SOCIAL BEHAVIOR AND REPRODUCTION

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THE subject of social behavior and reproduction requires delimitation in order to clarify the scope of this part of the symposium (see Auk, 69: 127–191, 1952, for other parts of the symposium). In its broadest sense social behavior apparently includes any behavior between or among individuals of a species. However, for this paper the term will be restricted to the aspects of social behavior that influence the reproduction of the species as a population. This is a rather functional viewpoint because it considers the results of the behavior in terms of reproductive success or failure. It seems obvious that social behavior has relations with reproduction in birds because insemination is necessary in all known species of birds. The act of copulation is of course a form of social behavior. However, this does not settle the problem, because birds have developed a bewildering complexity of behavior patterns associated with reproduction. Our task is to obtain an understanding of the extent of causal relation between social behavior and reproduction.

The general thesis to be developed is that a large proportion of the social behavior assures or at least increases the success of reproduction. This thesis is rather difficult to test because, obviously, those species that lacked the social behaviors that assured reproductive success are no longer present. Thus we must deduce that, because of the absence of these behavior patterns, the species vanished. This type of evidence is unsatisfactory from the experimental viewpoint. Furthermore, as will be described later, the detection of the factor that limits a population is very complex.

The discussion will be divided into three major parts: 1) Courtship behavior clearly influences the production of eggs and the raising of young; 2) Territorial behavior affects the supply of environmental requirements; and 3) Hierarchial behavior is another method of regulating the utilization of resources. These three aspects affect reproduction in somewhat different manners.

COURTSHIP AND THE NESTING CYCLE

Courtship behavior in general seems to ensure that, at the appropriate times, a mate will be available to fertilize the eggs and assist in the work of raising the young. Some species require two individuals for most of the reproductive cycle in order to breed successfully, while other species get along with the barest minimum of collaboration.

An example of the minimum is provided by Gould's Manakin, *Manacus vitellinus* (Chapman, 1935). This species is a rather primitive passerine bird living in the jungles of Central America. Several males of Gould's Manakins make courts in the underbrush of the jungle. Each bird clears all leaves and twigs from the ground and establishes a perch above the bare area. The males display toward one another by means of "bluffing," and especially by snapping the wings together behind the back, producing a sharp noise. The dull green female, as she approaches sexual readiness, tends to remain near the court. When she is ready she enters the court of one male and with him performs a fantastic mutual dance consisting of leaping in the air and passing over each other rhythmically. After a short period of dancing the birds disappear into the woods, presumably for copulation. The male returns to his court and the female completes the nesting activities alone.

This type of mating is found in other species. The Tailed Manakin, *Chiroxiphia caudata*, of Brazil performs a similar dance, although I have never seen more than three individuals at one spot. The birds do not clear the ground beneath the dancing area and are able to make only minor noises with their wings. Wagner (1945) describes the courtship dances of the closely related *Chiroxiphia linearis* of Mexico. This species clears the ground under the dancing area.

There are, of course, many other examples of species that meet for only a brief period of time to copulate. Some of the best known are the Ruff, *Philomachus pugnax*, and the Sage Grouse, *Centrocercus urophasianus*. These species differ in the details of their courtship behavior and reproductive patterns, but all appear to reproduce adequately to maintain the species. For example, the manakins as a group are definitely successful in South America. Many of the others are clearly thriving species.

Another group of species utilizes the courtship ceremonies to maintain the sexual bond for the period of building the nest and, in many cases, the entire nesting cycle. The nuptial bond is of course formed at or sometimes before copulation and in many species is maintained for a period beyond fertilization. Most passerine birds maintain courtship ceremonies during nest-building and beyond. Ducks, however, show a transitional phase. The birds pair on the wintering grounds (Hochbaum, 1944) and remain together until the nest is built and the incubation has started. No example comes to mind of a species in which the male helps to build the nest and then deserts the female. We can postulate that such a stage in the evolution of behavior probably existed, but that it disappeared due to the continuation of the mutual bond to almost the end of the nesting cycle.

In some species the male is the chief architect of the nest. The male House Wren, *Troglodytes aëdon*, constructs the major part of the nest before copulation and may, under some circumstances (Kendeigh, 1941), prepare several nests and be polygynous. A somewhat similar behavior occurs in the Baya Weaver Finch, *Ploceus philippinus*, (Ali, 1930) in which the number of females obtained by a male depends upon how many nests he can build. In these cases courtship hardly functions to provide the necessary structure for reproduction but does maintain the function of arranging a suitable meeting of the two birds.

Some more primitive species maintain elaborate courtship performances that appear to be related to the proper maintenance of incubation. Doves of many species share the incubation between the sexes and continue elaborate ritual during this time. Black-crowned Night Herons, *Nycticorax nycticorax* (Allen and Mangels, 1940) not only maintain courtship ceremonies but develop elaborate performances when the mates exchange incubation duties on the nest. The performances involve plume erection, bill-rattling, and weak call notes. It is perhaps significant that both sexes incubate in a large number of species that feed far from the nest. This may be assumed to be an adaptation for protecting and warming the eggs while one parent is absent for a long period of time. Thus species are able to utilize a distant source of food by developing incubation behavior in both sexes. The social behavior patterns of courtship maintain the members of the pair together, and the ceremonies at the nest permit a harmonious exchange of incubation duties.

The argument can be extended to the problem of feeding the young in the nest. To supply an adequate quantity of food for the young requires strenuous efforts by the parents. Presumably the activities of both adults of some species are necessary to keep the young fed. Thus the result of courtship performances is that the pair is maintained through the period of feeding young. Examples readily come to mind. The male Song Sparrow, *Melospiza melodia* (Nice, 1943:171) assists regularly in feeding the young even after they have left the nest. The male House Wren (Kendeigh, 1941), however, may begin another nesting cycle before the young have left the nest. It may be assumed, since both species reproduce at a rate adequate to maintain a population, that differences in the availability of food permit this slight difference in behavior.

Since the young soon learn to take care of themselves there is little need for the parents to continue their bonds for this function. However, Canada Geese, *Branta canadensis*, apparently mate for life and the families remain together at least until the late fall (Elder and

Elder, 1949). Presumably there is some advantage to the reproductive success of the species in this behavior.

The relation of courtship performances to territory is perhaps the most difficult to analyze. It seems likely that the original territory was around the site for copulation and that the territory has been extended both spatially and temporally. The courtship behavior serves to keep the pair united until a territory can be staked out. Kingbirds, *Tyrannus tyrannus* (Davis, 1941) pair before establishing a territory and perform courtship displays actively until the territory is firmly outlined.

This summary of the relation of the nesting cycle to courtship indicates that, at least in many species, the courtship behavior can have the function of keeping the pair together until the requirements of reproduction are satisfied.

TERRITORY AND REPRODUCTION

Territorial behavior is well known in all its multiplicity of forms. In general, it consists of song, posturing, or actual fighting, all of which serve to stake out a claim for land. In some sea birds that nest on cliffs the land may be only a foot or so in diameter. In some hawks the land may be several square miles. Many passerine birds have a territory of about one or two acres. It is not the purpose of this discussion to describe the details of the social behavior that is involved in the defense of the territory because the chief objective is to try to understand how social behavior, as reflected in territorialism, affects reproduction of the species.

If we assume that the primordial function of territorial behavior is to provide a site for copulation, then it is clear that this form of social behavior fosters reproduction and indeed seems necessary for reproduction. The tiny territories maintained by Gould's Manakins are adequate to ensure that reproduction can occur because the males are not interrupted during coition. Many other species require little more than a copulatory spot. The Ruff, many grouse, and many hummingbirds have only a limited duration of time for the relation of social behavior to reproduction.

Other species have a restricted territory around the nest. Some are colonial nesters, such as gulls, herons, and jackdaws, while some are practically solitary as, for example, some birds of prey. Again we conclude that, since these species are thriving, their social behavior is adequate for the maintenance of reproduction.

Still other species regulate their reproduction by means of social behavior that obtains an area of ground around the mating and nesting

site. The Great Crested Grebe, *Colymbus cristatus* (Huxley, 1934) and the Goldfinch, *Spinus tristis* (Stokes, 1950) defend a territory around the nest site but obtain most of the food elsewhere. We deduce that in these species their life history is such that it is unnecessary to have a social behavior that will obtain a feeding ground to ensure reproduction.

Perhaps the majority of passerine birds have a territory that includes a feeding area. For success in reproduction it seems necessary that the social behavior provide the means for obtaining adequate food. This is the classical territory as described by Howard (1920) for the buntings and warblers. In some species (Song Sparrow; Nice, 1943) the young are fed within the territory even after they have left the nest, but in other species (Black-capped Chickadee, *Parus atricapillus*, Odum, 1941) the young leave the territory a few days after fledging and are fed outside the territory. Howard in his chapter, "The relation of territory to the system of reproduction," discusses the food problem in great detail. I wish to defer my discussion of this problem till later in order to develop the background further.

In a small number of species, a colonial territory is defended by the birds. Rooks, *Corvus frugilegus* (Yeates, 1934) defend a territory as a group but remain in pairs for nesting. The anis (Davis, 1942) show the evolution of a colonial territory. A primitive species, *Guira guira*, defends a colonial territory, but the colony frequently divides up into pairs which defend a small territory within the colonial territory. Another species, *Crotophaga major*, nests communally, but the birds remain paired. The most evolved species, *C. ani*, nests communistically and has lost all social behaviors associated with pairing. The abundance and wide distribution of this species is proof that reproduction is adequate and that the social behavior associated with pairing is quite unnecessary for these conditions.

THE HIERARCHY AND REPRODUCTION

Social behavior is related to reproduction in still a third manner. Many species that live in groups develop within the group a ranking that is called the social hierarchy. The individuals in the group arrange themselves in order according to their dominance which usually depends upon strength in combat. Guhl and Warren (1946) showed clearly that the dominant cock in a group of three cocks fertilized more eggs and sired more viable chicks than did the other two cocks. Presumably this relationship holds for other species that have a social hierarchy. This behavior is thus positively related to reproduction by ensuring that the dominant individual produces most young. In

times of scarcity of food or other necessities it seems likely that the dominant individual will obtain his requirements and the subordinate individuals will starve. But reproduction will continue at about the same rate since the dominant individual performs most of it anyway in polygnous species. Thus the social behavior that produces a hierarchy enables the species to maintain reproduction in times of hardship.

DISCUSSION

We have now surveyed the relations of social behavior to reproduction and seen that three types of activities are involved: (1) courtship, (2) territory, (3) hierarchy. In all three types there is great variation of behavior from species to species, but we have concluded that, because a species is thriving or at least not extinct, the social behavior is adequate for reproduction. But this type of reasoning is circular and resembles the "survival of the fittest" reasoning that annoys the philosophers and logicians. Just as we define the fit as the ones that survive so we define adequate social behavior as that of the successfully reproducing species. This logical problem has not yet been resolved to the satisfaction of all in the evolutionary controversy, and even today there exists little experimental evidence that the fit ones actually do survive better than the less fit. Hence, we should not be discouraged in our attempt to obtain proof for the thesis that these social behavior patterns are adequate and necessary for reproduction.

Another difficulty with the present state of the thesis is that we have little evidence concerning the possibility that a change in social behavior might improve the reproduction of the species. We can very well ask, "Would Song Sparrows reproduce better if they had a colonial feeding territory or some other modification of their social behavior?" The evolution of social behavior in the Crotophaginae suggests that such changes may be beneficial. The least successful of the species, *Guira*, pairs and frequently defends a nesting territory. It is nowhere abundant and has a limited distribution in southern Brazil, Uruguay, and Argentina. In contrast, the most successful species, *Crotophaga ani*, has lost all pairing behavior. It is abundant throughout a wide range from southern Argentina north to the United States and including the West Indies. But without experimental analysis of the factors governing the population it is impossible to conclude that a change in social behavior caused an increase in population. All we can say is that the two are correlated.

The difficulty of experimentally testing the theory of territory bothered Howard, and he actually performed some experiments to

determine whether it was necessary that the adults have a supply of food within a short distance. His experiments agreed with the theory but were inadequate to prove anything conclusively. But unfortunately Howard developed the food requirement idea and hence received criticism from many persons, especially David and Lambert Lack (1933). This criticism pointed out that many species do not defend territory when they need food most, that is, after the young are hatched. Furthermore, there is little evidence that territory limits the number of pairs in a region.

The procedure for determining the factor that limits reproduction (or a population) is exceedingly complex. But this problem is basic to an understanding of the relation of social behavior to reproduction and also to determining the functions of social behavior. Let us therefore digress for a while into a discussion of regulatory factors and limiting factors. A regulatory factor affects the success of reproduction in some manner. For example, viability of sperm determines how many eggs are fertilized and thus affects reproduction. Similarly, courtship behavior must be adequate to stimulate copulation, and hence it affects reproduction. Or high temperature may hinder development of the embryos and hence may affect reproduction. It is obvious that there are a multitude of regulatory factors that are inextricably interrelated. Furthermore, the intensity of the effect may vary from year to year and from place to place so that an almost hopeless jungle of relations develops. Fortunately, however, some factor may act at a particular time and place as the minimum factor to limit the reproduction. This, of course, is similar to the situation described by the phrase, "A chain is no stronger than its weakest link." The regulatory factor which at a definite time and place determines the extent of reproduction is called the limiting factor. Thus it is possible that viability of sperm would be so low under certain conditions that only a small proportion of eggs would hatch. Under these circumstances courtship performances and food supply would be more than adequate for the few young. Or at some time courtship might be impeded by unfavorable conditions so that the fertility or food supply would be far in excess of the number of young. Or in some place the food supply might be inadequate for the young and hence limit the number raised. These examples are far simpler than nature usually is, but they should demonstrate that the limiting factor acts upon a particular relationship at a particular time and place.

For an understanding of the relation of social behavior to reproduction it is necessary to digress once more into the problem of limiting factors. Of the many factors that regulate reproduction of a popula-

tion of birds, or the population itself, competition within the species is frequently the limiting factor. Birds have largely avoided the limiting effects of ordinary variations of environmental factors by the development of migration, of homoiothermism, of incubation, and many other adaptations. Similarly birds have largely avoided the limiting action of predators and disease by developing protective coloration or behavior, or immunity and tolerance to infection. Thus these two groups of factors rarely in nature become significant as the limiting factor. Such climatic catastrophies as the sleet storm that practically destroyed the Bluebird, *Sialia sialis*, population of New England in 1908 or such epidemics as occurred in duck populations (Rosen and Bischoff, 1949) are, fortunately, not daily occurrences. The result of this situation is that the limiting factor in reproduction is usually some form of competition which obviously involves social behavior.

Let us now return to a specific example of the relation of social behavior to reproduction. Consider the classical case of the relation of territory to food supply. For Yellow Buntings, *Emberiza citrinella*, Howard concluded that a territory was necessary to provide adequate food for reproduction. This implied that food supply for Yellow Buntings regularly was the limiting factor and that other regulatory factors such as temperature, disease, predators, and nesting sites were all ineffective in limiting the reproduction. Under these circumstances the number of young produced depended upon the social behavior of the adults that ensured an adequate food supply. To quote from Howard, "This end the territory serves to promote; it roughly ensures that the bird population of a given area is in proportion to the available means of subsistence, and it thus reduces the risk of prolonged exposure to which young are always liable."

But subsistence is not always the limiting factor, and Howard gives an excellent example of the exchange of factors that limit a population. Under usual weather conditions the territory contains enough food so that the adult Yellow Buntings can find food and return to the young in time to prevent their chilling. But June of the year 1916 was exceptionally cold and the adults could not get enough food fast enough. Hence a high mortality of young resulted. The limiting factor in that year was therefore cold weather rather than territorial behavior.

Another example is provided by the data for Song Sparrow populations (Nice, 1937). From 1930 to 1935 the number of males varied as follows: 33, 31, 44, 29, 19, and 17. In brief, the history was that in 1933 there was a considerable destruction of cover, but that espe-

cially in 1931 and 1932 the environmental conditions were essentially the same. However, in 1931 there was a scarcity of Song Sparrows (only 31) in contrast to a population of 44 in 1932. Therefore, in 1931 some unknown factor, perhaps a winter mortality, had limited the population. But in 1932 almost every available piece of land was utilized, and hence the social behavior of territorialism limited the population. It is quite obvious that whether or not social behavior limits reproduction depends upon the circumstances.

We thus find that social behavior may and frequently does have very complex relations with reproduction. These relations are both on an individual basis and a population basis. We also find that it is extremely difficult to explore the relationships because of the difficulty of detecting the limiting factor in a particular situation. It is appropriate therefore that we outline some of the methods of testing the hypothesis that social behavior, as manifested by courtship, territorialism, or hierarchy, affects the reproductive rate of a species.

Perhaps the first method should be experimental. To test the hypothesis it is necessary to make certain that all other regulatory factors are available in excess of the requirements of the species and that an excess population of birds is present. It must then be observed that by means of some social behavior the reproduction is affected. An example is found in Nice's Song Sparrows for the year 1932. Apparently there was an ample population of birds and more food and shelter than needed. But the data are not sufficiently detailed to show that birds actually were driven from the area by territorial fighting. We can always ask the question, "Could another pair have squeezed in, if it had been present?" In 1933 the amount of cover was reduced and apparently became the limiting factor. It is impossible to claim that territorial behavior limited the reproduction that year because, according to the map, many of the territories did not join another territory.

An experiment with Barn Swallows, *Hirundo rustica*, is in progress and may be described although the results show nothing yet. These swallows are only slightly territorial but do defend a small area around the nest. The large barn under observation has an unlimited supply of nesting sites under the rafters and an ample supply of nesting material. The food supply is presumed to be ample because the swallows have for their use extensive fields and a barnyard with many animals. The supply of birds also is presumed to be ample because the species is abundant in the region. There is unfortunately no proof that these assumptions are true each year. However, under these conditions the number of swallows nesting in the barn should be limited by the

territorial requirements of the birds, that is, the social behavior should affect reproduction. This limitation should be manifested in a fixed upper limit to the population, at which time excess birds would be driven away. In 1949, eight pairs nested in the barn and in 1950, 18 pairs nested there. Clearly in 1949 the social behavior was not the limiting factor since in 1950 many more pairs were accommodated. Only additional evidence will tell whether 18 pairs is the maximum number. It should be possible to alter the number of nesting sites and thereby test the relationships.

Another experimental observation may be revealing. On an island in the Chesapeake Bay, four pairs of Ospreys, *Pandion haliaetus*, have nested since 1946 and according to the farmer for many years before. The birds are regularly spaced in the available area, although there seems to be plenty of food and nesting sites. In 1950 a fifth pair unsuccessfully tried to nest on a duck blind near the island, although more usual nest sites were available. It seems likely that social behavior restricts the number of breeding pairs to four on this island.

Another method for examining the thesis is to observe carefully the social behavior and relate it to success or failure of individual birds. Davis (1941) noted several times that the Kingbirds built nests but abandoned them. In one case a nest was started in an oak but abandoned. The pair nested later in an apple tree. In another case a pair built three nests in succession but never laid eggs. Hochbaum (1944) cites a case of a male Canvasback, *Aythya valisineria*, that lacked a territory. When he tried to copulate with his mate, other drakes interfered, showing that territory is essential in this case to reproduction. Indeed, in many species copulation outside the territory may be interrupted by other members of the species. As another type of failure, Skutch (1931) found that the cause of half of the nesting failure of Rieffer's Hummingbird, *Amazilia tzacatl*, was pilfering of the nest by other hummers. We can also obtain data of this type on the population level. The Heath Hen, *Tympanuchus c. cupido* (Gross, 1928) may have become extinct because the number of birds was so low that adequate social behavior was not attained. But to prove this contention requires very detailed observations. The same explanation has been given for the extinction of the Passenger Pigeon, *Ectopistes migratorius*. If enough observations of this type can be related to presence or absence of social behavior (courtship, territorial, or hierarchal behavior), then perhaps a causal correlation can be detected. This will be difficult because of the complexity and infrequency of observations and an understandable reluctance to study birds that failed to nest.

A last method for studying the thesis is by a comparative study of a group of closely related species. The studies of the Crotophaginae (Davis, 1942) have already been mentioned. The evidence available for three species suggests that low reproduction was correlated with the social behavior of territorialism and that high reproduction accompanied the loss of territorialism. This is no more than a correlation and is particularly weak because nothing is known of the mortalities of the several species.

Another example of comparative behavior is Friedmann's study (1929) of cowbirds. The two species that have lost their territorial behavior, *Molothrus ater* and *M. bonariensis*, are eminently successful as judged by their abundance and wide distribution. The territorial species are less successful, but again we know too little about the other factors to conclude much about relation of social behavior to reproduction.

Moreau and Moreau (1938) compared two closely related weaver finches. In one species, *Euplectes hordacea*, the maintenance of territory seems to limit the population, while in another species, *E. nigroventris*, the territories seem to be indefinitely compressible and hence do not limit the population. Unfortunately data directly applicable to the hypothesis are usually suitable for the development of correlations but not causal relations. Much work remains to be done in this complex field before the extent of causal relations of social behavior to reproduction can be determined. Let us illustrate the problem in its simplest terms. Given a species that performs social behaviors, A, B, and C, and reproduces at a known rate, what will that rate be if behavior C or B or A is eliminated? Or if behavior D is added or substituted? We now can rarely prove that these complex social behaviors have any significant effect on reproduction. They may merely be useless or at least innocuous accompaniments to the reproductive cycle. Until we can find out what happens in the absence of these behavior patterns, we will have to be content with tentative deductions based upon correlations.

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