

THE SIZE AND MEASUREMENT OF TERRITORY IN BIRDS

By HERBERT FRIEDMANN¹

EVER since H. Eliot Howard brought the concept of the breeding territory clearly before ornithologists its usefulness in understanding and interpreting the behavior of individual birds has increased in direct proportion to the number of students working intensively on life-history problems. In fact, so useful has this concept proved to be, that even if it were not based on a factual foundation it would still be worth keeping as a working hypothesis. A great mass of data was produced by Howard in support of his concept, and since the publication in 1920 of his book "Territory in Bird Life" a still greater amount of new data has been collected and put on record. The subject is one of intense interest to all students of bird behavior, and it is the purpose of this paper to attempt an analysis of one aspect of what has been learned of territorialism generally, the size of territories and the measurement of that size.

The idea of territory has always been looked upon as a matter of spatial dimensions. Thus, a certain bird with a given food-habit might need a large area to supply its wants and those of its young, while another species might need only a fraction of the geographical area occupied by the first one. Hence, the size of the territory varies with the species, and, to a lesser extent, within the species. Some forms, particularly sea-birds such as Gannets, Murres, Auks, etc., that nest on rocky ledges of sea-bound islets and have in common the foraging ground of the surrounding waters, have practically no individual spatial territories, the nests sometimes being so close together that the sitting birds actually touch one another. Still, while no bigger than the nest it contains, the territory of each bird is at least a theoretical reality; the relatively small number of nests containing mixed clutches of eggs speaks for the individuality of the breeding sites. Furthermore as intimated above, the concept of territory is so useful in correlating what would otherwise be isolated fragments of behavior that it behooves us to grant territoriality even in such extreme cases as these sea-birds, rather than to take the opposite view.

However, territory is not merely a matter of space-extension; it is also a matter of time-duration. The same spot cannot

¹Published by permission of the Secretary of the Smithsonian Institution.

serve as a breeding territory for two pairs of a species simultaneously, but may well do so if one pair comes after the other is gone. Hence it follows that the measure of a territory must be made in space-time units and not in those of space alone. The territory is the unit of local distribution just as the cell is the unit of biological structure, but in distributional data the factor of population numbers of a given species is correlated with the total of all the individual territories of that species in any given area. Hence it follows that if the actual geographical ranges of two species be wholly coincidental, and if in one of the two birds the same actual spatial areas may be used twice in a season as territories, while in the other they may be used but once, the former species has, to all intensive purposes, in a comparative sense, twice the distribution of the latter. We must distinguish between the meaning of distribution in the biology of the bird and in the statistics of the zoögeographer. Unfortunately the two are quite dissimilar.

Just as we find the size of the breeding territory varies in different species, so, too, we discover that the length of time the territory is occupied differs in different kinds of birds. On the whole, the time-duration of a territory in the case of the average small altricial bird is equal to the time of nest-building plus that of egg-laying plus that of incubation plus the nest life of the young plus at least a few days after the young leave the nest. Probably, to be more accurate, we should add on a few days at the beginning between the acquisition of the territory and the inception of nest-building. In precocial birds, on the other hand, such as ducks, gallinaceous birds, and some limicoline forms, the territory has a different time-duration; in these it is equal to the time of nest-building (which is sometimes negligible) plus that of egg-laying plus that of incubation and occasionally plus a few days after the young hatch out. The fact that the territory as such does not come into existence until very shortly before nest-building commences, in many species, is indicated by the non-individual territorial aspects of the "dancing-grounds" or "tournament-fields" of some gallinaceous birds, such as the Blackcock, or some shorebirds, such as the Ruff, etc. In these birds the courtship and securing of a mate are done, not in an individual territory, but in a common, gregarious playground. Furthermore, inasmuch as the incubation and nestling periods differ in various birds, it is obvious that the time-dimensions of the territories vary accordingly. In the case of birds that use old nests already present, the time-duration of the territory is shortened accordingly; in the case of parasitic birds in which the territorial complex has been studied, as in the Cowbirds, the time-duration is

rather peculiar in that it is equal to the time required for the nest-building and egg-laying periods of the victims, plus a few days over, but not including the total period of incubation, to say nothing of the nestling period. This last special type of time-duration appears to hold true for some of the Cuckoos of the Old World as well. Thus, Chance, Rey, and others have found that the European Cuckoo (*Cuculus canorus*) finds its victims' nests by watching them build. If the nests are destroyed and new ones built to replace them, the parasite continues to lay (in this way Chance was able to get over twenty eggs from one Cuckoo in one season), whereas ordinarily the parasite would stop laying after the nests of its particular host species had reached the incubation stage. The reason for this is that with the end of the egg-laying period of the victims the Cuckoo's territorial instincts begin to diminish and finally disappear. It is then that a second Cuckoo may invade the territory of the first one.

Thus, to summarize the facts outlined so far, we have a great many possible combinations of component parts of the life-history of a given bird, any one of which may be reflected in the dimensions (spatial and temporal) of its territory. It follows then that all territories are not necessarily comparable as they are not all based on the same ethological materials. But the end is not yet; a further complication awaits our attention. This has to do with the consideration of the territory of a pair of birds as a summation of, or as a compromise between, the individual territories of the two individual birds comprising the pair. Howard, Selous, and others have given many instances in which the territories of the male and of the female were not altogether identical; in fact, in most of our passerine birds that have been studied intensively the time-duration of the same identical spatial territory is different for the male and the female. The male usually arrives first in the spring and establishes the territory, which, therefore, has an earlier time-limit for him than for the female arriving later. Just as here we have the two sexes differing, with respect to territory, in time-dimensions, so we have numerous cases where the difference is in spatial terms. Thus, in tropical East Africa, a long-tailed Widow-bird, the Jackson's Whydah, (*Drepanoplectes jacksoni*), presents a striking example. Here the male makes a little individual dancing-ground, a small circle of depressed and trodden grass in a field of tall upright grasses. He remains in this little area and does all his courting displaying in it, until he has secured one or more mates. The important point for our immediate problem is that the location of the dancing territory bears no relation to the actual breeding

territory (including the nest-site) of the female. Here we have a case where the breeding territory is really the territory of the female; the same situation may be found in the Bower-birds of the Australian region (*Ptilonorhynchidae*). The other type of condition is that in which the display ground of the male (the singing-tree of Mousley and others) coincides to a greater or lesser extent with the breeding territory of the female (including the nest-site). This is the type found in most of our small birds. Exceptions or marked modifications are by no means uncommon, however; we need only recall such birds as those in which the male never comes near the nest, Hummingbirds, etc., or those in which the picture is the same but with the sexes reversed, as in the Phalaropes. As far as our attempt to measure territories in quantitative space-time units is concerned, we have here two different problems. In the first type, the breeding territory is a single entity, the territory of the female; in the second type the breeding territory is a welding of the territories of the male and the female; in other words the type that we have come to look upon, through abundant personal contact and experience, as the "normal" type is really a compromised summation of two territories into one. This naturally results in an extension of the limits, both in space and time, of the resulting territory. It seems, from the fact that separate male and female territories are found chiefly in the "lower" groups of birds (gallinaceous, limicoline, etc.) with relatively few cases among the "higher" families, that the separate condition may be the older one. With the advent and development of accelerated hatching time, resulting in the altricial natal state, there may have come about a tendency to merge the territories of the two responsible parents. This is really beside our problem, but we must realize in any scheme of measuring territories that we are sometimes dealing with a single "primal" territory, and sometimes with a double, secondarily unified one. The degree of unification or merging is another variable factor that has to be considered.

The actual measurement of a territory of a given species, in order to be of value in a comparative way, will have to be made with all these variables in mind. The day is not yet here when our knowledge of enough such specific territories is sufficient to enable us to make any generalizations of more than temporary value. The first step to be made is to classify territories of species according to their basic nature; whether they are primal or secondarily unified territories is the first criterion to be judged. These two words may well be adopted in describing the territorial picture in any species, primal or merged. With this as a basis we may then state the time-limits in terms of the

parts of the reproductive cycle actually spent in the spatial confines of the territory. The spatial dimensions would have to be in some convenient measure, such as square meters or yards. Thus, we might measure a hypothetical territory and express our results as follows: "The territory of—— species is of the primal type and occupies approximately 500 square meters over a period of nest-building (2 days) plus egg-laying (6 days) plus incubation (28 days) plus 3 days after hatching (precocial); a total of 39 days," or, again: "The territory of —— species is of a merged type and occupies approximately 100 square meters over a period of courtship (6 days) plus nest-building (4 days) plus egg-laying (5 days) plus incubation (15 days) plus nestling period (11 days) plus 5 post-nesting days, a total of 46 days. The male alone occupies the territory for the first 4 days."

The probabilities are that some simpler, better method will be found as the measurements of territories in many birds are attempted; the plan given here is more in the nature of a suggestion than anything else. The main point of this paper is to stress the various combinations of factors (other than food, which is obvious) that have a resulting influence on the size of the territories, and to distinguish between them.

BANDING WILSON'S PETRELS

By SAMUEL A. ELIOT, JR.

To any one becoming interested in the possibilities of bird-banding, the following passage could not but be suggestive. It is from "The Story of a Bird-Lover," by W. E. D. Scott, a prominent ornithologist of the last century, and refers to August, 1881.

"With a fisherman I left Chatham, Massachusetts, very early one morning and by daylight we were far out at sea. A gun and ammunition were part of my equipment, and as occasional birds were seen in the distance I thought it worth while to begin my preparations. I saw an amused look pass over the captain's face as he said to me, 'Better wait till we get where the birds are; it will be easier to get 'em!' After two hours' sail—we were now out of sight of land—he announced that we had arrived on the fishing-banks, and that he would make a try. This seemed to be entirely foreign to the work I had come out to do, but I did not interfere. Without anchoring the boat, simply heaving to, he baited a couple of codfish lines and lower-