

FLOCKING BEHAVIOR IN BIRDS

BY JOHN T. EMLÉN, JR.

MODERN studies of social behavior in birds have concentrated on two problems: 1) the mechanisms of integration of the organized social unit, and 2) the effects of the social environment on the activity, fecundity, and survival of the individual. The first of these has been brought to your attention by Dr. Collias in his discussion of the development of social behavior (Auk, 69: 127-159, 1952). The second will occupy the attention of the two remaining papers in this symposium, those by Dr. Davis and Dr. Darling (Auk, 69: 171-191, 1952). In the interim I would like to bring up for your consideration a third aspect of social behavior—that of flocking responses, gregariousness, and the various factors which determine the size and density characteristics of bird flocks.

The actuality of flocking behavior in birds does not need to be proved. It is everywhere in evidence, indeed it is difficult to find situations and species which do not show at least a trace of it. Large and dense bird flocks are familiar to the most casual observer. Chattering hordes of migrating blackbirds, swirling clouds of swallows in a pre-roosting flight, jostling crowds of sea-birds on a rocky islet; such scenes provide some of the most thrilling spectacles to be seen in bird life.

The term flock, while commonly associated with such spectacular phenomena, will be applied in this discussion to any aggregation of homogeneous individuals, regardless of size or density. The word homogeneous as used here is not to be interpreted in too strict a manner, but is employed in order to exclude the special heterogeneous groupings of sex and age categories occurring in the breeding pair and the parent-young family group. A flock in this broad sense might result simply from a convergence of independent individuals at a common, localized source of attraction such as a patch of shade or a feeding station. It might, on the other hand, arise as a result of a mutual attraction between individuals. In many bird flocks it is probable that both of these factors operate, the relative rôles of each varying with the species and with the circumstances.

SOCIAL FORCES IN BALANCE

The convergence of birds in response to external physical factors presents, in itself, no great problems to the student of bird behavior. Social responses, on the other hand, are highly complex and fraught with challenging problems.

The tendency of birds to respond positively to the presence of others of their kind, commonly referred to as gregariousness, is little understood despite its conspicuousness and widespread occurrence. Various writers have compared it with hunger, a craving or sensation of discomfort which arises in the absence of a physical requirement. Trotter (1916:30) described gregariousness as an impulse in individuals to be in and remain with the flock and to resist anything which tended to separate them from it. Craig (1918) classified it as an appetite, which he defined as "a state of agitation which continues so long as a certain stimulus—is absent," and which is resolved as soon as the appetized stimulus is received. Wheeler (1928:11) compared it with the appetites of hunger and sex and noted its persistent nature and its striking effects on segregated individuals. Various psychologists have regarded it as a condition of responsiveness to social stimuli which, if blocked, leads to frustration activities.

Illustrations of gregarious behavior are not hard to find. Nearly everyone has watched stragglers from a flock of Starlings hurry to join their confreres, or has seen passing Crows respond to a flock of their kind on the ground. Duck and goose hunters are thoroughly familiar with the effect that a group of decoys has on their quarry. Alverdes (1927:108) noted how the artificial isolation of a social animal such as a dog produces numerous signs of discomfort while the presence of a companion, even one belonging to another species, will quiet these "social cravings." Stresemann (1917) discussed the fascination which a flock of birds holds for a segregated individual.

While few would deny this positive social reaction among the members of a flock, Allee (1931) and others have pointed out that there is another factor operating in the formation and regulation of aggregations, the factor of tolerance of social encroachment.

Social tolerance may be considered as promoting flocking behavior by permitting the members of a population to converge in response to either environmental or internal (gregarious) factors. For our purposes, however, it is convenient to consider tolerance in its negative aspect as intolerance, an expression of independence or self-assertion acting in opposition to forces which tend to bring birds together into flocks. Social intolerance is functionally the antithesis of gregariousness. If we follow Craig in calling the craving for companionship an appetite, this second, negative factor is an "aversion," a state of agitation which continues so long as a certain stimulus is present but which ceases when that stimulus is withdrawn (Craig, 1918).

This negative reaction of individuals to crowding is of widespread occurrence in animal populations of all kinds and needs little elabora-

tion. It is particularly conspicuous in birds and is nowhere better illustrated than in the territorial behavior of both colonial and non-colonial species. It underlies most of the situations which lead to conflict between individuals in nature and is considered basic in our modern concepts of the mechanisms of population regulation. Problems of social tolerance and the rôle of aggression in the integration and regulation of bird flocks have recently been reviewed by Collias (1944).

We thus have two opposing forces, a positive force of mutual attraction and a negative force of mutual repulsion, interacting in the formation of bird flocks. The positive force initiates the process and acts centripetally in drawing membership; the negative force serves a regulatory rôle, limiting the size of the flock and preventing close crowding through its centrifugal action. Such a concept may be criticized by those who, encountering difficulties in elucidating emotions in subhuman subjects, object to the word "force" as applied to bird behavior. In the present case, however, I am not referring to any stored or penned-up energy but simply to the cause of the centripetal or centrifugal movements observed, whatever that might be (see Webster's unabridged dictionary, 2nd edition, definition No. 15). The responses might be regarded as essentially tropistic and comparable to the prototaxes proposed by Wallin (1927).

No matter what terminology we choose, there seems little doubt that positive and negative social responses occur and interact. Craig observed this interaction in the behavior of his caged Ring Doves as they settled on their roosts for the night. Each bird, he says sought a perch close to friendly companions, *but not too close*, and the difficulties involved in satisfying both the appetite for companionship and the aversion for crowding often kept the birds busy for more than an hour. I have observed similar performances in roosting crows and in loafing flocks of starlings and swallows. By way of illustration, I would like to relate some observations which I made on Cliff Swallows, *Petrochelidon pyrrhonota*, during the past summer.

Cliff Swallows near a group of nesting colonies at Moran, Wyoming, spent much of their time loafing on spans of telephone wires. Positive social forces were immediately apparent in this behavior for the distribution of the birds over the available perches on the roosts was far from random. Of the thousands of linear feet of wire to be found in the area only a few relatively small sections were used at any one time. One or two birds, alighting apparently at random, typically served as the nucleus for a potential gathering. Other birds followed until an aggregation of 100 or more had accumulated, all within a space of 100 to 150 feet.

Negative social forces were also apparent, for in spite of the overall compactness of the group no bird ever held a perch closer than about four inches from its nearest neighbor. Birds were constantly arriving and leaving, and an unstable situation occasionally arose when a bird attempted to secure a perch too close to another, already-settled bird.

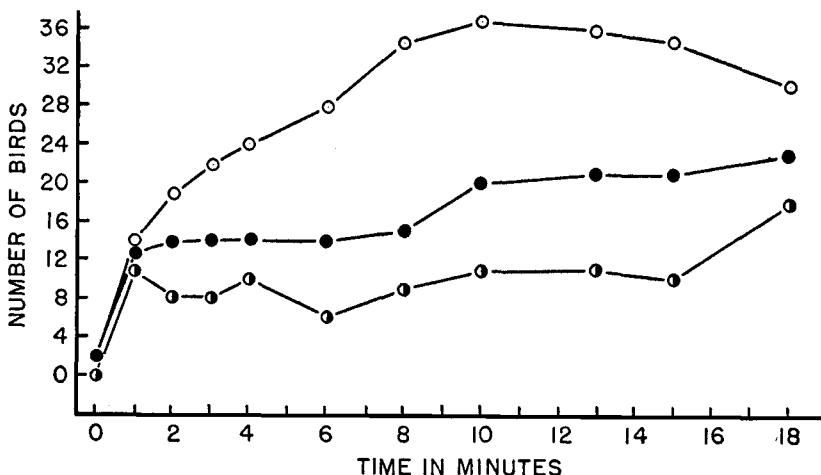


FIGURE 1. Sample curve showing increase in number of Cliff Swallows perching on the central third (open circles), east third (solid circles), and west third (half circles) of a section of telephone wires near Moran, Wyoming, August 4, 1950.

Shuffling and reshuffling inevitably followed until the proper spacing had been reestablished all down the line. Ten-inch gaps were filled centrally and without trouble, a six-inch space on the other hand was usually avoided and, if chosen, was invaded only with the accompaniment of aggressive displays and a local reshuffling of perches. Swallows move their feet but little when once settled and this tolerance limit of four inches may be related to the maximum reach of a bird from a fixed perch.

In an accumulating aggregation of this sort the central portion of the perching area tended to fill more rapidly than did the peripheral portions, and shifts from peripheral to central positions occurred more frequently than did shifts in the other direction. Thus when the perching area was optically divided by the observer into three comparable sections and the number of birds in each of the sections counted at one minute intervals, the central section was seen to grow most rapidly. If the process continued for some time, however, and the central section became filled to capacity, a change in the growth picture ensued and the central section stabilized or even declined while the peripheral sections advanced (Fig. 1).

Observations of territorial defense at the nests indicate that the same narrow but definite tolerance limitations that were seen in the resting flocks on telephone wires applied. The spatial arrangements of nests in the colonies also indicated that the proximity of nest openings was limited by the reach of a perching swallow. Details of these observations will be published shortly in another paper (Emlen, *in press*, Condor, 1952).

As I have already suggested, the size and density characteristics of a bird flock are determined by the balance of centripetal and centrifugal forces acting on an innate pattern of behavioral response. Without such forces we may assume that the dispersal of the members of a population over its range would be random. A positive social force acting alone on such a randomly distributed population would tend to produce clusters and might, if unchecked, lead to the complete aggregation of all individuals into one great and compact flock. Negative forces would presumably intervene, however, to limit and regulate this process of aggregation and, in balance with the positive forces, produce a pattern of small dispersed aggregations each in dynamic balance within itself and with neighboring aggregations.

Variations in the size and density characteristics of flocks may be interpreted as resulting from different balances of these positive and negative social forces. A few species under certain circumstances may exhibit the positive social attraction with very little of the negative element of intolerance. This apparently is the case in the sleeping clusters of tree swifts (Hemiprocnidae), wood swallows (Artamidae), and colies (Coliidae) (Allen, 1925:270; Pycraft, 1910:138). Roosting Passenger Pigeons were said by Kalm (1759) to pile up in heaps on the branches and by Audubon (1831:324) to form solid masses as large as hogsheads. Other examples of clustering occur, particularly among species which roost in cavities, but a far more common situation is to find the birds spaced and jealously defending their immediate surroundings even in large and dense flocks. Thus, swallows space themselves along telephone wires and rarely if ever tolerate physical contact with neighbors. Murres nest in dense colonies yet vigorously defend their immediate surroundings against others of their kind (Howard, 1920:143). Roosting crows, despite early accounts of clustering (Godman, 1842; Wright, 1897:178), characteristically adjust and re-adjust their perches on the outer twigs of the roosting trees until a suitable interval of three or four inches is achieved (unpublished personal observations made in California and New York).

Small flocks and flocks of low density may be regarded as representing a further shift in the balance through a reduced gregariousness,

an increased intolerance, or a combination of both. Even dispersed social groupings and territorial societies may be included in this concept as cases in which negative forces are strongly developed. Thus territorial Red-wings, *Agelaius phoeniceus*, for all their pugnacity, show many evidences of a colonial social bond (Robert Nero, unpubl. notes). Indeed, as Mr. Darling shows in the concluding paper of this symposium, social attraction may be an essential element of territorial display in relatively dispersed populations of non-colonial species.

The effects of non-social, physical factors of the environment such as a localized center of attraction or a localized source of repulsion may be superimposed on the pattern of dispersal set by the balance of social forces. When such factors are present aggregations may develop which violate the limits of social intolerance and precipitate fighting within the flock. Fighting, for instance, is common at winter feeding stations among species which rarely quarrel back in the brush where food is more generally dispersed.

Artificial confinement or other restrictions to free movement may have a similar effect. Fighting is frequent when birds are placed together in cages, and this is particularly noticeable among non-flocking species (Tompkins, 1933). It is also prevalent in very dense breeding populations of territorial birds where crowding creates the equivalent of spatial restriction (Palmer, 1941:100; Kendeigh, 1941:42). The increase in aggressiveness which accompanies the spring recrudescence of sexual activity in flocks of California Quail (Sumner, 1935:214) may perhaps reflect a temporary violation of social tolerance resulting from the inertia of the population in adjusting to internal changes in sociality.

With a fluctuating environment such as is encountered in northern and temperate latitudes and a fluctuating physiology such as is characteristic of nearly all birds, the balance of factors determining flocking behavior is obviously far from stable.

THE PHYSIOLOGY OF FLOCKING

Having noted the existence of centripetal forces related to social attraction and of centrifugal forces related to social repulsion operating in dynamic balance in bird flocks, it might be profitable to give brief attention to the physiological basis of flocking responses.

Since several forms of social behavior, such as those exhibited in the pairing relationship or in the parent-offspring relationship, are demonstrably stimulated and regulated by specific hormones, one is tempted to search for a hormonal basis for the definite and emotionally expressed social responses. No hormone for gregariousness has been

demonstrated, however. The emotional aspects of social behavior are probably related to nervous tensions arising as a result of frustrated attempts to follow a stereotyped neural pattern of social responsiveness.

Social intolerance, the disruptive element in flocking behavior, is, by contrast, often clearly related to the activity of specific hormones. Male sex hormones have been repeatedly shown to induce birds to fight with their flock associates, apparently as a part of the adjustment for sexual activity. Injections of a male hormone into free living California Quail in winter produced aggressive displays and, within a few days, withdrawal from the flock (Emlen and Lorenz, 1942). Castration, conversely, suppressed aggressiveness and fighting in male pigeons (Carpenter, 1932:522). Such responses in experimental birds suggest that the natural increase in sex hormone secretion by the gonads in spring is directly related to the disintegration of wintering flocks in many species.

Other hormones may influence general aggressiveness under special conditions. Prolactin induces maternal reactions (Riddle, 1935), a form of behavior which involves intolerance of flock associates. Thyroxin has little effect on domestic hens except at high levels when it decreases aggressiveness (Allee, Collias, and Beeman, 1940). Estradiol produces similar effects in hens at high levels (Allee and Collias, 1940).

It thus appears that flocking responses have their physiological basis in stereotyped neural patterns and are influenced by hormonal factors only as these incite disruptive responses associated with sexual or parental activity. The aggregated pattern of distribution, reflecting the unrestricted action of positive social responses of gregariousness may thus be regarded as the neutral or "resting" state, and any deviation from it toward a dispersed pattern, a state of tension effected by the introduction of negative social elements.

ENVIRONMENTAL FACTORS

The fluctuations in sociality which are characteristic of most if not all species of birds correlate with two great rhythms of the environment, the seasonal and the diurnal. In both of these the factors which are associated with increased flocking are those that may be considered unfavorable. This correlation of aggregative tendencies with unfavorable conditions has been noted and emphasized by Alverdes (1927) and various other writers concerned with a wide variety of organisms, both vertebrate and invertebrate. Such

generalizations should be extended with caution, however, for they may tend to hide the true relationships.

Seasonal factors fluctuate at a slower tempo than diurnal factors, and their effects may thus become integrated with the slower forms of response mechanisms in the bird's physiology, such as those which involve conspicuous morphological changes of the primary, secondary, and accessory sexual structures. Diurnal factors, on the other hand, fluctuate at a tempo which precludes major morphological adjustments, and behavioral fluctuations associated with them are more superficial.

Two factors associated with the seasonal cycle which commonly promote flocking are low temperature and low precipitation. These correlations may be seen in the normal seasonal activity cycles of many birds but are best illustrated, freed from the possible effects of innate rhythms, in the behavioral responses of local populations to irregular fluctuations of weather.

Although the spring recrudescence of sexual activity with its corollary aggressiveness is basically a physiological response to increased day-length, cold temperatures have a profound modifying influence. Red-winged Blackbirds, for instance, respond to a cold spell during early stages of the nesting cycle by abandoning their aggressively defended territories and returning to a winter flocking behavior (Beer and Tibbitts, 1950:63). Many other species behave similarly. Flocking should not be regarded as a general response to cold, however, for in those species which habitually breed in flocks, the effect of cold may be quite different. Thus Cliff Swallows in several colonies near Moran, Wyoming, in 1950 responded to an unseasonable cold spell early in the nesting season by temporarily abandoning their half-built nests and shifting for two days from one type of flocking behavior at the nesting site to another, slightly more dispersed type on foraging grounds several miles away (Emlen, *in press*, Condor, 1952).

Drought is another environmental factor which, occurring abnormally, may promote flocking responses during the non-flocking season. This has been noted in Gambel Quail, *Lophortyx gambelii*, in arid portions of southern California and Arizona where a failure of the usual spring rains inhibits the normal spring dispersal of the winter coveys (Leopold, 1936:28). Endocrine disturbances resulting from nutritional deficiencies are thought to be responsible (MacGregor and Inlay, 1951).

It thus appears that the behavioral responses of birds to unseasonable cold or drought constitute essentially a return to the non-breeding pattern of the species. This implies a suppression of sexual activity

and suggests a reduction either of hormone output or of responsiveness to persisting levels of hormone in the blood. Regardless of the mechanisms, however, we may conclude that unfavorable weather promotes flocking behavior by suppressing the disruptive element of social intolerance. There is no evidence that it directly modifies gregariousness itself.

Light intensity is the principal environmental variable of the diurnal cycle, and it is quite evident through observations of roosting behavior that darkness is associated with increased flocking in a great many species. One has only to recall the great roosting assemblages of such diverse birds as herons, gulls, vultures, pheasants, pigeons, swifts, crows, swallows, blackbirds, and robins to capture a realization of this response to the light cycle.

Such sudden fluctuations in sociality are probably not associated with hormonal changes such as those involved in the seasonal cycle; at least no such relationships have been demonstrated. Perhaps they can best be explained by relating them to the schedule of general activity imposed on the birds by alternating periods of light and dark. Night is a period of enforced inactivity for most birds, while the hours of daylight provide the only time during which foraging and other essential activities of self-maintenance can be performed. Self-maintenance calls for independent action which, while not necessarily involving social intolerance, entails a certain amount of freedom from interference. Thus, the members of a covey of quail disperse slightly from their compact roosting aggregation during the morning foraging period, may reunite to loaf during the noon hours, and then fan out again for a second feeding period before finally congregating for the night. The spectacular flights of blackbirds to and from their huge roosting assemblages reflect the same alternation of periods of activity and rest in a pattern and on a scale compatible with their special feeding habits and greater mobility. The limited acreage of a blackbird roosting-site could not conceivably support, even briefly, the hundreds of thousands of birds which congregate on it nightly.

Thus, after foraging in a relatively dispersed pattern, and in a relatively independent manner during the day, the members of a population are temporarily released from the demands of self-maintenance and are permitted to respond freely to their basic gregarious appetites.

RESUMÉ AND CONCLUSION

Symposia such as the present one provide perhaps a legitimate excuse for a little speculation. I hope that I have not abused this privilege and stepped too far beyond the firm shore of established facts.

My objective has been to develop a theoretical basis for interpreting flocking behavior and the various factors, both internal and external, which affect it. For this I have proposed that the form and density characteristics of bird flocks are determined by the interplay of positive and negative forces associated with gregariousness on the one hand and intolerance and independence on the other. Gregariousness has its basis in stereotyped neural patterns, and there is no evidence at present that it is affected directly by hormonal or environmental influences. Social intolerance and independence, on the other hand, are highly variable, and in their variations regulate and determine the dispersal or flocking pattern of the population. Flocking reaches its highest development when gregariousness is given free rein, unrestricted by conflicting demands of reproduction and self-maintenance.

LITERATURE CITED

- ALLEE, W. C. 1931. *Animal aggregations, a study in general sociology.* (Univ. Chicago Press, Chicago), pp. ix + 431.
- ALLEE, W. C., AND N. COLLIAS. 1940. The influence of estradiol on the social organization of flocks of hens. *Endocrinology*, 27:87-94.
- ALLEE, W. C., N. E. COLLIAS, AND E. BEEMAN. 1940. The effect of thyroxin on the social order in flocks of hens. *Endocrinology*, 27:827-835.
- ALLEN, G. M. 1925. *Birds and their attributes.* (Marshall Jones Co., Boston), pp. xiii + 338.
- ALVERDES, F. 1927. *Social life in the animal world.* (Transl. by K. C. Creasy). (Harcourt, Brace, New York), pp. ix + 216.
- AUDUBON, J. J. 1831. *Ornithological biography.* (Dobson & Porter, Philadelphia), pp. xxiv + 512.
- BEER, J., AND D. TIBBITTS. 1950. Nesting behavior of the Red-wing Blackbird. *Flicker*, 22:61-77.
- CARPENTER, C. R. 1932. Relation of the male avian gonad to responses pertinent to reproductive phenomena. *Physiol. Bull.*, 29:509-527.
- COLLIAS, N. 1944. Aggressive behavior among vertebrate animals. *Physiol. Zool.*, 17:83-123.
- CRAIG, W. 1918. Appetites and aversions as constituents of instincts. *Biol. Bull.*, 34:91-107.
- EMLÉN, J. T., AND F. W. LORENZ. 1942. Pairing responses of free-living Valley Quail to sex-hormone pellet implants. *Auk*, 59:369-378.
- GODMAN, J. D. 1842. *American natural history, Vol. II.* (H. Carey & I. Lea, Phila.), pp. 337.
- HOWARD, H. E. 1920. *Territory in bird life.* (John Murray, London), pp. xiii + 308.
- KALM, P. 1759. Beskrifning på de vilda Dufvor, som somliga år i så otrolig stor myckenhet komma til de södra Engelska nybyggen i Norra America. *Kongl. Vetenskaps-Akad. Handl. för ar 1759*, 20: 275-295 (transl. Gronberger, *Auk*, 28: 53, 1911).
- KENDEIGH, S. C. 1941. Territorial and mating behavior of the house wren. III. *Biol. Monog.*, 18: 1-120.

- LEOPOLD, A. 1936. Game management. (Scribner's, New York), pp. xxi + 481.
- MACGREGOR, W., AND M. INLAY. 1951. Observations on failure of Gambel Quail to breed. Calif. Fish and Game, 37: 218-219.
- PALMER, R. S. 1941. A behavior study of the common tern. Proc. Bost. Soc. Nat. Hist., 42: 1-119.
- PYCRAFT, W. P. 1910. A history of birds. (Methuen & Co., London), pp. xxxi + 458.
- RIDDLE, O. 1935. Aspects and implications of the hormonal control of the maternal instinct. Proc. Amer. Philos. Soc., 75(6): 521-525.
- STRESEMANN, E. 1917. Über gemischte Vogelschwärme. Verh. der Ornith. Ges. in Bayern, 13(2): 127-151.
- SUMNER, E. L., JR. 1935. A life history study of the California Quail with recommendations for its conservation and management. Calif. Fish and Game, 21: 167-256.
- TOMPKINS, G. 1933. Individuality and territoriality as displayed in winter by three passerine species. Condor, 35: 98-106.
- TROTTER, WM. 1916. Instincts of the herd in peace and war. (T. Fisher, Unwin. Ltd., London), pp. 213.
- WALLIN, I. E. 1927. Symbioticism and the origin of species. (Williams and Wilkins, Baltimore), pp. xi + 171.
- WHEELER, W. M. 1928. The social insects, their origin and evolution. (Harcourt Brace, New York), pp. xviii + 378.
- WRIGHT, J. S. 1897. Notes on crow roosts of western Indiana and eastern Illinois. Proc. Ind. Acad. Sci., 1897: 178-180.

*Department of Zoology, University of Wisconsin, Madison, Wisconsin,
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