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THE RELATION OF ABUNDANCE TO TERRITORIALISM IN TROPICAL BIRDS.

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THE concept of territorialism has proven to be a most fruitful generalization in biology for classifying the behavior of many species. For numerous kinds of birds the previously inexplicable fighting behavior has been shown to have a definite relation to a piece of land, while in other species, the fighting in relation to the sex partner has been delimited from other defence reactions. However, this concept has been based almost entirely on studies of temperate zone birds; the hypothesis originated exclusively from the observations of temperate region birds (Altum and Howard). Now it seems desirable to compare the manifestation of territorialism in the temperate regions with the territorial behavior of the birds in the tropics. In this paper the writer will synthesize his experiences in Cuba, British Guiana, Argentina and Panama with the pertinent literature and with the general problems of tropical populations. I am indebted to Margaret M. Nice for several suggestions concerning the manuscript.

TERRITORY CONCEPT

The concept of territorialism, in brief, states that a piece of land which serves for reproduction is defended. Implicit in this concept is the assumption that the birds have something to defend the territory against, that is, either birds of the same species or of another species. Territorialism obviously can not be manifested unless the species is sufficiently common so that there is the necessity of defending the territory. Abundance then is a prerequisite, not for territorialism, but for our recognition of territorialism. Clearly if no defence of the piece of land is observed, the investigator can not state that a species is territorial.

The characteristics of populations, as regards abundance, are very different in the tropics from those in the temperate regions. It is a recognized generalisation that in the tropics there is a large number of species but a small number of individuals of each species. This condition, as interrogated by Nice (1933), clearly means that the defence of territory will not occur frequently if at all, and that our subjective criterion for territorialism is no longer useful.

At this point it seems desirable to digress to present quantitative data to indicate that there is a greater number of species in the

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tropical than in the temperate regions. Since bird populations are related to the vegetation, it is of interest to consider the number of tree species. Davis and Richards (1934) in their studies of the vegetation in British Guiana state that "the rain forest can be divided into a number of distinct types as widely different as the oak and beech woodlands of western Europe." These types and the number of tree species over four inches in diameter are as follows: Mora (60); Morabukea (71); Mixed (91); Greenheart (95); Wallaba (74). The mixed association, occupying the optimum habitat, is the climatic climax. In its association the greenheart tree is dominant, comprising 43.3% of the trees over sixteen inches in diameter. Now comparing this tropical region with a typical temperate region, the maple-beech association of Michigan, the author in unpublished work found that there were, in five large areas of somewhat different edaphic and historical conditions, a total of no more than sixteen species of trees with specimens over two inches in diameter, and that of these specimens the two species *Fagus grandifolia* and *Acer sacharrum* comprised 81%. To further emphasize the contrast between the temperate and tropical regions the data from Nigeria are of interest. Richards (1939) lists the number of species with specimens sixteen inches or over in diameter on a plot of 160,000 square feet. In a swamp association he found eleven species while in a mixed forest he listed sixteen species, as compared with 31 in British Guiana and 32 in Sarawak. Richards further states that the Nigerian forest is relatively poor in species. These data bring out the contrast between the tropics and the temperate regions in the number of species existing in an area.

After having considered the plethora of tree species in the tropics let us consider the number of bird species. Beebe (1925) compares the number of bird species in a limited area in British Guiana (Kartabo) with the number found in New York State, and finds that while the whole state of New York has 330 species including migrants, Kartabo has 464. To further emphasize the number of species in the tropics the data from Barro Colorado Island, Panama, may be cited. On this island, less than 4,000 acres in area, 251 species have been recorded to date (Chapman, 1938). These data show that in the tropics there are many more species than in the temperate regions.

To compare the number of individuals of the various species to the corresponding numbers in the temperate regions requires accurate census methods and as yet an accurate census of tropical birds has not been published. Of the few data available, Winterbottom (1936) found in Rhodesia 260 birds per 100 acres of second growth forest by a census method which is at best only a rough approximation. This can be compared with the figures given by Lack (1937) for forest temperate regions where the number of birds per 100 acres ranged between 32 and 561 in various parts of the

world. In spite of lack of quantitative data, it is the concensus of opinion among ornithologists that in the tropics there are many fewer individuals of each species. To summarize these data, it may be stated that it can be quantitatively shown that in the tropics there is a plethora of species, each consisting of relatively few individuals.

To return now to the problem of the relation of the abundance of a given species to the manifestation of territorialism, it is clear that unless the species is at least fairly common, territorial fighting will not occur. For there will be no necessity of defending the territory even though the territorial defence is one of the behavior patterns of the species.

OBSERVATIONS ON TROPICAL BIRDS

Field observations of tropical birds must be the basis for a discussion of the defence of territory. In Argentina Davis (1940b) studied the manifestation of territorialism in the Furnariidae, a neotropical family of many species and wide distribution. Several species studied in detail (*Schoeniophylax phrynganophila, Furnarius rufus, Coryphistera alaudina, Synallaxis spixi*, and *Pseudoseisura lophotes*) showed typical territorialism of the fringillid (*Melospiza*) type. The males of these species all acquire territory, defend it by singing and fighting, and maintain this territory during the nesting time. These studies were done in subtemperate regions (30° south latitude) but since this family is eminently tropical and the territorialism is so widespread within the group, being present in all five subfamilies, it seems logical to conclude that territorialism is a basic pattern in the behavior of this tropical family.

In British Guiana other observations indicate that in the true tropics territorialism is as widespread as in any temperate region. Such characteristicaly tropical species as *Synallaxis cinnamomea, Pitangus sulphuratus, Volatina jacarina* and *Lathria cinerea* showed typical criteria of territorialism, defence and song. *Volatina*, for example, sings from a low perch, jumping up a foot at each burst of song, giving rise to the local name of "bouncing bird." *Lathria* inhabits the greenheart forests where magnificent trees give the appearance of a cathedral. Each bird remains in a territory and sings the melodious clear notes, answering one another. A loud noise, such as banging on a tree, will stimulate a chorus of splendid song. If one bird encroaches on another's territory, it is at once threatened by song and driven out. As in other regions a small number of species lack territorialism or demonstrate a peculiar manifestation as does the communistic *Crotophaga major*.

All the species mentioned so far are relatively common and therefore do not truely show the condition of populations in the tropics, but do prove that territorialism is the usual behavior in tropical families and in tropical birds. The tropical birds which are typical

in that the species is uncommon, belong to these families and live under the same ecological conditions and therefore it seems logical to conclude that these birds also are territorial, although it may not be manifested to us.

The importance of song in the maintenance of territory is perhaps even greater in the tropics than in the temperate regions. For a species which is rare or even uncommon, song can serve as a means of attracting mates and driving away undesirable males. Song must be recognized as one of the means of defence of territory. It is particularly useful in the tropics and is as common there as in the temperate regions.

In order to emphasize the point that territorial species may not have the opportunity to show this behavior it is desirable to discuss the behavior of *Crotophaga ani*. This species (Davis, 1940a), although social nesting, is extremely territorial in Cuba, and also in British Guiana and Argentina. Yet at Saladas, Province of Corrientes, Argentina, where the species is uncommon, several widely spaced colonies never showed any indication of territorialism, although watched over a period of a week in the breeding season. This species does not even have a song to indicate territory. In British Guiana the species inhabits open areas which are in many cases isolated patches of savanna along the rivers. These open spots are frequently so small that there is only space enough for one colony of *C. ani* and there is no other colony for perhaps a mile. In these cases also, no territorialism is manifested because there is no opportunty to defend the territory. Thus an investigator would conclude from the evidence that the species was not territorial, an entirely erroneous conclusion as shown by studies in other regions.

DISCUSSION

The data cited above show that in the tropics territorialism is present but that it must be interpreted in a broad sense. Many species are represented by only a few individuals and therefore seldom have opportunity to show their territorial behavior. It may be argued that territorialism is a phenomenon only of abundant species; that uncommon birds do not show territorialism and never will. But this line of reasoning leads to the conclusion that territorialism has developed independently numberless times in many families and even within the same family, a conclusion quite contrary to our knowledge of the uniformity of behavior within a family. As a further point against this conclusion, it seems less likey that this territorial behavior has developed to nearly an identical type from many independent origins, than that the behavior is common to the whole group but only manifest in some.

The strict definition of territorialism, at present difficult or even impossible, is made more difficult by consideration of the situation in the tropics. For when considering uncommon species it becomes

necessary to say that the territory *would* be defended if there *were* another bird to invade it. Clearly then we see the futility of trying to define territorialism strictly. We must admit that the behavior shown by any species is a stage in the evolution of the species, just as is a morphological character, and can not be abstracted from its relation to other species. The concept of territorialism should be grouped with such concepts as 'species' or 'community', ideas which have no objective existence and therefore should not be strictly defined. A flexible characterization of these ideas permits the variations in behavior between species to be grouped under one concept.

SUMMARY

1. In the tropics there is a plethora of species, each consisting of relatively few individuals. Unless a species is fairly common, territorial fighting will not have an opportunity to occur and our objective criterion for the recognition of territorialism fails.

2. The theory of territorialism, developed from studies in temperate regions, must take into account the scarcity of birds in the tropics.

3. Field observations show that in the tropics many species manifest territorialsm in a typical manner. Since these species belong to tropical families it is concluded that territorialism is present even in species whose rarity does not permit our recognition of the behavior.

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