SOCIAL BEHAVIOR AND SURVIVAL

BY F. FRASER DARLING

THE convener of this symposium has given me the enviable position of being the last speaker on the program (see Auk, 69: 127–182, 1952), but he has offset that by giving me the most difficult subject—at least so it seems to me—of social behavior and survival. One can certainly talk about gregariousness, the *development* of social behavior, and the fundamental factor of sociality in reproduction, but to be faced with commenting on social behavior and survival I feel that I am in serious danger of being teleological or of picking facts to support an argument, and that will never do. Perhaps it would be easier to show the part of social behavior in survival of the individual or of the species by a study of negative evidence, but we should all have a tedious half-hour.

Social behavior and survival are so closely linked that I feel I can do no more than emphasize the obvious. The animal cannot truly stand alone and, as we are now coming to understand, neither can a good many plants. The whole trend of ecological thought at present is towards a realization of the importance of community, and in this respect we are becoming increasingly aware of the social interactions between species and the whole complex of the ecologic association. But, of course, I must not beg the question by calling on the wide ecological field. The animal, as I say, cannot truly stand alone; the social interest is there, implicit and inherent, mainly to be derived—as I believe—from the fundamental need for reproduction. But there is more to it than that. I believe an animal needs to go outside itself, just as we do, and to enter into relationships with others of its kind. There seems to be in animal life a reciprocal responsiveness which in itself leads to a development of variability of behavior—and there can be no evolution without variability. It would be unscientific to say that this generic need for the awareness of other selves is designed to lead towards cooperative behavior, but cooperation undoubtedly develops. That inherent, unconscious, reciprocal responsiveness is, in fact, cooperation in its simplest sense.

How does this view square with the orthodox biology of the later nineteenth century? Darwin based his theory of natural selection on the survival of the fittest. There was an interminable struggle for existence. Darwin's followers took the bald hypothesis farther than he would have been prepared to go, I think, and the notion of "Nature red in tooth and claw" blinded us to the complementary notion of evolution, which implied survival, continuing through cooperative

effort as well. Kropotkin (1902) was so ingenuous and lacking in critical outlook that he may have retarded the emergence of a scientific view of sociality and survival.

It is only recently that zoological workers and those in comparative psychology have realized that the group is a major ecological factor in the life of the individual. Sociality is fundamental in life and not a cultivated development of the so-called highest form. Allee, in Chicago, has done 30 years of investigation of animal communities in the comparatively low forms of life in which we are not accustomed to acknowledge a high type of possibly conative behavior such as we see in some birds and mammals. It is his view that many advances in evolution may have come about through selection of cooperating groups rather than of individuals, and he has stated the beautiful concept that the two great natural principles: struggle for existence and cooperation, or reciprocal responsiveness, as I prefer to call it, are not wholly in opposition, but that each may have acted on the other in determining the trend of animal evolution. My own work has been confined to birds and mammals. In the study of a herd of red deer I found that sociality was intrinsic and, at least to my own satisfaction, it was clear that social behavior was intimately bound up with survival. The study of *behavior* in birds is fairly recent among men of science. It received its greatest impulse from the publication of Eliot Howard's (1920) researches on territory, work which in some ornithologists' minds tended to emphasize those types of territorial behavior which lead to the segregation of pairs, to active hostility to neighbors, and to independent or isolated behavior. Consequently, the social behavior of birds was somewhat overshadowed until a few years ago, since when numerous researches have not only enlightened us on this subject alone, but have given us new concepts in the study of evolution.

My own research on avian sociality was published over 12 years ago. It held the dual thesis of—the reality of social stimulation to reproductive condition in such birds as are social or colonial at some state of, or throughout, the breeding cycle; and the existence of a threshold of numbers in some colonial species, which might be critical as to whether the birds bred or not.

Naturally, the extent to which the social factor enters into the life of birds varies greatly. In some it appears to be sporadic, in others seasonal, and in others it constitutes the whole way of life. Whereas the benefits of sociality in the lower animals as studied by Allee (1931, 1938) and others appear to be physiological in origin, operation, and result, the basic element of *stimulation* in avian sociality seems to be psychological and psycho-physiological.

The life of a bird falls mainly into two linked parts—maintenance of its everyday activities and reproduction of its kind. Let us take some examples of aggregations and sociality in the maintenance activities of birds. It is obvious that within a population where members share a common medium as food, with common methods of obtaining it, flocking or grouping at a feeding ground is likely to arise, and it is one of the simplest forms of gregarious activity—an assemblage without any special social cohesion at a place of abundance of food. We do not know for sure whether these aggregations have survival value, though in some fishes and among domestic hens Allee found that more per head is eaten when several are present than when the creatures are solitary. The farmer observed the phenomenon in little pigs long before, but you may question the survival value of eating more, for it has been shown in the laboratory rat that a measure of inadequacy in food increases the life span. Gallet (1949) tells us that the Flamingo, *Phoenicopterus ruber roseus*, never feeds alone, unless it is ill or injured. As a species it is one of the most tightly coalesced into flocks. Bartholomew (1942), observing Double-crested Cormorants, *Phalacrocorax auritus*, in San Francisco Bay, showed that a flock of these birds was more active in fishing than individuals fishing alone, and the activity of a larger flock was greater than that of a smaller flock. Different methods of fishing were evident between large flocks, small flocks, and birds fishing alone. Bartholomew concluded that mass fishing was efficient, as a surprising number of birds made catches. The formation of one of these large fishing flocks is interesting. The first group to alight does not begin feeding but swims about slowly till other flocks join it, and it is thought the birds locate a large flock by sight. Bartholomew suggests that birds of a large flock are stimulated to maximum effort by the presence of a large number of easily-caught fish, but if this is so, they are not so stimulated by the fish alone, or the first-comers to the scene would become active immediately. A flock of Starlings, *Sturnus vulgaris*, searching pastures for insects move rapidly over the ground, each bird spurred on by its neighbors, and if one should startle an insect from a tuft of grass, a neighbor may obtain it, whereas the insect would perhaps have escaped if it had been startled by a solitary bird.

Simple assemblages of birds are typified by winter roosts of Starlings, finches, wagtails, and Wood Pigeons. Once more we cannot assess the survival value of such aggregations, but for the Starling the physical possibility of conservation of heat should not be overlooked. The rise of emotion in the roost resulting from numbers may in itself bring about physiological conditions helping the bird to endure the environ-

mental stress of the long winter night. But, of course, we do not know, and it would be valuable if the physiologically-minded from among us would devise some experiment for finding out. The onset of cold is a potent factor causing flocking in small birds.

The complicated and intricate structure of the multispecific flock has not yet been thoroughly studied, but Colquhoun and Morley (1943), working with tits, have found that the aggregation is evidently not merely for the sake of feeding, because each species tends to have its own vertical niche in the flock and is therefore feeding at a different level from the others. If the species are feeding in roughly stratified fashion, why need they feed together? Whatever the purpose, it must be fairly important, for with the Marsh Tit, *Parus palustris*, one of the species found in the flock, over 70 per cent of some ringed individuals were found in a flock for the eight months June to January. The concerted cries and call notes of the flock actually render it conspicuous to predators, more loudly declare its whereabouts, than if individuals were scattered.

Similarly, Roberts (1942) in Australia has described the winter flocking of the Pied Currawong, *Strepera graculina*, in which species it would seem that social contact stimulates psychic and physical qualities and that the common activities of the flock have a real, though not obvious, value in maintaining biological fitness during the non-breeding season.

Leaving aside the apparently haphazard aggregations, which still must not be dismissed as being without order, there are the flocks in which organization is obvious.

When we examine the social factor in relation to reproduction, we have more evidence than we have for maintenance. As one who has been responsible for postulating that social stimulation is of value in synchronization of breeding condition and that the display of the social group has value for the individuals, I do want to say that it is obvious that such a state of affairs does not appear in many species, and the principle does not apply all round, but that fact does not invalidate the principle in those species which *are* social and colonial nesters. Even here the principle varies in intensity and may be modified by fluctuating ecological conditions. It is not a good enough argument to say that because on two occasions a single pair of Gannets, *Morus bassanus*, has occupied a rock and nested successfully that the principle of social stimulation to breeding success does not apply in this species. The Fulmar Petrel, *Fulmarus glacialis*, appears to be a species in which the social factor is critical in reproduction. My own evidences, published in 1938, were slight, but they have since been con-

firmed statistically by Fisher (in press) who has just completed a monumental study of this species. There can be no doubt of the greater biological success of the larger colonies and the figure of 8 to 12 pairs seems correct for the all-or-none reproductive threshold. As an example of how social nesting may *adversely* affect survival, I should mention the work of Lees (1946) on the Rock Dove, *Columba livia*, who shows that where the species is colonial, if one pair deserts or loses its nest, the other pairs in the colony follow suit.

There is not space to go through the body of work published in the last ten years which supports the biological survival value of social stimulation. Instead, I want to draw special attention to what we call aggressive behavior and its place in social stimulation. True fights do occur, but they are rare, and I think that the uniqueness of the combative nature of our own species tends to make us interpret the formalized fighting of birds too literally. Aggressive display is one of those facets of the complex of bird life which evolution has seized upon for development of a different kind. For example, in Johnson's study (1941) of the Atlantic Murre, *Uria aalge*, a bird in which crowding seems a necessity for reproduction, he observed frequent fights regardless of sex. The fights seemed to intensify the urge to incubation rather than vanquish a neighbor as a competitor for space. The greater the amount of fighting, social preening, crowding, and calling, the greater the amount of apparent general satisfaction and welfare. Crowding occurs in spite of there being unoccupied ledges. Lockley (*in litt.*) found much the same conditions on Skokholm, and so did I on North Rona. Perry (1940) found that the tempo of activity of individuals of this species without young increases when hatching of the eggs of a colony causes an increase in the fishing activity of the parents and that on crowded stacks the delivery of the fish to the chick tended to be more immediate than on sparsely populated ledges. This, of course, could be interpreted that the avarice of neighbors, and fear of having the fish snatched from them, caused parents on crowded ledges not to dally in passing the morsel over, but Perry elsewhere observes that if the parent does so dally the chick often abandons its attempts to secure the food and burrows again into its brooding parent.

Williamson (1949) remarks on the aggressive flight of the Arctic Skua, *Stercorarius parasiticus*, against human intruders being common throughout the nesting cycle in the colony, but absent from the behavior of solitary pairs. He suggests that this behavior needs a certain level of mutual stimulation not attainable by solitary or widely scattered pairs. Williamson also mentions that Arctic Terns, *Sterna*

paradisaea, strike the intruder more readily in large than in small colonies.

It is perhaps significant that species living in a difficult and hazardous environment are social in the breeding season, a sociability reaching extreme lengths in the Emperor Penguin, *Aptenodytes forsteri*, where incubation of the egg is shared among a group. Other birds, such as the Flamingo, Sandwich Tern (*Sterna sandvicensis*), and Shelduck (*Tadorna tadorna*), form crêches, the young banding together and being reared by adults not necessarily their parents. There is a strict adherence to age-groups in these crêches. This is definitely of value for survival, for fledglings of contemporary age and powers band together into a more compact flock than one composed of youngsters of different levels of performance; and the more compact the band the safer are the individuals composing it from their predators, the gulls.

Many species of birds which nest in separate, fairly extensive breeding territories, and which establish and defend these by apparent fighting are for the most part indulging in no more than aggressive display. May (1949) remarks that a group of territories of the Willow-Warbler, *Phylloscopus trochilus*, by reason of the volume of song, has more chance of attracting females than has an isolated territory. Even with the pugnacious European Robin, *Erithacus rubecula*, Lack (1948) finds that winter territories in English woods tend to be bunched, though the conditions overall seemed so similar that they could have been widely separated. He says, "Perhaps the singing of one individual, though repelling others from the actual territory, attracts them to settle near by." Nice (1937) observed the bunching of territories of the Song Sparrow, *Melospiza melodia*, apparently from preference and not from limitation of the habitat. Bickering was frequent on the peripheries. Likewise Yeates observed a tendency for the territories of Snow Buntings, *Plectrophenax nivalis*, to be together. Armstrong (1947) says the birds, in spite of their territorialism, are attracted to each other and benefit, by mutual stimulation. My own remark here is that the phrase "in spite of territorialism" is as a pair of blinkers to the point of view that territorialism is one aspect of social behavior. The aggressive quality of bird song has, I think, been overemphasized. Proclamation, yes; *apparently* aggressive, yes; no more combative than a military tournament of befrogged dragoons, but probably even more stimulating. So-called fighting, and singing, are in my opinion often a form of social stimulation and have indirect survival value as aids to development of reproductive condition. I should think the term "aggressive behavior" could be dropped for a great deal of true display.

Morley (1941) found in Starlings that the eviction of interlopers to the territory caused the members of a pair to display to one another, and that owners' visits to nest sites in their territory greatly interested their neighbors. She also found in Marsh-Tits (1943) that after territorial clashes the pair was stimulated to visit possible nest sites. Ruttledge (1946) notes in the Irish Coal-Tit, *Parus ater hibernicus*, that the volume of song is much dependent on birds of adjacent territories being close to one another. A bird whose territory is seldom invaded or which spends much time in the center of the territory is rarely heard to sing. Perry (1940) records for the Puffin, *Fratercula arctica*, that the mere sight of another Puffin alighting on the same terrace provokes display between the pair, and so do squabbles between neighbors, while *display* or vocalizing in burrows stimulates a great deal of interest among other Puffins around.

The most highly developed social aggressive display is apparent in some game birds such as the Blackcock (*Lyrurus tetrix*) and the Prairie Chicken (*Tympanuchus*), and in some waders such as the Ruff (*Philomachus pugnax*). Here the formalized fighting has reached such a degree of organization that it is doubtful whether successful reproduction would be possible without it. The social stimulation is of critical survival value, but do not let us ever think of it as aggressive behavior.

I have been strengthened in this view in later observations in breeding territories in red deer and in Atlantic seals. Fighting does occur, but formalized fencing by stags and display of canine teeth and claws by bull seals is much more common. I have noticed in red deer that the large female groups mean several harems close together, which phenomenon means more challenging behavior on the part of the stags, and as the females in season solicit the stags in a beautiful courtship display, the stags are quicker in response when they are kept in a state of excitement by their challenging of other stags. The whole subject of challenge and vocal display needs fuller investigation as a social phenomenon with survival value.

The breeding behavior of the Lapwing, *Vanellus vanellus*, provides an example of a link between the social aggressive display of males and the social display between sexes and social nesting. Rinkel (1940) in Holland speaks of *colonies* of Lapwings, as a number of territories are always found together. He found that, far from avoiding clashes, the males seemed to need them and the emotional stimulation they gave, and the birds sought opportunities for them. Meanwhile the females do not desert the display ground for egg-laying, but lay in territories within sight and sound of their fellows.

I would like to put forward the hypothesis that one of the important functions of territory in breeding birds is the provision of *periphery*—periphery being defined as that kind of edge where there is another bird of the same species occupying a territory. One pair of warblers in a wood have, in effect, no territory at all; they are merely existing in space. But by pushing up against each other, rather than spreading themselves out, the birds are giving themselves peripheries, and there are doubtless optimum peripheries for each species. The breeding territory has little to do with a sufficiency of feeding ground for raising the brood. It is a place with a focal point or two—the nest site and the singing post—and periphery. Southern and Morley (1950) show that there is a considerable concentration of Marsh-Tits on what they call the "defended" boundaries of territories, with less interest in the neutral margins. If this hypothesis is correct, then *territorial behavior as a whole is a social phenomenon, and it has survival value.* We also begin to see functional survival value in autumnal territorial sexual behavior among birds (Morley, 1943).

We cannot go into the complicated subject of social flocking for migration and the possible survival value. Those who may have watched geese preparing for migration, and the behavior when they arrive at their wintering ground, the flocks having tended to break up and time being given to building up again before even feeding, can have little doubt that the social behavior has survival value for the individual and the species; but we do not have it well analyzed. Lorenz, in his "Kumpan" paper (1935), gave us new standards of inquiry, but we have not followed them up as fast as we might have. The field is varied and all of it is important, not only in bird studies but in comparative psychology and a whole socio-ecology which includes our own species. This symposium shows something of achievements and of deficiencies, and the best it can do for us here is to stimulate *us* to further research—social or otherwise.

LITERATURE CITED

ALLEE, W. C. 1931. Animal aggregations: a study in general sociology. (Univ. Chicago Press, Chicago), ix + 431 pp.

ALLEE, W. C. 1938. The social life of animals. (W. W. Norton Co., Inc., New York), 293 pp.

ARMSTRONG, EDWARD A., 1947. Bird display and behaviour. (Oxford Univ. Press, New York), 431 pp.

BARTHOLOMEW, GEORGE A., JR. 1942. The fishing activities of Double-crested Cormorants on San Francisco Bay. Condor, 44:13–21.

COLQUHOUN, M. K., AND AVERIL MORLEY. 1943. Vertical zonation in woodland bird communities. Journ. Animal Ecol., 12:75–81.

DARLING, F. FRASER. 1938. Bird flocks and the breeding cycle. (Cambridge Univ. Press, Cambridge), x + 124 pp.

FISHER, JAMES. (Monograph on the Fulmar Petrel.) In press.

GALLET, ETIENNE. 1949. Les Flamants Roses de Camargue. (Librairie Payot, Lausanne), 128 pp.

HOWARD, H. ELIOT. 1920. Territory in bird life. (John Murray, London), xiii + 308 pp.

JOHNSON. R. A. 1941. Nesting behavior of the Atlantic Murre. Auk, 58:153–163.

KROPOTKIN, P. 1902. Mutual aid: a factor in evolution. (McClure, Phillips & Co., New York), xix + 348 pp.

LACK, DAVID. 1948. Notes on the ecology of the Robin. Ibis, 90:252–279.

LEES, JOHN. 1946. All the year breeding of the Rock-Dove. Brit. Birds, 39:136–141.

LORENZ, KONRAD. 1935. Der Kumpan in der Umwelt des Vogels. Journ. für Ornith., 83:137–213, 289–413.

MAY, D. J. 1949. Studies on a community of Willow Warblers. Ibis, 91:24–54.

MORLEY, AVERIL. 1941. The behaviour of a group of resident British Starlings (*Sturnus v. vulgaris* Linn.). Naturalist, 788:55–61.

MORLEY, AVERIL. 1942. Effects of baiting on the Marsh-tit. Brit. Birds, 35: 261–266.

MORLEY, AVERIL. 1943. Sexual behavior in British birds from October to January. Ibis, 85:132–158.

NICE, MARGARET MORSE. 1937. Studies in the life history of the Song Sparrow I. Trans. Linnaean Soc. N. Y., 4:1–247.

PERRY, RICHARD. 1940. Lundy: Isle of Puffins. (Lindsay Drummond, London), 267 pp.

RINKEL, G. L. 1940. Waarnemingen over het gedrag van de Kievit (*Vanellus vanellus* (L.)) gedurende de broedtijd. Ardea, 29:108–147.

ROBERTS, N. L. 1942. The winter flocking of the Pied Currawong. Emu, 42: 17–24.

RUTTLEDGE, ROBERT F. 1946. Roosting habits of the Irish Coal-Tit, with some observations on other habits. Brit. Birds, 39:326–333.

SOUTHERN, H. N., AND AVERIL MORLEY. 1950. Marsh-Tit territories over six years. Brit. Birds, 43:33–47.

WILLIAMSON, KENNETH. 1949. The distraction behaviour of the Arctic Skua. Ibis, 91:307–313.

The Old Rectory, Lilley, Newbury, Berkshire, England, October 12, 1950.