# SOCIAL BEHAVIOR OF NESTING BREWER'S BLACKBIRDS

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Clumped distributions of animals in space and time pose several interesting questions. Is the clumping due to a common response to an external stimulus or is it a result of an aggregating tendency in the animals themselves? If it is the latter, how do the animals communicate and synchronize their activities?

Darling (1938) addressed these questions when he observed a correlation between the number of sea birds in a colony and their average clutch size. He also noted that the larger colonies were earlier and more nearly synchronous in their breeding than smaller ones. Accordingly, he suggested that contagious social behavior stimulates the physiological preparations for breeding. Darling's observations have been given alternative explanations (Fisher 1954; Coulson and White 1956, 1960), but his work has stimulated further hypotheses about the mechanisms behind synchronous nesting. These mechanisms have been reviewed by Hailman (1964): (1) a common response of all pairs to temporal cues in the environment; (2) a concommitant of normal behavioral responses, such as the approach to conspecifics for pair formation or the progression of responses to displays of a mate; (3) an increased recruitment of individuals to places already occupied by birds in like reproductive condition (after Orians 1961); and (4) a positive contagion of displays that influence reproductive condition (after Darling 1938).

I have previously analyzed the adaptive significance of spatial and temporal clumping in nesting Brewer's Blackbirds (*Euphagus cyanocephalus*), finding that this clumping improves their foraging efficiency and predator avoidance only when the colony is built in a large expanse of nesting habitat, surrounded by abundant, but patchily distributed, food (Horn 1968). Since such ideal sites are rare relative to the number of breeding blackbirds, it is appropriate to ask whether these groups are really colonies, or passive aggregations of birds in the most favorable localities.

Following Hailman's outline, I shall first examine the characteristic features of the environment that supports nesting colonies of Brewer's Blackbird in eastern Washington. I shall then describe the normal mating behavior of the birds and, finally, examine the effect of contagious behavior on the synchrony of nesting.

## STUDY AREA AND METHODS

The area of this study is about 30 km<sup>2</sup> of channeled scabland in Grant and Adams Counties, Washington, known locally as the "Potholes." Parts of the study site are on the Columbia National Wildlife Refuge. Since the area receives only 20 cm of precipitation annually, most of the standing water seeps from a rising water table, charged by irrigation that began locally at the turn of the century and increased in 1951 through the efforts of the U.S. Bureau of Reclamation. It is unlikely that Brewer's Blackbirds bred on the study area prior to the formation of ponds and streams. The upland steppe vegetation is dominated by sagebrush (Artemesia tridentata), bluegrass (Poa sp.), and bunchgrass (Agropyron spicatum). Rabbitbush (Chrysothamnus viscidiflorus) and greasewood (Sarcobatus vermiculatus) dominate sandy areas and alkaline pans, respectively. Cheatgrass (Bromus tectorum) covers heavily grazed and well-watered areas. Sedges (Carex sp.), Scirpus, and a few patches of cattail (Typha angustifolia) border standing water and streams. Willows (Salix amygdaloides) are found along the older streams.

In 1964 and 1965 I camped continuously in the Potholes from mid-April to mid-June; in 1966, from late April through May. The nine colonies that I studied and the lakes for which they were named are mapped in figure 1, along with several other colonies and areas with scattered single nests. Each colony had 10-30 pairs of nesting birds, few enough to allow me to observe the behavior of individual pairs and their contributions to the behavior of the whole colony. In 1966 I pitched my tent in the middle of the Pit-Teal colony to watch mating displays at close range without disturbing the birds. To record and play back the vocalizations of displaying birds and to time behavioral sequences, I used a Uher Report-S 4000 portable tape recorder and a transistorized timer that gives an audio signal at fixed intervals. The activities around each nest were recorded in a daily or bi-daily log, and the position of each nest was mapped on 15X enlargements of aerial photographs obtained from the U.S. Agricultural Stabilization and Conservation Service. From these maps I could measure the distance of each nest from the "centroid" of the colony; that is, the point that has as coordinates the mean coordinates of the nests considered. Further details of my methods are recorded in Horn (1966).

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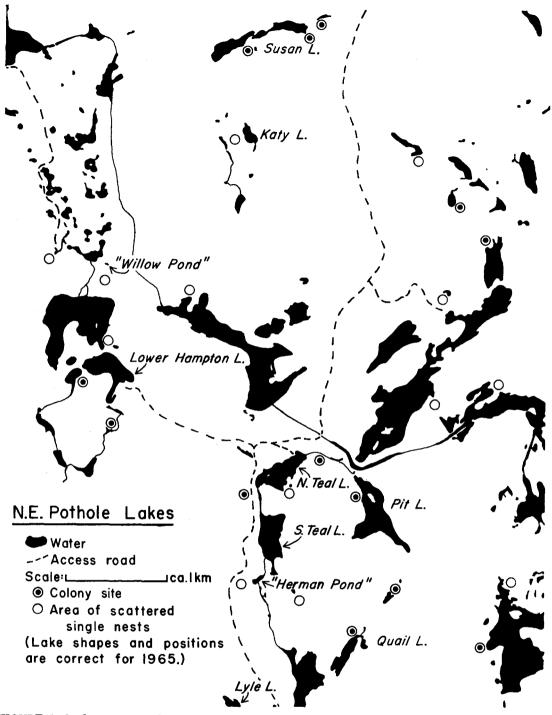


FIGURE 1. Study sites in northeastern Pothole Lakes. Circled dots show the locations of colonies of Brewer's Blackbird found from 1963 through 1966. The colonies studied are near the named lakes.

## RESULTS AND INTERPRETATIONS ENVIRONMENT

From figure 1, it is obvious that the nests of Brewer's Blackbirds in the Potholes are always near water. Thus the clumped distribution of nesting blackbirds may be due in part to the patchy distribution of standing water. However, there are three other features characteristic of the environment that supports nesting colonies of Brewer's Blackbird. These are a nearby foraging area, nesting sites, and a relatively high perch from which the nest sites are visible. The adult birds forage in short grass along the borders of

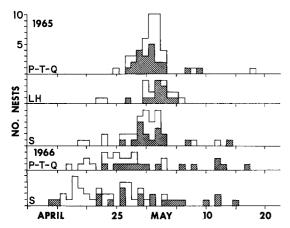


FIGURE 2. Nesting dates of Brewer's Blackbirds. The number of nests in which the first egg was laid on a given date is plotted for each date. Data are pooled for colonies near each other (fig. 1): 5 colonies near Pit, Teal, and Quail Lakes (P-T-Q); 2 colonies near Lower Hampton Lake (LH); and 3 colonies near Susan Lake (S). The shaded entries are nests ultimately destroyed by predators. Later nests were subjected to heavier predation than early nests.

watercourses where they collect naiads and tenerals of recently emerged damselflies (Coenagrionidae). Nests are built in the more densely foliated sagebrush. The males stand guard on high perches near the colony while the females are incubating; from these perches they fly out to harry potential predators (Horn 1968).

I searched the study area to find sites where two of these features were found in the absence of the third. No colonies were found in the absence of water bordered by short grass, although foraging Brewer's Blackbirds were occasionally seen near water bordered by either a bluff or tall emergent vegetation. Single nests were occasionally found where there were no extensive areas of densely foliated sagebrush, but no nests were found in sites that lacked the high perch. All sites that had all three features, the foraging and nesting areas and a nearby perch, had either active colonies or a number of nests left over from former years. Since the favorable areas are few, relative to the amount of food to be found nearby (Orians and Horn, in press), a patchy distribution of nest sites is in part responsible for the spatial contagion of nesting Brewer's Blackbirds.

The gross timing of breeding is probably also controlled by cues in the environment. Figure 2 shows that peak periods of nesting are coincident in widely separated areas of the Potholes. The variation of nesting times changes from year to year, but this pattern is also common to widely separated areas.

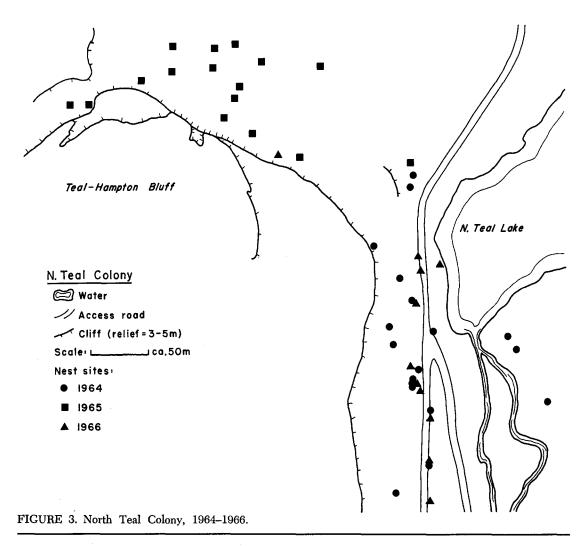
The first evidence that colonies are more than passive aggregations comes from observed changes of colony site. Each colony dislocated from its 1964 position moved as a unit to a new location in 1965. Figure 3 shows the locations of nests in the N. Teal colony in 1964, 1965, and 1966. In 1964 the nests were in a line beneath a cliff, close to the main foraging area, a stream and sedge meadow, and the north end of S. Teal Lake. In late April of 1965 at least 12 pairs of birds were present in the area of the 1964 colony and I saw five females defending prospective nest sites. On 25 April the fishing season opened and refugees from civilization swarmed over the area between the road and the stream, which had been closed to fishing in 1964. The birds were apparently disturbed at a critical time, as they immediately relocated their activities in a dry canyon to the northwest. When the fishing season opened in 1966 (17 April) the birds had not yet chosen nest sites, and in spite of the garrulous throng of fishermen nearby, they nested again in the area of the 1964 colony.

Similar relocations of the Quail and Pit-Teal colonies occurred in 1965, the former in response to deterioration of the sagebrush in a portion of the old colony area, the latter because a Loggerhead Shrike (Lanius ludovicianus) nested in the old area and drove the blackbirds out of a portion of it. In both of these colonies, as in the N. Teal colony, the birds in 1965 continued to forage in the areas used in 1964, often flying greater distances than if they had nested in the old areas. At least a few sites in the old areas were suitable for nesting in 1965, and in fact used again in 1966. Thus relocations seemed to involve the whole colony, including individuals who could have occupied parts of the old area to their advantage.

## MATING DISPLAYS

The unitary movement of each colony suggests that the birds affect each other's behavior during nest-building, which further suggests that some patterns of behavior are contagious between nesting pairs. Such contagious behavior must, of course, be interpreted in the context of the normal behavior of independent pairs.

Pairing takes place in foraging flocks during late winter and early spring. Thus the birds arriving at a prospective colony site are already paired. In the Potholes a slight surplus of unpaired males is found early in the breed-



ing season. The paired birds stay together in all their activities, the male following the female as she chooses and defends a nest site, builds the nest, and forages. Presumably the guarding behavior of the male during this period increases the likelihood that his mate's offspring will also be his own.

The ethology of breeding Brewer's Blackbirds has been described by Williams (1952) for a colony in Carmel, California. I have used terminology that differs slightly from that of Williams, not because of any substantial difference in the behavior of birds in the Potholes, but because I wish to include the call as part of a display, and I did not distinguish some of the subtler differences that Williams noted.

The displays are briefly described below, with Williams' equivalents in parentheses.

Song. The wings and tail are spread out and downward and most of the visible contour feathers are ruffed out (Ruff-out) while the bird utters what passes for song in this species. This display is frequently exchanged between members of a pair. It is also used by the male in response to a precopulatory display by the female and prior to copulation.

Precopulatory display. The wings are lowered and fluttered and the tail is cocked (includes the Female precoitional display, Female generalized display, and Male elevated tail display of Williams 1952), while a repeated staccato note is uttered. This display is used by the female soliciting copulation. The female also uses this display when leaving the nest site early in nest-building; her mate follows immediately. During the nestbuilding and egg-laying stages of a colony, the female uses this display quite often, invariably with an attracting effect on her mate and any other males nearby. The male occasionally uses a similar display, often alternated rapidly with the song display, when his mate has given a short precopulatory display or initiated a sexual chase but shows no further interest in copulation.

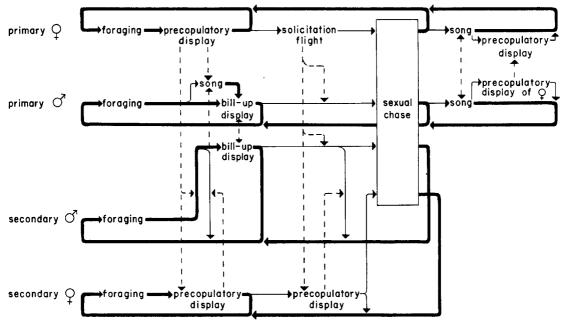


FIGURE 4. Interaction of sexual displays in Brewer's Blackbirds. The abscissa is time (except for return to foraging). The ordinate approximates the spatial positions of the birds. A heavy arrow shows a transformation observed in 3/4 or more of the observation periods. A light, solid arrow shows a transformation observed in 1/4 or fewer of the observation periods. A broken arrow points to an action that (if it occurs) is invariably preceded by the action whence the arrow originates.

Bill-up display. The bill is pointed almost vertically and the feathers sleeked (Head-up display); no call is given. This display is exchanged between males who are close together in the presence of one or more females. It is also used by females in defending nest sites against other females and against males other than their mates.

Sexual chase. The female is pursued by her mate and usually several other males (Chase). The sexual chase is usually initiated by a sudden advance of the male (Dart), but the female may initiate it with a solicitation flight, in which she flies with a slow, stalling wingbeat.

The information that these displays communicate is clarified by a discussion of figure 4, which summarizes observations of 46 encounters between foraging pairs. When a female gives a precopulatory display, the males of nearby pairs are attracted. Their females then give the same display, often drawing them back. Males in proximity to each other exchange the bill-up display until one of them is intimidated. A solicitation flight attracts all nearby males, whose females may then give precopulatory displays to draw them back. After a sexual chase, a male may give a display similar to the precopulatory display of the female, eliciting further precopulatory display by the female.

The use by males of a display identical to the soliciting posture of the female has been noted in certain Fringillidae, Spermestidae, and Ploceidae (Morris 1954; Hinde 1955-6; Marler 1956; Andrew 1957; Immelmann 1962; Crook 1964). The motivation of this behavior has been discussed by Hinde, who interprets the display as sharing tendencies of sexual and escape responses. Such a motivational analysis of the display by Brewer's Blackbirds seems unnecessary. The display clearly elicits solicitation by the female. Given the contagion of the precopulatory display among females, which presumably has evolved as a mechanism for retention of a mate in the presence of other displaying females, a similar display by the male might be expected to elicit further display by the female. Thus the observed effect of the male display could account for its function, motivation, and derivation.

The performance of the precopulatory display by a given female increases the likelihood of the same display by nearby females. This observation was confirmed experimentally in 1966. I recorded the calls of a displaying female in the Pit-Teal colony. Within the next hour I played the recording six times at irregular intervals. Each time I played the recording, the nearest female (the one recorded, and always within about 10

TABLE 1. Contagion of precopulatory calls of Brewer's Blackbirds.

No. calls initiated per 10-sec interval:	0	1	2	3 or more
Observed Poisson with	67	20	24	14
same mean	51	46	20	6

m of my tent) immediately gave a precopulatory display. On one of these six occasions an additional female also displayed immediately.

Contagion of precopulatory displays has also been noticed by Howell and Bartholomew (1952, 1954) in studies of the responses of Brewer's Blackbirds to various models of a female in the copulatory stance.

#### SYNCHRONY OF NESTING

The contagious displays in a colony of Brewer's Blackbirds contain information about the reproductive states of the birds. I could easily assess the state of nesting in a given area by observing the birds for a few minutes in the morning or evening. But do the birds actually communicate their reproductive states to each other and use this information in a way that affects their nesting pattern?

Precopulatory display is particularly frequent at the nest site during the last two days of nest-building, when the lining of the nest is formed. The tendency for precopulatory display by one female to increase the likelihood of display by nearby females should result in a synchronization of precopulatory displays within a colony. Data confirming the expected synchronization are presented in table 1. The number of precopulatory calls initiated per 10-sec interval was recorded in the 1965 Pit colony 2 days before the peak period of laying first eggs. There were significantly more periods with several displays than would be expected were the displays of individual females independent of each other. Since the likelihood of a precopulatory display by a given female in a given 10-sec interval is extremely small, comparison with the Poisson series (Fisher 1958:54) is appropriate as a measure of randomness. The observations are significantly different from the Poisson series, since the chi-square measure of the difference is 25.45, while chisquare for P = 0.05, with 3 df = 7.8.

If communication of breeding condition reduces the variation in nesting times, there should be a correlation between the synchrony of nesting and some measure of the compactness of the colony. The efficiency

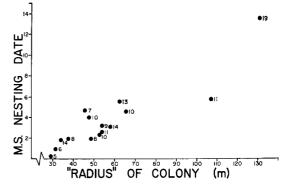


FIGURE 5. Synchrony of nesting and spacing of the nests of Brewer's Blackbirds. The mean square (an estimate of variance) of the date when the first egg was laid is plotted against the mean distance to the centroid of the nests considered. Next to each point is the number of nests in the colony.

of vocal and visual communication should vary inversely with the average distance between pairs and the total area over which they are spread. In testing for such a correlation, I used only those nests that were in sight of each other and excluded single nests that were built more than two days before or after other nests in the colony. I excluded the latter nests for two reasons. First, their owners were not exposed to the peak period of display by the other birds; second, the inclusion of the extreme nests would have inflated the measure of synchrony disproportionately. The synchrony of nests in each colony was measured by the mean square (an estimate of variance) of the date when the first egg was laid. A high mean square indicates little synchrony; a low mean square indicates a high degree of synchrony. Compactness of the nests was measured by the mean distance to their centroid, a measure that varies inversely with the density of the nests and directly with the area over which they are spread.

The data of figure 5 show that breeding synchrony is correlated with the compactness of the colony. The Kendall rank correlation coefficient (Siegel 1956:213, 223) is 0.85, a significant value. When the effect of joint correlations with the number of nests is removed, the partial correlation between synchrony and compactness is 0.79, still a relatively high value. (A significant inverse correlation between synchrony and the number of nests in the colony is reduced from 0.55 to 0.09 when the effect of joint correlation with mean distance to the centroid is removed.) The correlation of synchrony with the spacing of the nests suggests that the observed contagion of mating displays may be in part responsible for the synchronization of nesting.

## DISCUSSION

The correlation of synchrony with spacing is evidence that contagious displays synchronize nesting, but a correlation of synchrony with the number of birds in the colony is uninformative. In small samples, early and late nesters are typically ignored since they have a disproportionate effect on the measure of synchrony (e.g., Coulson and White 1956; this study). When samples are larger, however, values that were rejected in small samples are less likely to be considered extreme. Therefore the variance of nesting in small colonies will underestimate the variance of the population as a whole, while the variance of larger colonies will more accurately estimate that of the population. (This statement does not vitiate the selection of data since we are measuring synchrony in a specific colony, not estimating a parameter of the population.)

The effect of interactions between birds will be superimposed on this basic pattern of increasing variance in larger colonies. If contagious display accelerates the development of reproductive condition and if, as Darling (1938) suggests, the acceleration is proportional to the number of birds displaying, then the variance of nesting should be reduced by a greater amount in larger than in smaller colonies, decreasing or even reversing the correlation between variance and colony size. If, on the other hand, a colony recruited birds that are in the same reproductive state as those already established in the colony, as suggested by Orians (1961), then the correlation between colony size and variance of nesting time should be preserved. The more birds there are in the colony, the greater is the chance of attracting extreme nesters. Thus Darling's hypothesis does not give a clear a priori prediction of a correlation between synchrony and colony size. The effect predicted by Orians' hypothesis cannot be easily distinguished from the effect of selecting data to give a uniform measure of synchrony.

Neither does the correlation of synchrony with spacing discriminate the mechanism by which synchrony is achieved. Stimulation of gonadal growth by displays of conspecifics other than the prospective mate has been demonstrated only for the Budgerigar, *Melopsittacus undulatus*, (Brockway 1964, 1965) and the Ring Dove, *Streptopelia risoria* (Lott et al. 1967). However, experiments showing the stimulating effect of displays by a mate (Polikarpova 1940; Warren and Hinde 1961) give some hope that the phenomenon may be as general as it is often assumed to be (cf. Lehrman 1959). An alternative mechanism, the recruitment of pairs to places already occupied by pairs in like reproductive condition (Orians 1961), has yet to receive a critical test. However, this "contagious recruitment" is not a satisfactory explanation the increased synchrony of compact for colonies of Brewer's Blackbird, because the nest sites are chosen at least a week before the peak period of sexual display. Whatever the mechanism, it is clear that the nesting of a colony is more nearly synchronous than would be the nesting of independent pairs of Brewer's Blackbirds.

It is perhaps easier to get unequivocal results from field studies of the survival value of synchronous breeding. Darling (1938) suggested that if the rate of predation is constant with time and fairly low, birds that breed during the peak period of nesting are less likely to lose their nests than birds that nest earlier or later. Darling's suggestion has been applied interpretively to colonies of gulls and terns (Cullen 1960; Ashmole 1963; Kruuk 1964), and Patterson (1965) has confirmed it in the Black-headed Gull (Larus ridibundus) by demonstrating a correlation between the proportion of nests started in a given five-day period and the surviving fraction of eggs laid during that period.

A similar mechanism could conceivably favor synchrony in the Brewer's Blackbird, but the data of figure 2 do not show it. The adaptive significance of synchronous breeding must in this case be related to the advantages of coactive behavior in foraging and avoiding predation (Horn 1968). A substantial net advantage to synchrony, even if based on coactive behavior, should be demonstrable by an analysis like that of Patterson, but the colony size of the Brewer's Blackbird is too small to demonstrate any but the grossest effects by this analysis.

## CONCLUSIONS

Though both the nesting site and the timing of breeding are largely determined by the suitability of the environment, adjustments in both are made by the birds. The adjustments of each pair are affected by the behavior of other pairs. Thus there is evidence that colonies of the Brewer's Blackbird are more than passive aggregations of birds in the most favorable sites.

A common response to factors in the external environment is probably important in the choice of a suitable nesting site, and in the gross timing of the breeding cycle. The initial aggregation of birds synchronizes the normal activities of individual pairs. In particular, the contagion of displays of pairs might be expected as a consequence of the evolution of individual behavior. Either these displays are stimulatory or there is a similar contagion of recruitment to the colony, as evidenced by the correlation between synchrony of nesting and spacing of the nests. The distinction between these mechanisms is physiological; both give the same ecological result, synchronizing breeding in a given area. Both involve communication of reproductive state among pairs of birds, and therefore both suggest that the colony is more than a passive aggregation of independent pairs.

The results of this study apply only to the Brewer's Blackbird. However, the methods are generally applicable to test a cautious hypothesis that any species is indeed colonial.

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