

BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. VII

JANUARY, 1936

No. 1

THE FUNCTION OF SEXUAL FIGHTING IN BIRDS; AND THE PROBLEM OF THE ORIGIN OF "TERRITORY"

By N. TINBERGEN

THE problem of the function of "territory" originated as the problem of the function of fighting of male birds in spring. This question was first raised by Darwin. It was Darwin who concluded that the fighting of male birds in spring was "over the females", and that a female would choose a strong and victorious male in preference to a weak male to mate with. Doubtless this hypothesis was originally intended to interpret the *function* of the fighting, not to serve as a psychological interpretation of the motives of the fighting males. Owing to the position of psychology at that time, Darwin's formulation, and perhaps his conclusion itself, were not so cautious as to be particular on this point.

Howard's theory of the "territorial" function of the fighting was in some respects a reaction from the Darwinistic explanation. It became impossible to assume that the males fought "over the females" because the fighting begins when the females are still absent. This, it should be noted, is a psychological argument. Territory, however, is present from the beginning of the battles, and therefore Howard(1), seeing a correlation between fighting and "settling on a territory", concluded that fighting was "for territories."¹ In the course of his argument Howard passes from a psychological to a functional interpretation, and considers the securing of a territory to be the only function of fighting. It is my opinion, that considering the function of fighting, the new interpretation is just as incomplete as the former one.

Psychologically speaking, that is, seeking for the motives of the fighting bird, and for the circumstances which stimulate and direct its fighting, both formulations are uncritically expressed, and it is therefore difficult to discuss them. What is "fighting for" something? The expression "fighting for" or "fighting over" implies a hypothesis about the state of a bird's mind which has failed as a basis for the interpretation of many facts of bird behavior known

¹"The males do not fight over the females; they fight for territory." M. M. Nice in: *Fifty Years Progress of American Ornithology*. 1933.

at present. When no special psychological background is accepted, the expression ought to be more sharply defined; otherwise it is too vague a term to permit discussion.

As Howard's hypothesis tries to explain the function of fighting, and a satisfactory formulation has not yet been found (many facts do not fit in with Howard's scheme), another formulation about the function of the fighting will be discussed here. Therefore it will be necessary to discuss fighting first, in order not to focus attention on territory at once. It is the fighting that is the observed fact: territory as a function of fighting is the hypothesis.

That the attention was concentrated on the defense of a territory as the only, or at least the main, function of the fighting, is largely due to the fact that comparison, which is so important an aid for functional interpretation, was restricted to birds only, and even to rather few kinds of birds. It is, however, necessary to compare bird-behavior with corresponding behavior among other animals. It is seen, then, that there occurs much fighting between members of one sex in many kinds of animals, culminating in the period of the formation of pairs. It is this kind of fighting which reaches its maximum intensity before and during mating, that was considered by Howard. That he did not sufficiently exclude the defending of nest and young against predatory animals, has been emphasized by Lack (2), with whose criticism I quite agree, so far as this point is concerned.

Before considering the function of special cases of fighting, it is necessary to agree on the way to determine it. The function of a process must be judged by the effect it has. Now the fighting in spring is never fighting under all circumstances but it is always spatially restricted; that is to say, fighting is restricted to the vicinity of something. The animal does not merely fight; it remains at the same time in the neighborhood of something, and along this line "defense" originates. When we see that the fighting is always exhibited in the presence of some particular object, then it is undeniable that the fighting has the effect of assuring the possession of that object and we conclude that the fighting has the function of assuring its possession for the fighting animal.

Now when we find evidence of fighting outside the territory, or even independent of the presence of a territory, we cannot assume it to be a case of fighting for territory. We are not able to see its function in assuring of territory. In a comparative review of fighting behavior before or during pairing (which I will call "sexual fighting"), many instances appear in which fighting is not restricted to territory, and is even independent of territory. The latter case is, so far as I know, not known among birds; and an explanation of this curious fact will be given farther on. The former case, however, of fighting which is not restricted to territory, does indeed occur.

In some species of birds, fighting is not restricted to a special

territory, but also occurs at many places outside it. Instances are the Great Crested Grebe, Huxley (3); the Avocet, Makkink (in MS.).

Secondly, in most "territorial" birds, it often happens that a male that has settled on a territory fights outside of it under special circumstances. One of these is that a female, having no idea of the borders of the territory of its mate (which is often the case), goes outside it. Sometimes the male will follow her into strange territory. Here they will be attacked by the owners of that territory, and then the male will fight the strange male. This he will never do as long as both of them are unmated. In other cases an unpaired male crosses its own borders to visit the female of its neighbor. Upon being attacked by the latter, he will often fight; if there is no female, he will not fight, but will flee. Instances of both cases are reported by Howard himself; furthermore, I have observed several instances in the Snow Bunting.² Here the males fight in presence of the female while temporarily deserting the territory.

Thirdly, in many species the females also fight. Now, in the Snow Bunting, the female does not know the borders of the male's territory, and often trespasses outside of them; Brock (6) describes the same occurrence among Willow Wrens. Nevertheless, the female Snow Buntings fight furiously. They attack almost exclusively other females.³ The females fight only in the presence of the males. The function of this fighting of the females, therefore, cannot be sought in the defense of territory alone, for it results in securing a mate, as they do not allow another female to come near the male. To a certain degree, however, their fighting helps in defending the territory, because the females remain in the neighborhood of their mates, and these remain in their territories.

Territory alone fails to explain these instances of fighting. Fighting before and during mating occurs, as remarked above, in many species of animals besides birds. Some few instances will be mentioned.

A very interesting instance is the fresh-water fish *Rhodeus amarus*, a species which lays eggs in the gills of the mussel *Anodonta cygnæ a*. In the spring the male settles in the neighborhood of a mussel, and fights furiously against other males of the same species, thereby actually "defending" this mussel and remaining in its immediate vicinity. It does not matter that the mussel is constantly moving about; the fish is connected with it and not with a certain topo-

² The Snow Bunting, which I had opportunity to study intensively, is a strictly territorial bird, notwithstanding the opinion of Mrs. Nice (4), which was based on the observations of Nicholson (5). Nicholson's observations were made at the end of the reproductive season, on individuals which were collecting food for their young. In this stage many birds collect food outside their territories, in places where they seldom fight.

³ Howard, defending his view on the function of fighting, calls attention to the fact that not only males fight males, but pairs fight against pairs, and argues that the function of those latter fights cannot be anything else than defending the territory. In the Snow Bunting, all fights between pairs are in reality double fights, one of male against male and another of female against female. This makes a considerable difference!

graphically limited area, Wunder (7). It is impossible to speak of territory here, as the area covered constantly changes.

The sexual fights of many Ungulates, of which the Moose (*Alces alces*) will be taken as an example, is not connected with territory. The fighting of the male Moose is restricted to the vicinity of his herd of females and is independent of the actual place in which they stay at the moment of the encounter. The area in which he attacks a strange male, and which moves about with the females, is much smaller than the ground they are moving about in in the pairing season. Although the latter is also a rather limited area, it is not a territory in the sense of Howard's concept, *as it is not defended*. Here we feel the lack of that strict definition which Howard has failed to give. Farther on a definition will be discussed.

These few instances will suffice to show that fighting in the pairing season has not always the effect of securing a territory. In the two cases mentioned above, there is a connection with other things (mussel, female) only; in the case of the birds there is a connection with territory, and *a connection with the sex partner besides*.

Another method by which we can trace objectively the function of fighting is to look for common characters in all individuals that are attacked by the fighting bird; for the attacked birds are competitors in some respect.

Here, however, one restriction must be made. The fighting bird has, without any doubt, an inborn disposition to react on special kinds of birds by driving them off. This disposition reacts on the visual stimulation, as birds recognize other birds in the first place by sight. We can expect, therefore, reactions on birds which are not competitors, but which are "mistaken" for the real competitor, owing to optical resemblance. Such "errors" are known to every field observer, not specially in the case of fighting birds, but more often in the case of the discrimination of a bird of prey (for which Swifts and Pigeons are often taken by birds), or of the discrimination of parent birds by young, etc.

The same may apply to auditory orientation, although I cannot now cite any instances.

Applying this method and looking for common characters in the attacked birds, we find puzzling facts which do not exactly fit in with the scheme of birds defending territories alone. For instance, in the great majority of species, males fight against males, and females against females. As territory-competitors, for a male, strange females are as bad as strange males.

By comparative observation we find in various species a great many different objects "defended" against competitors. We conclude that an object is "defended" when we see the fighting restricted to its vicinity. *It is well to emphasize that our knowledge of these objects is no hypothesis, but a fact*. When we consider these objects, they all appear to have one character in common: they are, without

any exception, necessary for the successful accomplishment of reproduction. *The fighting before and during the formation of sexual bonds, therefore, serves to secure objects or situations which are indispensable for reproduction.* A closer definition cannot be given without excluding many facts known.

This situation is different for different species, according to their ecological needs. In most birds, territory is included as one element in this situation, as a consequence of their laying in a certain place, eggs which have to be incubated in that same place. In most birds, the sex partner is another element of the situation. In the Moose, the sex partner is the only element. In *Rhodeus*, the mussel is one element, the female another one.

Let us now consider the case of birds more closely.

In many species, as was remarked above, the females do a certain amount of fighting. This occurs especially in monogamous species. The fighting of these females may be, as it is the case in the Snow Bunting, and certainly in many other species too, independent of territory, and dependent on the sex partner only. In the Snow Bunting, it is indirectly connected with territory: the female remains in the vicinity of the male, leaving him for short excursions only, and as the male remains in his territory, the female remains there too. The fighting of the females, and, less exclusively, the fighting of the males, here serves as a means of establishing monogamy, and monogamy is biologically most important in connection with the rearing of young.

A definition of "territory" is necessary when it has to be discussed. Howard does not give a definition, and many of his critics have also forgotten to define it; and as the meaning of the word "territory" in daily life is much wider than in Howard's discussion, the word has been applied to many territories of quite another kind. It will appear from what I have said that in my opinion *we must define "territory" as an area which is defended by a fighting bird shortly before and during the formation of a sexual bond.* This definition does not differ essentially from Ernst Mayr's definition, which runs: "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." (8). I have two objections to Mayr's definition: First, in some species, it is the female that secures territory (Phalarope), Tinbergen (9) and second, no reference is made to the fact that the territory is established shortly before and during mating, though Mayr expresses this indirectly by a reference to some courtship actions by which the birds make themselves conspicuous. This behavior runs parallel with the mating behavior, and it appears, therefore, that no essential differences exist between both formulations; I consider my formulation to be the more direct, and therefore prefer it to Mayr's.

A territory in this sense (which is certainly identical with the

"territory" Howard had in mind) occurs in many more species of birds than is recognized. In their criticism of Howard, the Lacks speak of "colonial birds" as opposed to "territorial birds." This is based on observations of Bertram and Lack on Guillemots, which are observed "to brood each other's eggs and young indiscriminately." (10). This, however, does not imply, that "territory" does not exist among Guillemots, but only that the orientation of the Guillemot is such as to make errors possible. I suppose, judging from comparable observations on Terns, that a Guillemot which is incubating on a wrong nest will defend this nest against trespassers, because it considers the egg which it is incubating as its own. My own observations on a colonial bird, the Herring Gull, show that every pair has a strictly defined territory which is defended against other Herring Gulls, especially by the male, but to a certain degree by the female also. Males fight with males principally, and females with females. In Terns the case is nearly identical; every pair has a territory around its nest. In Huxley's film of the Gannet, incubating birds are seen pecking at trespassers which come too near the nest; fights between neighbors seem to occur regularly. *A colonial bird may be just as territorial as a solitary bird.*

The territory that plays a part in the sexual life of birds is by no means of the same importance and significance in different species. It remains one of Howard's many merits, that he has clearly shown that the value of the territory in one species of bird is very different from that in other species. That he could not give more than tentative suggestions was due to a lack of knowledge about the ecological needs of most birds, a lack of knowledge which still exists in nearly the same degree. Still, careful observation has made a rough analysis possible in some cases. In the Grey Heron, for instance, the territory is a place where a nest can be built, Verwey (11); a territory of a Kestrel is a place where a nest is present, L. Tinbergen (12); in Howard's Buntings, as well as in the Snow Bunting, the territory must contain not only a nesting-site, but surely something more, and the question of the food for the young certainly is of importance, though it is yet impossible to see its exact value.

Although, in the case of birds, the area in which the nest will be built is always included in the "defended situation," it is quite possible that the sex partner in some species is a more important element than the territory. Such a state could be recognised by the greater amount of "free fighting," of fighting occurring outside the territory but in the presence of the sex partner. In the Snow Bunting, and doubtless in many other truly territorial species, those "free fights" are rare, and the bird always shows much hesitation before it crosses its own boundaries to follow its mate (which, having no knowledge of these boundaries, often crosses them) and fights outside the territory.

In other birds, the concentration of the fights within the limits of the territory is much less complete, as for instance in the Northern or Red-necked Phalarope (where the female does the fighting) and, according to Huxley (13) in the Black-tailed Godwit. In other species, again, it apparently is difficult to discover any connection between fighting and territory at all; this connection I believe to be questionable in the Great Crested Grebs, Huxley (3) and in the Avocet, Makkink (in MS.). This can be concluded, as was explained above, from the great number of free fights. The result in these cases is a rather vaguely defined territory. That a territory results at all is caused by the fact that the bird concentrates its activities around a certain topographical center (the place of the future nest). The difference with the strictly territorial species, which do so likewise, is that in the latter no strange bird of the same species and sex is tolerated within the area in which the bird fights, whereas in the former it is not so much the fact that the strange bird is on the territory which urges the attacking bird to fight as that the strange bird comes, for instance, into the vicinity of the female. It is, therefore, *a priori* possible that such an ill-defined territory contains no essential factor for reproduction, but that it is an unessential by-product. To find these cases, however, the available methods seem to be inadequate.

The fact that the significance of "territory" as the function of the sexual fighting in birds has been overemphasized has several reasons. Firstly, the origin of the territory theory as a reaction from the Darwinistic interpretation caused an over emphasis on the other side. Secondly, the function of the fighting in many species of birds is really the securing of a territory in the first place, for a reason which has been pointed out above. Thirdly, the situation in many birds shows a complication; though the fighting shows functional connection with the sex partner, it may begin when the latter is still absent. But as the female is attracted only by a male in full sexual condition, and a male in full sexual condition has a territory, a territory is, to the male, a "potential female;" it is absolutely the same (functionally), if a female is present in the territory at once, or if it will be present after some time. Howard's objection to the Darwinistic interpretation was a psychological one: he could not assume that the males could be induced to fight for something absent. The functional connection between fighting and the sex partner here takes a roundabout way. Owing to a bird's living in the present and not in the future, such a roundabout way is psychologically impossible. After the arrival of the female, however, the behavior of the male shows, not only the functional, but also the psychological connection with the female, as he is stimulated by her presence to fight in places where he would otherwise withdraw.

To summarize: It is argued that the problem of territory is in origin the question of the function of sexual fighting, that is,

fighting shortly before and during the formation of sexual bonds. Objections are made to the overemphasizing of territory as the function of sexual fighting. The fighting does not occur in the presence of the territory only, but in several cases in the presence of the sex partner, which is "defended" in much the same way. Further comparison with other animals shows, that sexual fighting may often occur without any connection with territory. In birds, this does not occur, owing to the fact that birds lay eggs which have to be incubated at one and the same spot; therefore fighting, if occurring at all, has always a connection with territory.⁴ In general, it must be said that the sexual fighting in all animals serves to secure one or more objects or situations which are necessary for reproduction. These objects are generally a territory and a sex partner. In the case of many female birds, the object is primarily the sex partner; in most cases of male birds territory and sex partner both are included. When both sexes fight, monogamy is promoted, which is of great importance to the rearing of the young.

It has not been my intention to write an elaborate treatise on the subject, though this certainly would be necessary to fill up many gaps; my intention has been only to point out several causes for the unsatisfactory formulation of the actual problem about "territory." It is caused by a vague formulation of the original question, by the lack of definitions of discussed concepts, and by the fact that the problem has drifted away from the function of fighting to the meaning of territory.

Zoölogical Laboratory, Leiden, Holland.

LITERATURE CITED

- (1) Howard (1920): *Territory in Bird Life*, London.
- (2) Lack (1933) in: *Brit. Birds*, 27.
- (3) Huxley (1914) in: *Proc. Zoöl. Soc.*, London.
- (4) Nice (1935) in: *Bird-Banding*, 6.
- (5) Nicholson (1930) in: *The Ibis*, 12, VI.
- (6) Brock (1910) in: *Zoölogist*, 14.
- (7) Wunder (1933) in: *Zoöl. Anz. Suppl.*, Band 6.
- (8) Mayr (1935) in: *Linnean Soc. of New York*, 45, 46.
- (9) Tinbergen (1935) in: *Ardea*, 24.
- (10) Bertram and Lack, (1932) cited after Lack (1933).
- (11) Verwey (1930) in: *Zoöl. Jahrb. Allg. Zoöl. u. Physiol.*, 48.
- (12) Tinbergen (1935) in: *De Levende Natuur*, 40.
- (13) Huxley (1926) in: *The Ibis*, 12, II.

⁴ It is possible that, in birds which pair before settling on a territory, sexual fighting occurs only in the flock, and then misses the connection with territory. I know of no instance which has been studied satisfactorily.