

SOCIAL STIMULATION WITHIN BLACKBIRD COLONIES

By GORDON H. ORIANS

In 1938, F. F. Darling, writing about breeding colonies of gulls, suggested that (p. 3) "The social group and its magnitude, in birds which are gregarious at the breeding season, are themselves exteroceptive factors in the development and synchronization of reproductive condition in the members of individual pairs of birds and throughout the flock."

Support for this hypothesis was drawn from three types of evidence: the time of initiation of breeding; the synchrony of colony members; and the comparative breeding success of large and small colonies. On the basis of his results, Darling also postulated a number of corollaries, but it is important to note that the validity of the main thesis does not rest upon the truth of these corollaries. First, he suggested that synchrony was of value in reducing the loss of young to predators because the vulnerable stages were concentrated into a shorter period of time. Second, he believed that there was a threshold of numbers below which breeding would be unsuccessful. He did recognize, however, that this number may change with ecological conditions. Finally, he postulated that sexual dimorphism and elaborate displays had evolved because they stimulated the pituitary glands of other members of the breeding group. This explanation was thought to avoid some of the traditional difficulties felt in the Darwinian theory of sexual selection.

More recently, Darling (1952) extended his main thesis to cover territorial birds as well, postulating that the main value of a territory was that it provided a periphery of contact between pairs, thus offering greater opportunities for social stimulation. According to this view the area is defended primarily because the act of defense provides the stimulation necessary to bring the birds into reproductive condition and not because the area provides any vital requisites. The concentration of territories of breeding birds into pockets in what appears to be a uniform environment was offered as suggestive evidence in support of the hypothesis.

Early it was brought out that some of the supposed differences in success observed by Darling could be explained by variable age distributions (Lack, 1943; Armstrong, 1947), and it was subsequently demonstrated that Darling's original data were statistically insignificant (Haartman, 1945). Nonetheless, belief in the effectiveness of the "Darling Effect" became widespread (Lockley, 1942; Lowe, 1954) and it was even suggested that interspecific stimulation was important in mixed breeding colonies (Fisher and Lockley, 1954). However, neither the original ideas of Darling nor the suggestion of Lack and Armstrong were subjected to critical investigation until recently (Coulson and White, 1956, 1958, 1960).

Extensive data gathered on the ecology of social organization in Redwinged (*Agelaius phoeniceus*) and Tricolored (*A. tricolor*) blackbirds in north-central California (Orians, in press) afford the opportunity to examine timing, synchrony and breeding success in relation to colony size in these two species. The Redwing is not colonial in the strict sense of the word, but the size of territories is small and the males engage in conspicuous perched and aerial displays above the vegetation so that opportunities for social stimulation are good. The Tricolored Blackbird, on the other hand, is the most highly colonial of North American passerines (Neff, 1937; Lack and Emlen, 1939), and up to 100,000 nests may be concentrated in a few acres of marsh. Here, conditions for social stimulation should be maximal.

THE REDWINGED BLACKBIRD

In the Redwing, the time at which territories are first occupied and the amount of time spent on them early in the season vary greatly from place to place, but this is not correlated with colony size. Since all suitable habitat is fully occupied, the size of the breeding population is determined primarily by the size of the marsh and secondarily by the nature of the surrounding vegetation. Where extensive feeding areas immediately surround the emergent vegetation in which the nests are placed, most of the food is gathered off the territories and territories are the smallest (Orians, in press). Peripheral territories that are most advantageously located with respect to feeding grounds are most fiercely contested and are occupied first during the breeding season. The time of arrival of females and the onset of nest building parallels the pattern of territory establishment by the males, and territory contests among females are also most severe for peripheral areas. Therefore, breeding may on the average be later in larger marshes simply because there is less periphery per unit of nesting area. In California, where the breeding period comes at the end of the rainy season, the peak populations of insects are present earlier on the grasslands, which dry up in May or June, than on the marshes. Since peripherally located birds feed more away from the marsh than birds with territories in the interior of the marsh, it is reasonable to assume that this difference in timing is adapted to coincide with the maximum availability of food and not with any effects of social stimulation. No significant differences in time of breeding in Redwing colonies of different sizes were found by Mayr (1941) or Smith (1943).

Synchrony in this species is poor because of polygamy and the tendency of the several females of each male to be out of phase with each other. Renestings and second broods further complicate the picture. However, data are available on the dates at which first nests were started in seven small, isolated cattail patches at the East Park Reservoir, Colusa County, California, in 1960. Even when data for all seven areas are lumped together, 51 of 72 first nests were started within three days, the closest synchrony I have observed in this species. The spread of time during which first nests were started in the main marsh on the reservoir extended over a much longer period of time because nesting in central territories started later than in peripheral territories as already indicated. It is probably generally true in this species that the spread of breeding is greater in larger colonies (Smith, *op. cit.*).

Insufficient data are available to compare nesting success in colonies of different size. The nesting area at Jewel Lake, near Berkeley, California, was surrounded by oak forest with the result that the chief source of mortality was predation by the Scrub Jay (*Aphelocoma coerulescens*). In the dry foothills of Colusa County, on the other hand, starvation was the major cause of mortality. For any meaningful analysis of the influence of colony size on breeding success, colonies of varying size in comparable environmental situations would have to be studied, and such studies are not available. No differences in reproductive success correlated with colony size were discovered in Illinois by Smith (*op. cit.*).

THE TRICOLORED BLACKBIRD

Data on the date at which nest building started are available for 25 colonies of the Tricolored Blackbird ranging in size from 50 to about 100,000 nests (table 1). On the average, the larger colonies started later but this difference is related to the ecology of the breeding area rather than colony size *per se*. The breeding habitats of this species in California can be grouped into three main categories: the foothills, valley cropland with no rice, and the rice-growing country. Breeding begins first in the foothills and last in the rice-growing country (table 2). In the foothills, where there is little or no irriga-

tion, the insect supply doubtless diminishes sharply when the grasses dry up in May or early June. In the valley, where much of the land is irrigated, the country remains productive of insects for a much longer period. Moreover, the rice fields are not seeded until late April or early May, and until the grass has sprouted and the water level in the fields lowered three weeks later, there are neither feeding grounds nor food supplies

TABLE 1
TIME OF BREEDING IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Colony size	Number of colonies	Mean starting date	Range of starting dates
Less than 1000 nests	7	May 2	Apr. 21-May 17
1000-10,000 nests	5	Apr. 28	Apr. 15-May 17
More than 10,000 nests	13	May 9	Apr. 1-May 28

for the birds. It is not until the vigorous growth of the crop in the warm shallow water is fully under way in June that the maximum feeding potential of the area is realized. Since the rice country provides the best conditions for the breeding of the Tricolor and supports the largest colonies, the larger colonies tend to start later, and no influence of social stimulation can be detected.

Colonies of Tricolored Blackbirds of all sizes are characterized by remarkable synchrony of nesting. Normally, all nests are completed within a period of one week, but sometimes colonies grow peripherally and, rarely, new nests may be constructed throughout the colony (Orians, 1960). In colonies studied by me, the largest had the longest duration of egg laying. But if those colonies growing peripherally are excluded, synchrony is comparable in all size classes (table 3). There is thus no evidence of a stimulating effect of numbers upon synchrony.

If numbers are important in stimulating the reproductive cycles of colony members it might be expected that clutch sizes would, on the average, be larger in large colonies

TABLE 2
TIME OF BREEDING IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO HABITAT

Habitat	Number of colonies	Mean starting date	Range of starting dates
Foothills	8	Apr. 23	Apr. 1-May 17
Valley cropland (no rice)	6	May 2	Apr. 18-May 23
Rice country	11	May 15	May 1-May 28

than in small colonies. However, the results of determinations of clutch size in seven colonies (table 4) show no signs of the effects of social stimulation.

Nesting success in colonial species is notoriously difficult to determine. In the Tricolor desertions sometimes occur, probably in response to unfavorable feeding conditions in the surrounding environment (Orians, 1960). Moreover, the chance of loss to predators probably depends not only on colony size but also on the location of the colony with respect to habitat suitable for different predators and the accessibility of the nests. The effects of colony size *per se* in increasing the nesting success could only be determined if sufficient colonies of all sizes were available for a wide variety of environmental situations. As yet no such data are available nor are they likely to be obtained easily because, since colony size varies with environmental conditions, it is difficult, if not impossible, to find colonies of all sizes in all situations. Nonetheless, I have been able to determine the average size of colonies which failed completely (table 5). Complete failure has been more common in smaller colonies but in only some of these instances

could it be attributed to predators. In some cases desertion due to drought is indicated and usually it is the smaller colonies that are located in marginal situations where the effects of adverse weather are most strongly felt. Thus, nesting success does not appear to be very useful in evaluating the possible effects of social stimulation upon the breeding colonies.

TABLE 3

BREEDING SYNCHRONY IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Colony size	Number of colonies	Mean duration of egg laying	Range
Less than 1000 nests	6	7.5 days	5-18 days
1000-10,000 nests	5	6.2	4-10
More than 10,000 nests (Excluding concentrically growing colonies)	13 (7)	19.1 (7.1 days)	5-41 (5-10 days)

The three types of evidence which Darling sought in support of his thesis provide no support for the operation of social stimulation in colonies of Tricolored Blackbirds. It might be argued that all colonies of this species which I investigated were large enough to provide maximal stimulation to their constituents, but such an answer automatically relegates social stimulation to a position of minor significance. However, although it has been shown that time of breeding is not correlated with colony size but rather is related to feeding conditions in different habitats, certain features of timing remain unexplained. Outside the breeding period Tricolored Blackbirds are highly nomadic and are found largely within the Great Valley of California. Often flocks appear suddenly in areas from which they have been absent for months and immediately breed. Frequently, colonies in close proximity to each other may be strongly out of phase with each other. For example, three colonies in the rice fields north of Sacramento started on May 1,

TABLE 4

CLUTCH SIZE IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Colony size	Number of colonies	Total number of clutches counted	Mean clutch size	Range of mean clutch sizes
Less than 1000 nests	3	425	3.40	3.29-3.44
1000-10,000 nests	2	311	3.11	3.01-3.33
More than 10,000 nests	2	1433	3.09	3.09-3.11

May 8, and May 15, 1959, in spite of their being in uniform country and within two miles of each other. Unfortunately, I was not present when these particular birds appeared and so I could not determine whether or not they arrived in three separate, already integrated flocks. Although the possibility of subtle environmental differences between these sites, such as differences in the time of planting of the rice, cannot be ruled out, it is likely that there is considerable social stimulation within these nomadic flocks which results in their spectacularly synchronous breeding because the birds are probably in an advanced state of gonadal preparation while still wandering about. Social stimulation would be highly advantageous for a nomadic, colonial species adapted for utilizing ecological opportunities whenever and wherever they occur, because it would enable the wandering flocks to be able to respond immediately and simultaneously to favorable situations whose duration may be short as well as temporally and spatially unpredictable. It is important to note, however, that such social stimulation, if subsequently shown to be true, is not related to the territorial and mating displays which are used once breeding begins and which were the basis for Darling's original postulation.

DISCUSSION

In view of the difficulty in obtaining convincing evidence of the "Darling Effect" in spite of repeated efforts, and because of the widespread uncritical acceptance of the theory despite the lack of supporting evidence, it is desirable to consider whether the failure to obtain evidence lies with the hypothesis in general or with the sorts of evidence sought or both.

Theoretically, the hypothesis of social stimulation is certainly plausible, a fact which probably is responsible for no small part of its acceptance. Moreover, it is known that the maturation of female reproductive tracts lags behind that of the males in many

TABLE 5
NESTING SUCCESS IN COLONIES OF TRICOLORED BLACKBIRDS IN RELATION TO COLONY SIZE

Degree of success	Mean colony size	Range
Complete failure	2080 nests	600-6000 nests
At least partial success	36,570	50-100,000

species and that the females come into breeding condition only when they reach suitable breeding grounds where the males are already displaying. The evolution of this response is perhaps best explained in terms of the selective consequences of the relative energy expenditures of maturing and maintaining testes and ovaries (Orians, in press). In any case, there appear to be no good theoretical grounds for rejecting the operation of some form of social stimulation among birds even if one wished to reject its use to explain the evolution of coloniality or territoriality.

However, more serious objections may be raised to the three types of evidence which Darling sought in support of his hypothesis, because important ecological variables were ignored. For example, it is necessary to assume that the modal breeding period of any species is the most advantageous time at which to breed. In species raising more than one brood, timing problems are more complex but the general principle holds. If this were not true the time of the breeding period would be shifting in one direction or the other under the influence of natural selection. This immediately raises the problem of the supposed selective advantage of earlier breeding in the larger colonies. Apparently neither Darling nor Coulson and White (1960) attached particular selective significance to these differences, but any feature of reproductive biology is likely to be under strong selective pressure and we must conclude that any tendency toward earlier breeding which might be fostered by social stimulation must necessarily be opposed by the action of natural selection. Moreover, differences in timing are already apparent at the time the birds arrive on the breeding grounds so that it is necessary to postulate that the effects of social stimulation carry over from one season to the next but this is highly unlikely. In any case, this makes social stimulation into quite a different phenomenon than originally constituted.

It was early pointed out by Lack (1943) and Armstrong (1947) that age composition of colonies of such birds as gulls and fulmars had been ignored by Darling and others subsequently applying his ideas. Since older individuals are known to breed earlier than younger ones and since many small colonies are composed of young birds, differences observed among colonies might be due to this cause. Apparently this suggestion was without effect until Coulson and White (1956, 1958, 1960) carefully investigated the age structure of colonies of the Kittiwake (*Rissa tridactyla*) and the influence of age on time of breeding. Through intensive studies of marked individuals they determined that birds bred progressively earlier in subsequent years and that the small colonies they

investigated contained a higher percentage of younger birds. Nonetheless, differences in time of breeding which could be attributed to age composition could account for only part of the differences observed. Apparently no selective advantage for earlier breeding by older individuals has been suggested, but it may be that because of their greater efficiency in food gathering older birds are able to do better earlier when the total food supply is less. Alternately, the advantage may be related to the obtaining of the best nesting sites.

Darling assumed that synchrony was necessarily good, and it is true that short duration of food supply, the advantages of communal exploitation, or the action of predators may favor synchrony, but there are good ecological reasons for believing that asynchrony may be more advantageous under many circumstances. If the food resources exploited by the breeding population are available for relatively long periods of time and, moreover, if there is recruitment to the food supply during that period, it may be decidedly advantageous to a population to spread its breeding effort rather than to concentrate it. Thus, lack of synchrony cannot be interpreted as detrimental to any species unless a careful ecological study has revealed this to be so.

Comparative data on breeding success are even more difficult to obtain and interpret. It is well known that in most species breeding occurs in suboptimal as well as optimal habitats. In territorial species the territories are smallest in the latter and in colonial species the colonies are largest. This was clearly demonstrated in the case of the Tricolored Blackbird, and other instances are discussed by Lack (1954). There is also evidence that breeding is less successful in suboptimal habitat than in optimal although it is not known how widespread this is (Kluyver, 1951; Lack, 1958; Orians, in press). Thus it is to be expected that small colonies of birds would have poorer breeding success than larger colonies, social stimulation or not. In Darling's analysis of breeding success, and in all subsequent analyses as well, the size and density of breeding colonies are the only variables which have been considered. Investigators have readily assumed that the environment is uniformly suitable for all breeding localities under consideration. Whereas it may be relatively easy for a terrestrial human to ignore spatial and temporal variations in the oceanic environment which are of significance to birds, it is difficult to ignore them in terrestrial conditions. Nonetheless, this has been done in previous studies of the Redwing (Mayr, 1941; Smith, 1943) although Smith clearly recognized the presence of spatial variability. Coulson and White also assumed ecological uniformity of environment for colonies of Kittiwakes. This assumption may be all the more hazardous in colonial species in which, because of the large numbers of individuals utilizing the environment from a single spot, the distance an individual must fly to procure food for the young and the searching time for, as well as the energy content of, individual food items become of paramount importance. These may be strongly influenced by the number of birds involved and the precise location of colonies with respect to suitable feeding areas that doubtless vary both spatially and temporally. Therefore, it may be strongly doubted whether pursuit of the three types of evidence originally suggested by Darling will prove very fruitful in determining the role of social stimulation in avian social organization.

Darling originally thought that there would prove to be a lower limit to colony size below which successful breeding was impossible. It has since been repeatedly shown that isolated pairs of normally colonial birds are physiologically quite capable of successful reproduction. The extension of the hypothesis to territorial species demands more careful attention however. It was first suggested by the clumping of territories in apparently uniform habitat. We may consider the possibility of both accepting and rejecting the assumption of uniformity of the habitat. It is obvious that caution is always necessary because what appears uniform to the human observer may not be uniform to the bird

in question. However, it is possible to press this argument too far inasmuch as no two places are ever identical and thus the critic can always find subtle differences to which he can point. To determine whether these differences are really responsible for the clumping is no easy matter.

Alternately we may accept the postulate of environmental uniformity in these cases and ask whether clumping might nevertheless result irrespective of any stimulatory effect of displays upon reproductive physiology. The most likely possibility is that one of the cues which a bird uses to evaluate the suitability of a habitat is the presence of other birds of the same species. Such a response should be advantageous because presumably earlier arrivals would have departed had the area not been suitable. It is this attraction of newly arriving birds to individuals already present which forms the basis for the use of decoys in duck hunting, probably a special case of a widespread phenomenon. Thus, clumping might be produced in this manner in the absence of any need for social stimulation in the narrower sense in which Darling employed the term.

It might be argued that since continued efforts have failed to produce good evidence of the Darling Effect and since the interpretation of data is fraught with difficulties, that the effect is nonexistent, or, if existent, not demonstrable, but neither conclusion necessarily follows.

In spite of the ecological difficulties inherent in any investigation of social stimulation, modified techniques may prove to be useful. Data from the Tricolored Blackbird suggest that in nomadic species where the flock may be very close-knit prior to the initiation of breeding, and where the selective value of rapid and synchronous response to suitable conditions is great, social stimulation is likely to play an important role, even though this role is somewhat modified from the sort of stimulation envisioned by Darling. Nomadic species are unable to use the standard environmental clues, such as daylength, in the same manner as species with predictable breeding periods in more stable environments (Marshall, 1959). As yet, however, the gonadal cycles of nomadic species are largely unknown and even less is known of the responses of their reproductive systems to various environmental factors. Information currently being gathered in Australia indicates that nomadic species may remain for long periods with gonads in relatively advanced states waiting for suitable environmental conditions. When rain falls, breeding may be dramatically sudden (Allen Keast, personal communication) and the role of mutual stimulation may be important. Whatever the outcome of these investigations, nomadic species would seem to be better suited to studies of the significance of the Darling Effect than stationary colonial or territorial species where ecological variability appears to exert the dominant influence upon differences in timing, synchrony and nesting success. The evolution of territorial and colonial forms of social organization is strongly influenced by the ecology of environmental exploitation by the populations (Orians and Pitelka, MS), and any stimulation which appears is probably a minor secondary phenomenon in such species.

SUMMARY

Data from breeding colonies of Redwinged and Tricolored blackbirds in California were analyzed to determine the role of social stimulation in time of breeding, synchrony, and reproductive success. Variations in timing and synchrony in the Redwing were correlated with the nature of the marsh and its surrounding vegetation and not with size of the breeding population. In the Tricolored Blackbird time of breeding, synchrony, and clutch size were also found to be independent of colony size. Nesting success in both species could not be evaluated with respect to colony size *per se*.

Nonetheless, although most variability appears to be ecologically rather than socially

induced, there remain differences in time of breeding in colonies of Tricolors in close proximity to each other not obviously explained in this manner. Since flocks appear suddenly and breed immediately in areas from which they have been absent for months, group stimulation may operate in the nomadic flocks prior to the initiation of breeding.

The social stimulation theory currently fails to consider the selective significance of proposed changes in timing and synchrony and neglects important aspects of the ecology of the environment which may vary temporally and spatially. When these are taken into account the usual information sought in support of social stimulation is seen to be of limited use. Nomadic, colonial species are suggested as the best subjects for future studies of the "Darling Effect."

LITERATURE CITED

- Armstrong, E. A.
1947. Bird display and behaviour (L. Drummond, London).
- Coulson, J. C., and White, E.
1956. A study of colonies of the kittiwake *Rissa tridactyla* (L.). *Ibis*, 98:63-79.
1958. The effect of age on the breeding biology of the kittiwake *Rissa tridactyla*. *Ibis*, 100:40-51.
1960. The effect of age and density of breeding birds on the time of breeding of the kittiwake *Rissa tridactyla*. *Ibis*, 102:71-86.
- Darling, F. F.
1938. Bird flocks and the breeding cycle (Univ. Press, Cambridge [England]).
1952. Social behavior and survival. *Auk*, 69:183-191.
- Fisher, J., and Lockley, R. M.
1954. Sea-birds (Collins, London).
- Haartman, L. von
1945. Zur Biologie der Wasser- und Ufervogel in Scharenmeer Sudwest-Finnlands. *Acta Zool. Fenn.*, 44:1-120.
- Kluijver, H. N.
1951. The population ecology of the great tit, *Parus m. major* L. *Ardea*, 39:1-135.
- Lack, D.
1943. Fisher and Waterston on the fulmar. *Ibis*, 85:115-116.
1954. The natural regulation of animal numbers (Clarendon Press, Oxford).
1958. A quantitative breeding study of British tits. *Ardea*, 46:91-124.
- Lack, D., and Emlen, J. T.
1939. Observations on breeding behavior in tricolored redwings. *Condor*, 41:225-230.
- Lockley, R. M.
1942. Shearwaters. Reprinted 1946 (J. M. Dent and Sons, London).
- Lowe, F. A.
1954. The heron (Collins, London).
- Marshall, A. J.
1959. Internal and environmental control of breeding. *Ibis*, 101:456-478.
- Mayr, E.
1941. Red-wing observations of 1940. *Proc. Linn. Soc. N. Y.*, 52-53:75-83.
- Neff, J.
1937. Nesting distribution of the tri-colored redwing. *Condor*, 39:61-81.
- Orians, G. H.
1960. Autumnal breeding in the tricolored blackbird. *Auk*, 77:379-398.
In press. The ecology of blackbird social systems. *Ecol. Monog.*, in press.
- Smith, H. M.
1943. Size of breeding populations in relation to egg-laying and reproductive success in the eastern red-wing (*Agelaius p. phoeniceus*). *Ecology*, 24:183-207.

Museum of Vertebrate Zoology, University of California, Berkeley, California;
present address, *Department of Zoology, University of Washington, December 9, 1960.*