recognized as song. Objective criteria that may be found as a result of such a study may be used as a basis for this definition.

In daily life the word song is applied to sounds that are both beautiful and not too short. The aesthetic appreciation, being a very subjective and delicate criterion, cannot, of course, be used for our purpose. The duration of the song, too, is a very unsuitable criterion, as the songs of songbirds vary so widely in this respect.

Another character of the song of most songbirds, however, appears to be much more important: its loudness and far-reaching capacity. I propose, therefore, to call the type of song with which I will deal here "advertising" song. In many cases this advertising song is most intensive at the beginning of the reproductive period during the premating phase. In several species, it is even strictly confined to it. It is, in this season, uttered by one sex only, mostly the male.

As a provisional definition, therefore, I will consider as advertising song those loud sounds that are given by birds of one sex especially at the beginning of the reproductive period. As is well known, the advertising song may be heard during the off season too, a phenomenon which will be discussed below.

By defining the reaction in this way, we do not confine song to the songbirds alone. We have to apply it to many sounds with the same characters in other birds, such as the *Liebeslockruf* of the Blue Heron (Verwey 1930), the sound accompanying the spring flight of the Lapwing, the ceremonial flight of the Phalarope (Tinbergen 1935), of the Black-tailed Godwit (Huxley and Montague 1926) and of many other Limicolæ, some of the drumming sounds of Woodpeckers (Tracy 1938), the peculiar sounds during the spring flights of the Ptarmigan and other gallinaceous birds, the rattling of the European Nightjar (Heinroth 1909, Lack 1930a, 1930b, 1933), the boom of the American Nighthawk, the bleating of the Snipe etc. etc. It is irrelevant, then, whether the sound is made with the syrinx or not (Bittern, instrumental music of Woodpeckers and Snipe).

THE CAUSES OF ADVERTISING SONG

Known facts bearing on this problem are few. Our knowledge is relatively best in the case of birds of the northern temperate zone, to which the following discussion applies. As was remarked above, advertising song shows a seasonal periodicity, being most intense at the beginning of the reproductive period. This shows that, in general, advertising song runs parallel with the development of the gonads. It must be said, however, that the experimental evidence as to the linkage of gonadal development with song is still very unsatisfactory. Yet attention should be called to some indirect evidence.

It is well-known fact that increasing length of day causes gonadal development not only in birds, but in many other vertebrates of our geographical zone as well (Rowan 1938, Bissonnette 1936). Now experimental day lengthening is practised by Dutch bird catchers in order to get males to sing in autumn, a technique probably developed generations ago (Hoos 1937). Some Japanese cage birds are treated in the same way (*yogai*) (Miyazaki 1934). Similar facts will certainly be known locally.

We may assume, therefore, that development of advertising song is either caused by gonadal development, or, at least, by the same factors that control gonadal development.

Another indirect way of testing this question is the study of the gonadal condition in a series of birds collected at different phases of the development of their song. This method was followed by Böker (1923). His facts, however, are entirely insufficient. In spring, he collected at different intervals a small number of male Chaffinches. With a few exceptions, he did not observe the behavior of the collected individuals, and therefore did not know whether they were singing territorial birds, or migrants that would have come into oestrum much later. Considering the enormous individual differences in the condition of the gonads of a mixed population of Chaffinches in spring, a correlation of the histological data with the general development of reproduction could hardly be expected. Furthermore, Böker argues that song, if it should be a sexual function, has to coincide with the formation of ripe spermatozoa in the testis. He thus ignores the well-known fact that song is, in the Chaffinch, not an accompaniment of coition, but of a much earlier phase of reproduction. Song is most intense before mating, and therefore *a priori* singing birds can be expected to show the beginning of testis development, and development of song must run parallel with, yet precede the actual formation of the spermatozoa, which is the very last step in spermatogenesis. In spite of the small series, and of the very inaccurate method of collecting the necessary ethological facts, Böker's birds indeed show a certain positive correlation between song and spermatogenesis. But since song and the formation of spermatozoa did not actually coincide, Böker concludes that "the song of birds has no causal relation to the sexual drive" (translation mine, N. T.).

It seems to me that his facts, if in any way conclusive, point in exactly the opposite direction. The facts so far known justify the hypothesis of a close causal relation between gonadal growth and song. In order to test this hypothesis, a much more careful study than Böker's will be necessary.

Miyazaki (1934), studying the effect of the lengthening of the day on the mating song of *Zosterops palpebrosa japonica* (Temm. & Schl.) reports that his experimental birds showed a testis progression coincident with increase in mating song intensity.

Temperature has a marked influence on song. Exact data, however, are scarce in literature. Nice (1937) shows that the first attempts at song of a male Song Sparrow in early spring are dependent on the temperature, the threshold getting lower as the season advances. I have captive males of the European Song Thrush, which can be induced to start their complete spring song in midwinter by an artificial sudden rise of temperature.

Direct experiments on the influence of castration and of injection of testis hormone on advertising song are not known to me. Yet in several cases the effect of such experiments on the development of the plumage has been studied. These experiments have seldom been carried out with a species that has a typical song; moreover, the behavior of the animals was rarely described. However some studies contain observations that point in the direction of our conclusion, either by showing influence of the gonads on song itself, or on other premating activities (Pigeons: Carpenter 1933; Turkey: van Oordt 1931; *Philomachus*: van Oordt and Junge 1936; see further Groebbels 1937).

It is quite possible, therefore, that a close study of progression and regression of the spermatogenesis, parallel with careful observation of the behavior of the individual birds, will reveal a very close connection between the two processes.

Opposed to the assumption of a causal relation between song and testis development are the numerous instances of autumn and winter song. Many song-birds resume singing in autumn, even migrants may sing rather intensively, especially in mild weather and there are several reports of migrating species singing in their subtropical and even tropical winter quarters.

These facts will have to be grouped in at least two categories. One comprises those birds that have winter territories, the other those that have not. The latter group will be treated first.

A priori it should be expected that if song were dependent on a certain phase of gonadal development, it would not cease suddenly, but diminish gradually in intensity, following the gradual decrease of testis activity. This gradual fading of the song is not actually observed; in general autumn song is a new peak after a quiescent period. It must be said, however, that in any given species autumn song seldom reaches the full intensity of spring song.

There are several important facts that tend to throw light, first on the occurrence of the quiescent period, second on the autumnal increase of song activity.

With the Snow Bunting, there is one factor that instantly inhibits song: the arrival of a female. A newly mated male is absolutely silent for several days, and only after an interval of some days may again sing a little. The polygamous male that is mentioned on p. 35 stopped singing as soon as he was mated, and started singing again in full force when his second female refused copulation. This male not only resumed singing, but behaved in detail like an unmated male. Inhibition of song occurred only during the short combined fourth and fifth periods and the bird then fell back to the third period again.

Sudden resumption of song after the loss of the female is reported by Allen (1934) with two male Song Sparrows: "On July 8 one of the most severe hail storms I have ever experienced destroyed both nests, and the female birds disappeared. What became of them I do not know—nor apparently did the male Song Sparrows, for almost immediately their song, which had almost ceased, was resumed with springtime fervor. . ." (p. 196).

In species that have more than one brood each season, the resumption of song after the first brood is fledged is often very striking.

Sudden inhibition of song by the arrival of the female has been observed in several species. Brock (1910) mentions it for the Willow Wren, Howard (1907-1914) for the Grasshopper Warbler, the Reed Warbler, the Garden Warbler and the Wood Warbler, Nice (1933) for the Song Sparrow, and Burkitt (1925) for the English Robin. The *Liebeslockruf* of the Blue Heron, which, according to our provisional definition, is analogous to the song of the *Passeres*, is instantly inhibited by the arrival of a female (Verwey 1930).

In many species, the inhibitory influence of the presence of the female decreases after some days but frequency and intensity of the song remain very low.

At the end of the breeding season, another inhibiting factor begins operating: the molt. In most species that display autumn song, this begins shortly after the completion of the molt. Presence of the female, and molt, therefore, easily account for the gap in song between premating period and autumn song.

A second question is whether autumn song really coincides with more or less active testes. I do not know of any careful observations of the condition of the testes of birds singing in autumn. It is likely, however, 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. This has, for instance, been observed in the European Starling, a species that is normally single brooded (Heinroth 1928).

The song during autumn migration and during the stay in the winter quarters has not yet been studied very intensively, but so much is certain that the weather influences its occurrence. In the winter quarters song appears not to be connected with fighting. A psychological interpretation of this phenomenon is certainly premature as long as more detailed observations are lacking.

Next the song of those species that have winter territories may be considered. These species form special cases, not to be treated like those birds that live gregariously and lack winter song. We possess several good descriptions of species with winter territories: the English Robin (Burkitt 1924-26), the Loggerhead Shrike (Miller 1931), the Song Sparrow (Nice 1933), the Mockingbird (Michener and Michener 1935), and the Wren-Tit (Erickson 1938). In the English Robin, the Loggerhead Shrike, the Mockingbird, and the Wren-Tit both male and female defend their winter territories and in all of them the female gives the male song more or less regularly during winter, or at least gives very similar calls.

It is not known whether song and territorial fighting are the only reproductive activities displayed by such birds (other less conspicuous sexual activities may often escape attention), nor whether the gonads of winter-fighting and winter-singing birds are somewhat progressed. As it seems to me that both these assumptions are rather improbable, I might suggest that in these species song is dependent on other internal and external causes than in those species lacking winter territories. Investigations directed especially toward these problems are certainly needed.

Even in those species that exhibit a typical advertising song and in which increase in song activity and gonadal progression apparently run parallel, song is often uttered on occasions when neither gonadal activity nor the absence of the female can be the immediate cause. For instance, birds that have just had a narrow escape from an attacking hawk, or birds that are alarmed by an owl or a fox, often utter song of great intensity. As has been worked out elsewhere (Tinbergen 1939b) there is evidence in favor of the interpretation of such cases as substitute activities, arising in situations where the reaction that is evoked by the circumstances is either blocked or exhausted. For a fuller discussion the reader may be referred to the original paper.

The Functions of Advertising Song

On this question there exists not nearly so much diversity of opinion as on the problem of the causes of song. The most important function of advertising song no doubt is, in most species, the attraction of a mate from afar. A strong support of this supposition is the fact that song is always most intense in unmated birds. In the Snow Bunting, this connection of song with the unmated status is so extreme that a mated male will instantly sing when he perceives that his mate is absent. As a female often temporarily leaves its mate, such an observation can be made several times a day.

Those authors who have intensively studied one single species with a conspicuous advertising song all agree that it must have an attracting influence on the other sex. In very few instances, however, is this opinion based on conclusive evidence, such as natural or artificial experiments. Strong supporting observations have been made, *e.g.,* on the Turkey (Heinroth 1910), the Blue Heron (Verwey 1930) and the Northern Phalarope (Tinbergen 1935).

It is generally assumed that song may have another function, *viz*: that it repels individuals of the same sex. Although convincing observations or experiments are few, several authors give supporting evidence. Often, for instance, neighboring males react to each other's singing, and regular song duels may result, the opponents alternating in outbursts of song (see *e.g.* Erickson's account of the Wren-Tit, 1938). This shows at least that the advertising song has an influence on another territorial male.

The advertising song of a male Snow Bunting may have different effects on another male, dependent on the condition of each. A singing male has a strong challenging influence on another male when on its own territory, for it is much more vigorously attacked than all other birds, as was described on p. 17. For a male that is outside its own territory, the song of another male is the cause of all kinds of avoiding behavior; dependent on the circumstances, he either crouches or flees. Both results, challenge and flight, tend to support the effect of other territorial behavior, and song, therefore, certainly has a function in the prevention of overcrowding.

Our conclusion as to the function of advertising song is, therefore, that it serves to attract potential mates from afar, and to warn off rivals. With some species the first function may be the more important, in others the second. 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 premating 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.

After this short statement of the functions of advertising song, a more complete definition may be proposed that contains some description of these functions: *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.*

It will be clear that a closer study of song in different species, when special attention is given to causes and functions, will reveal many cases where song does not fit this definition. I may point again to the instances given at the beginning of this chapter.

Special mention should be made of sub-song, a term introduced by Nicholson (1929). This author does not give a sufficiently sharp definition, and in my opinion, includes under this term several different phenomena, agreeing only in so far as they resemble true song, but are softer. The warbling song of the young birds as well as the incipient song of the adults in early spring or autumn are entitled sub-song. It seems to me that, before putting such insufficiently studied phenomena together under a common name and thus prematurely introducing a new conception, many more facts will have to be collected.

This treatise on the questions of fighting, territory and song has been purposely kept highly schematic. Many detailed questions have been omitted. Due partially to my imperfect knowledge of the vast literature on these subjects, it has been done rather with the intention of focusing attention on these problems that appear to be of fundamental importance. I should like to stress again the fact that my conclusions apply only to part of the complex of phenomena that commonly are entitled fighting, territory and song, and that, in order to designate special categories, the concepts of sexual fighting, sexual territory, and advertising song were developed. Many related phenomena are left undiscussed.

Research in this maze of detailed questions suffers from lack of organization of the problems. To stimulate this organization by proposing a first tentative step, not to dictate its form, has been the aim of this discussion.

IV. SUMMARY

Daily observations of the reproductive behavior of Snow Buntings in East Greenland were carried out from the end of March until the middle of July, 1933, with the main purpose of studying the problem of territory. The facts collected during this time, though fragmentary owing to several restrictions, were considered to be of sufficient interest to justify a general discussion of the territory problem. Observations of a more occasional nature, bearing on other problems of bird behavior, are mentioned and discussed partly in the descriptive section, partly in special chapters. Of these questions, only that of the discrimination of the other sex will be summarized below.

Fighting, Territory and Song

The words fighting, territory, and song have been used to denote more than one concept each, as there are several kinds of fighting, several kinds of territory and several kinds of song. In this paper, Howard's conception of territory is defined as sexual territory, the fighting reactions by which a sexual territory is settled are called sexual fighting and the song of territorial birds is called advertising song.

The differences between these types of fighting, territory and song and other types are discussed.

Since the causes of a bird's reaction cannot be sought in a knowledge of the reaction's function on the part of the bird, causes and functions of the discussed behavior patterns are treated separately.

Little is known about the internal causes of the periodicity of sexual fighting. The external causes of the reaction are different for male and female and for different species. It is shown that many birds not only fight in their territory alone, but that the presence of a mate may urge them to fight outside the territory. In some species sexual fighting is independent of territory, and depends entirely on the sex partner.

The general function of sexual fighting in birds and in other animals is the defense against sexual competitors of something that is indispensable for reproduction. This something may be a territory, a mate or some other object; in the Bitterling it is a mussel that serves as a host for the parasitic eggs.

The function of a territory in many Passerines is the reservation of a certain amount of food in the immediate vicinity of the nest, which enables the parents to brood the newly born young at sufficiently short intervals. Many of the arguments found in the literature about the food value of territory are irrelevant. The functions of other types of territory are only known in some few instances, and may be quite different.

It is argued that the word "song" applies to a great variety of different phenomena, and that a further analysis demands the discrimination of different types of song. The type called advertising song is discussed and defined. Böker's views about the causes of advertising song are rejected, and a close connection with gonadal progression must be assumed.

With most species advertising song has the double function of attracting potential sex partners and of warning off sexual competitors; with some of these species the first function will be the more important, with others, as the birds with winter territories, the second function prevails.

Although several of these questions and conclusions have been expressed in the literature in some form, the author believes that these have been formulated too vaguely and that further analysis is possible only by defining conceptions as clearly as possible. His discussion is intended to be a step toward a sharper definition of problems and toward a reorganization of the separate questions. For this reason, the chapter on territory has, in many respects, more the character of a program than of a conclusion.

Discrimination of the Other Sex

In many species of birds and animals, a male in sexual condition responds to approaching males in exactly the same way as to approaching females. There is evidence for the conclusion that this first reaction has a neural coupling with a sense impression of a very vague nature, built up of only a few recognition marks. Slight differences in the intensity of the first reactions to males and females respectively cannot be explained satisfactorily as long as further data are lacking.

New stimuli of a more special nature are required for the next reaction of the male. This next reaction is always different, dependent on the sex of the other bird. The recognition marks that enable the bird to discriminate between the sexes in this phase of mating behavior are different for each species. They 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.

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LIST OF NAMES OF SPECIES MENTIONED IN THE TEXT

Invertebrates

Mussel, Freshwater—*Anodonta spec.*
Great Diving Water Beetle—*Dytiscus marginalis* L.
Cuttlefish—*Sepia officinalis* L.

Fishes

Acara, Blue—*Aequidens pulcher* (Gill.)
Bitterling—*Rhodeus amarus* (Bl.)
Fighting Fish—*Betta splendens* Regan
Jewel Fish—*Hemichromus bimaculatus* Gill.
Stickleback, Three-spined — *Gasterosteus aculeatus* L.

Reptiles

Fence Lizard — *Sceloporus undulatus* (Latr.)

Mammals

Fox, Arctic—*Canis lagopus* L.
Deer, Red—*Cervus elaphus* L.
Hermine—*Mustela erminea* L.
Moose—*Alces alces* L.
Musk Ox—*Ovibos moschatus* (Zimm.)

Birds

Avocet, European—*Recurvirostra avosetta* L.
Bishopbird—*Euplectes h. hordeacea* (L.)
Bittern, European Great—*Botaurus st. stellaris* (L.)
Blackbird—*Turdus m. merula* L.
Blackbird, Redwing—*Agelaius ph. phoeniceus* (L.)
Bluebird—*Sialia sialis* (L.)
Bunting, Corn—*Emberiza c. calandra* L.
Bunting, Reed—*Emberiza sch. schoeniclus* (L.)
Bunting, Yellow—*Emberiza c. citrinella* L.
Chaffinch—*Fringilla c. coelebs* L.
Chiffchaff — *Phylloscopus c. collybita* (Vieill.)
Crow, Carrion—*Corvus c. corone* L.
Curlew—*Numenius a. arquatus* (L.)
Duck, Musk—*Cairina moschata* (L.)
Falcon, Peregrine — *Falco peregrinus* Tunst.
Flycatcher, Spotted—*Muscicapa str. striata* (Pall.)
Fowl, Jungle—*Gallus gallus* (L.)
Gannet—*Sula bassana* (L.)
Godwit, Black-tailed—*Limosa l. limosa* (L.)
Goldcrest—*Regulus r. regulus* (L.)
Grebe, Great Crested—*Podiceps cr. cristatus* (L.)
Grebe, Little—*Podiceps r. ruficollis* (Pallas)
Greenfinch—*Chloris chl. chloris* (L.)
Grouse, Ruffed—*Bonasa u. umbellus* L.
Guillemot—*Uria aalge hyperborea* Salomonsen
Gull, Herring—*Larus a. argentatus* Pontopp.
Harrier, Montague's—*Circus pygargus* (L.)
Harrier, Hen—*Circus cyaneus* (L.)
Hawfinch—*Coccothraustes c. coccothraustes* (L.)
Hawk, European Sparrow—*Accipiter n. nisus* (L.)
Heron, European Blue—*Ardea cinerea* L.
Hobby, *Falco s. subbuteo* L.
Jackdaw—*Coloeus monedula spermologus* (Vieill.)
Jay, European—*Garrulus g. glandarius* (L.)
Kestrel, European—*Falco t. tinnunculus* L.
Lapwing—*Vanellus vanellus* (L.)
Lark, Prairie Horned—*Otocoris alpestris* (L.)

Longspur, Lapland—*Calcarius l. lapponicus* (L.)
Manakin, Gould's—*Manacus v. vitellinus* (Gould)
Merlin—*Falco columbarius aesalon* Tunst.
Mockingbird—*Mimus polyglottus leucopterus* (Vig.)
Moorhen—*Gallinula chl. chloropus* L.
Nighthawk, American — *Chordeiles m. minor* (Forster)
Nightjar—*Caprimulgus eu. europaeus* L.
Oriole, Baltimore—*Icterus galbula* (L.)
Owl, Snowy—*Nyctea scandiaca* (L.)
Parrakeet, Shell—*Melopsittacus undulatus* (Shaw)
Phalarope, Northern—*Phalaropus lobatus* L.
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Robin, English—*Erithacus rubecula melophilus* Hart.
Rook—*Corvus fr. frugilegus* L.
Ruff—*Philomachus pugnax* (L.)
Sandpiper, Purple — *Calidris maritima* (Brünn.)
Shrike, Great Gray—*Lanius c. excubitor* L.
Shrike, Loggerhead—*Lanius ludovicianus* (L.)
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Skua—*Catharacta s. skua* Brünn.
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Snipe—*Capella g. gallinago* (L.)
Sparrow, Henslow's — *Passerherbulus henslowi susurrans* Brewster
Sparrow, Mississippi Song — *Melospiza melodia euphonia* (Wetmore)
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Stork, White—*Ciconia c. ciconia* (L.)
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Warbler, Garden — *Sylvia b. borin* (Bodd.)
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Warbler, Great Reed—*Acrocephalus sc. scirpaceus* (Herm.)
Warbler, Willow—*Phylloscopus tr. trochilus* (L.)
Warbler, Wood—*Phylloscopus s. sibilatrix* (Bechst.)
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