

THE EVOLUTION OF DIVERSITY IN AVIAN TERRITORIAL SYSTEMS

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WHAT are the conditions which facilitate or hinder the evolution of territoriality? No generally accepted solution to this problem has yet been found—perhaps because too specific an answer has been sought for too general a question. Instead, the *diversity* of systems of territorial and other aggressive behavior has come to be well appreciated, as evidenced in recent reviews of territoriality (e.g., Kuroda, 1960; Carpenter, 1958; Hinde, 1956), and the impossibility of providing a specific answer applicable to all types of territoriality is now realized.

Arguments over which are the primary selection pressures leading to certain types of territoriality continue, however, as shown in the recent contributions bearing on the “function” of territoriality by Stenger (1958), Wynne-Edwards (1962), Kalela (1958), Kuroda (1960), Peters (1962), and others.

The present paper offers a new orientation to the problem by presenting a general theory for the evolution of territoriality with special reference to its diversity among species. Since most of the previous theories have already been shown to be untenable or severely limited (see especially Carpenter, 1958; Tinbergen, 1957; and Hinde, 1956, for criticism of them), little attention will be given to them here.

GENERAL THEORY

A theoretical framework for the consideration of some of the mechanisms promoting and limiting the evolution of territorial behavior is outlined in Fig. 1.

Aggressive behavior is generally employed by individuals in the acquisition of goals which tend to *maximize individual survival and reproduction*. Natural selection should favor aggressive behavior within a population when these goals are consistently and easily accessible to individuals through aggression but should not favor it when they are not accessible. For example, when a food supply cannot be feasibly defended, because of its mobility or transient nature, generally no territorial system is evolved to defend it; and the territory, if present, may be restricted only to the nest and the area reachable by the parents on the nest. Such cases are found in colonial sea birds, nomadic and social feeding passerine species, and aerial feeders. In these species the goal of increased or guaranteed food supply is unlikely to be attained through aggression.

On the other hand, if the individual depends for its nesting requirements,

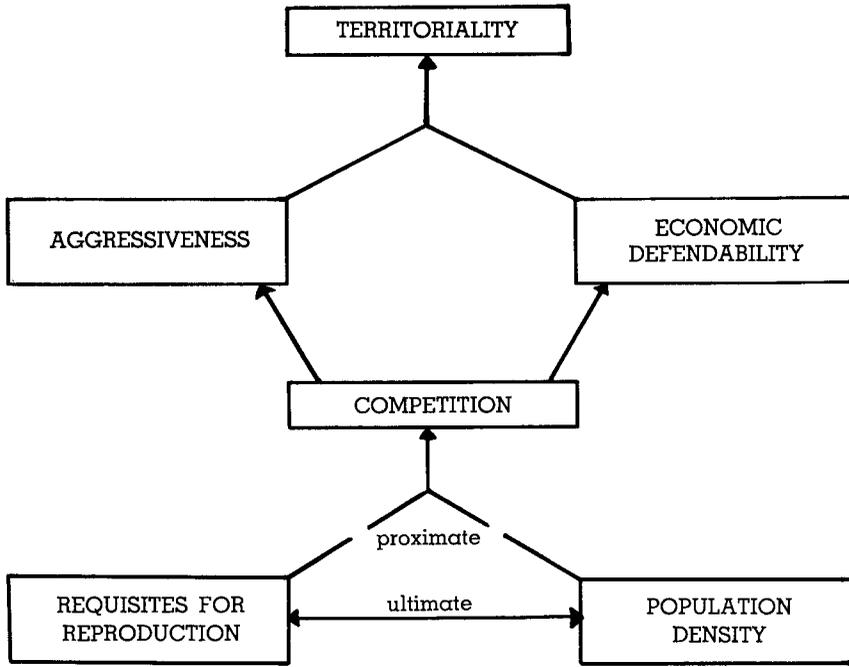


FIG. 1. A general theory of the evolution of diversity in avian intraspecific territorial systems.

food supply, and attraction of a mate on a relatively fixed and well-defined area, then this all-important area is typically defendable and becomes the classical territory. In short, *defendability* of the food supply, mate, mating place, nest, or other requisite for reproduction or survival is one of the most important determinants of the system of territorial behavior which is attained through natural selection. "Defendability" should be conceived in terms of the time and energy budgets of an individual as well as in purely physical terms.

Since intraspecific aggressiveness is primarily a behavioral response to competition for ecological requisites in short supply, *the predominant single factor tending to increase aggressiveness through natural selection should be competition*. Competition, as used in this discussion, may be said to exist when any ecological requisite exists in a quantity less than optimal for the total number of individuals which exploit it. Competition may exist for mates, food, roosting spots, breeding space, or any other necessity for reproduction in short supply. Competition is not necessarily expressed through aggression or threat but it frequently engenders such behavior.

On this logical assumption it follows that the value of site-dependent aggressiveness should tend to be in proportion to the intensity of competition—defendability allowing. The intensity of competition is directly dependent on the density of the population and inversely dependent on the supply of the requisites in question (Fig. 1). It is, consequently, complexly related to productivity, natality, mortality, and to all ecological and species characters affecting them.

Too much aggression in the absence of a short supply of the disputed requisite would eventually be detrimental. Consequently, a balance must be achieved between the positive values of acquired food, mate, nesting area, protection of family, etc., and the negative values of loss of time, energy, and opportunities, and risk of injury. Where this balance may lie in any particular species is influenced by a great variety of factors—to name a few: population density, physiological limitations and susceptibilities of the species, nest construction and site requirements, distance to food from nest, stage of development of young at birth, foraging time necessary to raise young, clutch size, time necessary to protect young, reaction of potential mate to too much or too little aggressiveness, conspicuousness to predators, migration, climate, weather, size of bird, and richness of food supply.

Within the population those *individuals* with the *optimal balance* of the genetic factors working for and against a particular form of aggressiveness would leave the most surviving and reproducing offspring; the type and degree of aggressiveness exhibited by these individuals would become, through natural selection, the norms for the population.

In short, it is argued that the type of territoriality evolved in a species depends on the types of requisites for which competition exists and upon the degree to which they are economically defendable in terms of balance between advantages and disadvantages of such defense to individuals (not the population). The problem for a particular species then becomes that of demonstrating which requisites are in short supply, which are not, and how it is economical for certain ones to be defended and not others.

APPLICATIONS OF THE THEORY

The general applicability of a theory based on competition and economic defendability to species exhibiting diverse types of territoriality may be illustrated with the following examples.

Colonial nesters.—A simple form of territoriality is exhibited by the Brandt's Cormorant (*Phalacrocorax penicillatus*), which was studied by Williams (1942). This species nests along the Pacific Coast of North America on islands and cliffs. At the start of the breeding season males begin giving

an advertising display in a small area a little larger than the size of the future nest; copulation occurs at the nest. The territory consists of the nest and a barren area extending a few feet or more around it. It is used in the attraction of a mate, for copulation, and defense of the family. All food is obtained from the sea under conditions which make the defense of a feeding area completely impractical if not impossible. Consequently, no matter how intense competition for food might be, the evolution of a territory used for feeding would be blocked through lack of defendability. On the other hand, the small area used for mating and family defense is feasibly defendable, and competition for the often limited optimal nesting space probably intensifies the necessity of defense of the nesting territory in this species.

Leks.—For the special evolutionary problems offered by the lek type of social organization the Sage Grouse (*Centrocercus urophasianus*) serves as an example. The data below have been taken from the extensive study by Patterson (1952). Sage Grouse live for most of the year in loose social groups of predominantly one sex. At the start of the breeding season cocks defend small display territories in a communal display area. Within the group of displaying males are a few dominants, each surrounded by a few subordinate "guard cocks." The females come to the display ground for copulation, usually choosing a dominant male. Aggressiveness is important for a male to achieve a dominant position; fighting and birds with blood-stained plumage are commonly seen on the lek. Nesting is performed by the female alone, who generally chooses an area well away from the lek where a richer supply of food, water, and cover exists. After the last egg has hatched the chicks leave the nest and are led by the hen to areas of suitable food and cover sometimes as much as 460 yards away. In summer and fall males and hens which were unsuccessful nesters move to areas of richer food supply, either higher altitudes or crop lands (up to 1 to 5 miles away).

According to the theory outlined here, the form of territoriality evolved in a species is determined primarily by competition and defendability. It is necessary, therefore, to relate the lek system to the environmental requirements of the Sage Grouse and to determine those requisites for which competition does and does not exist and whether or not they are economically defendable. Food, in the opinion of Patterson, was not a limiting factor on his study areas. He wrote, "... environmental deficiencies in the form of food, cover, and water are believed to be practically non-existent as sage grouse decimating factors, once the breeding season has been inaugurated" (p. 139). Consequently, "there seems to be no competition between individuals for the essentials of daily survival such as food, cover, or water" (p. 176). Patterson estimated juvenile mortality as 95% of the total mortality for the population and considered that, "losses to natural enemies probably constitute the

greatest source of juvenile mortality" (p. 139). Although a richer food supply might theoretically allow a higher population density and the occupancy of an increased area of suitable habitat, *for the individuals which are alive during the reproductive period*, food availability apparently does not limit reproduction. Consequently, competition for a food supply for the young in this species appears to be negligible, and any time or energy devoted to intraspecific defense of a food supply would be a net loss to the individuals concerned. The food supply may be considered as physically but not economically defendable under these conditions.

Furthermore, since protection against predators capitalizes on protective coloration and immobility of the precocious young, inconspicuousness of the family is necessary. Defense of an area around the nest would be detrimental by attracting predators, and the absence of the male from the nesting area is advantageous by decreasing conspicuousness of the family, and by reducing the potential prey population there (even if he were protectively colored). Furthermore, since the young do not have to be fed by the parents, the presence of the male is not necessary for that purpose.

Thus freed from the responsibilities of protection and care of nest and young, the males have full freedom of competition for the fertilization of females. To this end have evolved the elaborate and conspicuous plumage and display in the males and the lek system of mate selection. Once evolved, the lek system tends to perpetuate itself through the demonstrated preferential success of the dominant males within the lek (74% of 174 observed matings). Copulations at the periphery of the lek or outside of it are rare.

Summarizing, in the Sage Grouse although a food supply for the young might be physically defendable, it would not be economically defendable by the male during the breeding season because of the absence of competition for food at that season and the importance of predation in reducing productivity. Consequently, no large feeding and breeding territory is maintained by natural selection; competition among males for females has intensified, and, *together with other characteristics of the species and physical environment*, made possible the lek type of social organization. A similar explanation in principle for the evolution of the lek system in the Black and white Manakin (*Manacus manacus*) was given by Snow (1962).

Large territories.—The type of territory in which feeding, mating, and rearing of the young are all carried out together poses the most difficult problem for any theory of the evolution of territoriality, for the evidence is as contradictory as are the opinions of the many authors who have treated the subject. The fact that large territories occur only in species which utilize them for feeding would suggest that this type of territoriality has evolved in response to competition for food. This viewpoint is favored by Stenger

(1958) and Pitelka (pers. comm.) but opposed by Lack (1954) and Hinde (1956).

If this type of territory had evolved and were maintained in response to competition for food for the young, it would first be necessary to show that the nestling and fledgling mortality were commonly and in most populations of the species attributable ultimately to food shortage and only proximately to predation. However, the evidence presented by Lack (1954) on the causes of such mortality in thrushes favors stark predation uncomplicated by food shortage. There is but little reliable evidence bearing directly on this point in other species.

Despite the small amount of actual evidence that competition specifically for a food supply for the young commonly exists during or before the period when the young are being fed, the nature of the evolution of clutch size suggests that food may frequently be in short supply at that time. Clutch size probably tends to be increased through natural selection to the most productive number (in terms of eventual reproduction of the young produced) that the environment allows. Since the environmental limit to productivity in nests not affected by predation or parasitism is probably set primarily by the rate at which food can be brought to the young, it seems possible that competition for food for the young would frequently exist.

Another type of evidence offered in defense of food shortage as the primary cause for the evolution of large territories is the correlation between territory size and food supply. It is generally known that territorial (and nonterritorial) species have denser populations (and usually smaller feeding areas) in habitats where their food supply is better. This has been demonstrated quantitatively by Kluyver (1951) for the Great Tit (*Parus major*) and by Stenger (1958) for the Ovenbird (*Seiurus aurocapillus*). But if territory size is adjustable within limits to the breeding density in these species (as it apparently is), the correlation between territory size and food supply could be wholly a result of the normal habitat preference of the species and not directly related to the evolution of territoriality.

A more universal and easily demonstrable reason for the evolution of this type of territoriality is that it is dependent on competition for the *opportunity to breed*, as determined by ownership of a suitable area (in terms of feeding and nesting habitat). It may be debated whether the food density at the time the young are fed is adequate or not, but there is no question for many species with large territories, that possession of a territory is a prerequisite for the opportunity to mate and begin nesting. Even in a nidifugous species for which food is more than ample for the reproductive effort of all the individuals in any one area (assuming static clutch size), competition for space may result in restriction of the breeding population to those who by their aggres-

siveness are capable of holding a territory in an area of habitat acceptable to both sexes (e.g., certain Parulidae during high densities of spruce budworm, Stewart and Aldrich, 1951; Hensley and Cope, 1951). This would result in restriction of the maximum breeding density to the most aggressive birds. Such restriction has been indicated to occur in tits (Kluyver and L. Tinbergen, 1953; Gibb, 1956), Red-winged Blackbirds (Orians, 1961), Song Sparrows (Tompa, 1962), and strongly suggested to occur in many passerine species by studies of repopulation of artificially depopulated areas (Hensley and Cope, 1951; Stewart and Aldrich, 1951) and numerous other observations on the rapid remating of marked birds upon loss of their mate (e.g., Magpies, Minton, 1958; Shannon, 1958).

It should not be inferred that if the competition is not for food that it must be for mates, for many passerine species with large territories are monogamous with as many females as males in the breeding population.

The aggressiveness necessary to establish a large, exclusive territory may gain relatively little in terms of food, cover, and mates when they are already in adequate supply for the population as a whole; but by mere possession of an opportunity to breed, the territory owners would leave more reproducing offspring than the nonowners. As long as counter selection against aggressiveness were weak, *aggressiveness per se would be maintained in the population merely by the exclusion of less aggressive birds from breeding.*

The fact that the peak of territorial defense in some species (in terms of area and behavior) occurs before the young must be fed and often before the female arrives (e.g., Odum and Kuenzler, 1955) tends to support this idea. The males can afford to devote excess energies to territory defense during the period when they have little else to do but forage for themselves. After the mate arrives there is, of course, a selective advantage to protecting her from other males, but this could be done more efficiently by accompanying her and would not require a territory.

The correlation between large territories and their utilization for feeding might also be explainable on the basis of competition for space in which to breed. If aggressiveness were maintained in the population mainly by the exclusion of less aggressive individuals from breeding, the usage of the territorial space in foraging would be secondary to the fact that an aggressive individual was spending 100% of his time in a discrete area and defending it.

It seems likely that *both* limited food and exclusion by aggressiveness *per se* have been important selective agencies in the evolution of large territories. Under conditions of limited food density and medium to high population densities competition both for food and for space *per se* may be expected to be operative. Under the unusual conditions of high food density and low

population density, neither type of competition would constitute an effective selective force and territory defense would be absent or minimal. If both food density and population density were high, exclusion by aggressiveness would be the primary factor (e.g., Bay-breasted Warbler, *Dendroica castanea*, during outbreaks of the spruce budworm). If food density and population density were low, then defense of the food supply would be the primary factor.

Regardless of whether competition in this specific type of territoriality is for opportunity to breed, food, mate insurance, or some combination of factors, the general theory proposed in this paper would apply. For the object of the competition is not necessarily specified in the general case—only that it be economically defensible.

POPULATION CONTROL

Since territoriality appears in some species to participate in the control of population density (e.g., Kluyver and L. Tinbergen, 1953; Gibb, 1956; Tinbergen, 1957; Orians, 1961; Tompa, 1962), the hypothesis has been advanced (Wynne-Edwards, 1962) that territoriality and much of the ritualized agonistic behavior which characterizes it in many species have evolved to serve as mechanisms of population control. The argument fails primarily because it does not take account of the fact that changes in gene frequency are the result of competitive advantages accruing to individual genotypes rather than to the group as a whole.

It is not sufficient to demonstrate that genetic changes in some individuals in the direction of increased territoriality and efficiency of population control benefit all members of the population *equally*, including those individuals lacking these genetic changes. For, if the benefits of territoriality were equally distributed among all members of the population, then according to the Hardy-Weinberg equation the frequencies of the genes determining the increased territoriality would remain unchanged in successive generation rather than increasing. Consequently, it is impossible to account for the evolution within a population of territoriality, "epideictic displays," and population control on such a basis, notwithstanding the massive documentation assembled by Wynne-Edwards (1962). His proposal does not give a solution to the problem of how individuals in which territoriality is more strongly developed than others in the same population are adaptively superior to them.

The proposal that territoriality in a species may have evolved through extinction of nonterritorial populations and survival of territorial ones (Wynne-Edwards, 1962) is an insufficient explanation for two reasons. In the first place, the proposal does not explain how territoriality evolved in the original territorial populations. Secondly, the magnitude of the differences in

territoriality which occur between local populations of a species and between closely related species make it seem probable that such differences can evolve rapidly within a population in response to local conditions and do not usually require the processes of extinction of whole populations and invasion by others. The vast differences in territoriality exhibited by such closely related pairs of species as the Red-winged and Tricolored Blackbirds (Orians, 1961) and the Scrub and Mexican Jays (Brown, 1963) support this view.

SUMMARY

Recognition of the diversity of systems of territoriality among species has clearly indicated that an understanding of the evolution of territoriality requires a theory which accounts for the diversity according to more general ecological principles than those which have been proposed in the past.

A general theory of territoriality is proposed which depends upon the influence of two primary variables, *competition* and *economic defendability*, and on the adaptive value of aggressiveness under various conditions of these variables. Examples of application of the theory in different types of social systems (colonies, leks, and large territories) are given.

It is suggested that in species with large territories used for both feeding and nesting, territoriality might, under certain conditions, be maintained or selected for in a population merely through the exclusion of less aggressive individuals from the opportunity to breed in a suitable habitat. Such exclusion would, however, be limited by counter-selection pressures when aggressiveness became too detrimental to reproduction.

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