

EVIDENCE CONCERNING THE FUNCTION OF NOCTURNAL CALL NOTES OF MIGRATORY BIRDS

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Nearly all birds which migrate at night give characteristic flight calls, but only recently has any attempt been made to investigate these quantitatively. Ball (1952) and Vleugel (1954, 1960) relied on the unaided ear to register the notes of migrants aloft. Graber and Cochran (1959, 1960) have successfully recorded call notes with a parabola pointed skyward. A tape recorder automatically monitored a 1½ minute portion of each 10-minute interval through the night. The data collected in these studies have been used to interpret the volume of migration, its species composition, and the conditions under which it takes place.

The function of night calls has not been a major concern of these workers. There has been no lack of speculation concerning the significance of night calls, however. Some suggest that the calls are not adaptive. Ball (1952) supposed that the dawn surge of call notes of thrushes might be inspired by hunger and light from the oncoming dawn. Hudson (1923) postulated that the calls were an expression of fear in the unfamiliar night, an idea shared by a number of others. But it seems unlikely that a behavior pattern which is so frequent and characteristic is functionless. A frequently suggested function of the night calls is that they serve to hold flocks together. A corollary to this is the suggestion that young benefit from the experience of adults by travelling in their company (Brewster, 1886). Another related idea implies that the calls are mutually stimulating, each call urging flight partners onward (Tyler, 1916; others). Lowery and Newman (1955) suggest that the calls may serve an "echosounding" function, facilitating the landing process. This suggestion, while perhaps reasonable, is not considered here for lack of evidence. The evidence presented here is based on analysis of the calls of caged birds exhibiting migratory restlessness and calls given by free flying migrants. Both lines of evidence clearly indicate that for at least some passerine species the calls are communicatory.

METHODS AND MATERIALS

Most of the captive Bobolinks (*Dolichonyx oryzivorus*) used in this study were taken as adults near Kenmare, North Dakota, following the breeding seasons of 1959 and 1960. Additional birds of unknown breeding origin were taken from a transient flock at Gainesville, Florida, in early May, 1960. Three birds were hand reared in June, 1960, after being taken as nestlings near Ithaca, New York. All these birds were held in individual cages and maintained on a diet of Purina game bird startena.

Each bird was maintained in an individual holding cage with two perches. Those perches were attached to the lever arm of a microswitch so that every new perching movement was recorded on an Esterline-Angus chart. Occasionally the bird might trip the switch twice in landing, but at slow chart speeds this showed as a single deflection. The purpose of this monitoring was to ascertain when an individual bird was night-active and might provide suitable material for orientation experiments in the cylindrical orientation test apparatus (see Hamilton, 1962). But in addition, these holding cages provided considerable information on the temporal pattern of activity. These data were heavily supplemented by direct observation, either of the fearless hand-reared birds in the holding cages or of wild-caught birds in the orientation apparatus. In the latter case observations were made from below and the bird was unaware of the observer's presence.

BEHAVIOR OF NIGHT-ACTIVE CAGED BOBOLINKS

Preliminary movements.—Under natural skies all birds ceased activity in the evening at about the same time, whether or not they were going to be active later. Following the characteristic twilight period of inactivity, lasting 30 minutes or more, nocturnal activity began. Occasionally the initial response was delayed until later in the night or even until early morning. The first action usually was sporadic preening especially directed to the carpal joint of the wings. The bird stretched occasionally, and the feathers might be rearranged with a rapid back and forth motion, the shaking behavior typical of most birds. Shaking was particularly prominent and persistent when a bird was responding weakly. In early August of 1960 the young Bobolinks taken from their nests only two months earlier initiated these night activities. At first they limited their movements to feather ruffling and shaking, sometimes pursuing this activity almost continuously for two hours or more. An occasional preening movement might be interspersed between these shaking maneuvers but the bird became inactive again without moving appreciably from its place on the perch.

As the season progressed and activity became more intense a new behavior pattern emerged. With bill tilted upward the bird extended the wings and fluttered, perhaps slowly at first, then more rapidly until finally the wings moved so quickly that there was only a blur. Usually this fluttering lasted less than three seconds, although it might be repeated again and again. Occasionally such a burst of fluttering lasted 10 seconds or more. Between fluttering movements, preening was rare and shaking only occasional. When fluttering under clear night skies in the experimental apparatus, the bird aligned its body along the migratory direction, generally north in the spring and south in the fall (Hamilton, 1962).

Calls.—Calling began with the fluttering movements. Usually calls were given with or immediately before fluttering. Calling seemed to indicate even more intense motivation than fluttering alone, for it was restricted to the most frequent and continuous fluttering bouts. These observations seem to suggest that the calls correspond to the migratory calls of night migrants. Given at night, the calls are associated with fluttering, and the directional component of this behavior correlates well with what is known of the migratory route of this species (Hamilton, 1962).

In an isolated solitary bird the sequence of increasingly intensive response is roughly as follows: stretch and/or preen, shake, flutter, and call.

Response to the calls.—In the preliminary experiments with Bobolinks in the fall of 1959, the cages were placed in full view of one another in a small windowless shed atop the Life Sciences Building at the University of California, Berkeley. Both during the day and night the record of activity of individuals showed unexpected synchrony. Because of the isolated location of the birds, it seems improbable that this synchrony was a result of frequent disturbances, affecting all the responding birds simultaneously. Nor could such an interpretation explain why some birds responded together at night while others remained inactive. Similar over-all temporal patterns of activity could not have been the basis of the synchronous pattern either, since the synchrony was of a very precise short-term nature.

I assumed that the sight of active birds in adjacent cages was influencing the pattern of response and accordingly designed a holding box to impede direct visibility. But while the new holding boxes with thin light-tight plywood walls between individuals reduced the synchrony, they did not eliminate it entirely.

In the spring of 1960 the operation was moved to the roof of the California Academy of Sciences in Golden Gate Park, San Francisco. Direct observations were initiated to

measure the facing of fluttering birds from below. The birds used were taken only a few weeks earlier from flocks of migrants at Gainesville, Florida, and many of them showed strong fluttering responses. These birds were kept under the natural San Francisco sky only 20 yards from the site of the experimental apparatus (Hamilton, 1962). It was difficult to obtain responses in the experimental apparatus. Apparently fear induced by handling inhibited the migratory response of these recently wild birds. However, when nearby caged birds began calling, the motionless birds in the apparatus called back and became active. In following nights this happened repeatedly. Birds which had been motionless for hours were aroused from sleep and triggered to action by a call. The synchrony of action of the caged birds was in part explained. Call notes were triggering mutual responses.

In the hope that these call notes might be useful in stimulating migratory behavior in the Bobolinks and thus facilitate the orientation studies, I recorded a series of calls to play back to the birds. The data summarized in table 1 were obtained by placing the recorder at the side of a bank of cages.

Response of inactive birds to recordings of calls.—Birds which had not demonstrated night activity during previous nights and had been inactive earlier in the night of the test were relatively unresponsive to the calls. Some did not respond at all (table 1), either remaining motionless or stretching and shaking briefly. Other individuals moved about briefly, fluttered a bit, then lapsed into inactivity. When the tape recording of the night calls, playing several calls a minute, was allowed to run for 30 minutes or more, activity could sometimes be induced. The weak response of N.D. 23 (fig. 1) demonstrates this aspect of the response, although it is of course uncertain at this latter stage of the experiment whether the bird was influenced by the recording or by other birds which had been stimulated by this recording.

Response of active birds to the recordings.—Much more dramatic responses to the playback of the taped calls were obtained from birds which had responded "spontane-

TABLE 1
ACTIVITY RESPONSE TO ALTERNATE 20-MINUTE INTERVALS OF SILENCE AND PLAYBACK
OF MIGRATION CALLS, OCTOBER 4, 1960

Prior counts	Bird number and source									
	N.Y. 21, 25 Fla. 9		N. D. 24		N.D. 23		Fla. 4		Total	
	0	39	0	2	
Off	0	8	0	3	11
On	0	6	1	5	12
Off	0	3	0	1	4
On	0	8	2	5	15
Off	0	7	0	2	9
On	0	6	8	13	27
Off	0	6	2	1	9
On	0	6	5	14	25
Off	0	5	0	1	6
On	0	14	4	4	22
Total off	0	29	2	8	39
Total on	0	40	20	41	101

The response is measured by the number of automatically registered perch movements. Note that three birds did not respond either before or after the initiation of the recording. Prior counts indicate night activity level on October 4 before the initiation of the experiment.

ously" on the previous night or had become active without experimental influence on the night of the test (table 1). Usually if there was activity earlier in the evening, the fluttering response to the taped calls was immediate. The response of N.Y. 21 in figure 1

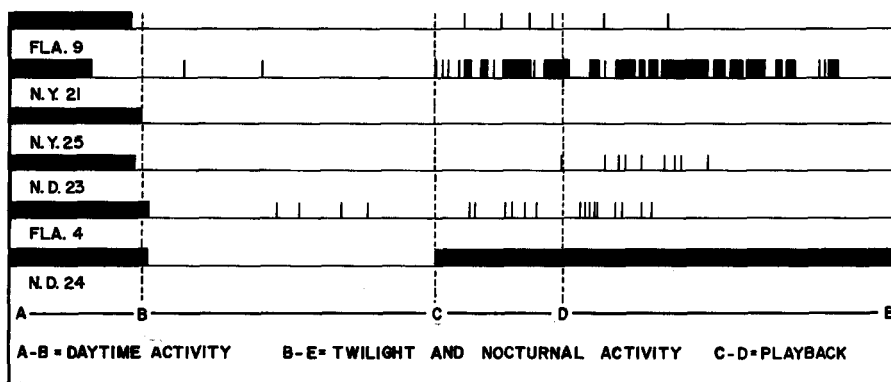


Fig. 1. Response of caged Bobolinks to the playback of recordings of call notes on September 25, 1960. Solid black bars indicate continuous activity, vertical lines single movements. The geographic origin of each individual is indicated by the state abbreviation prefixing the experimental record number. North Dakota 24 was given 5 mg. of testosterone propionate at 4 p.m. on this date. Normally this dosage either blocks or enhances the response. In this case it seems that the blockage was overcome by the call playback. Point B, 5 p.m.; C, 6:30 p.m.; D, 7:10 p.m.

is typical of numerous additional tests in the orientation apparatus with birds which showed little promise of making any vigorous response at all but which quickly responded to the playing of call notes. Often the bird called back and would frequently fly up, dashing into the lid of the apparatus.

The fly-up response may be especially significant. When the birds first responded by fluttering in the apparatus, the most continuous fluttering often terminated as the bird actually flew up from the perch, crashing into the Plexiglas lid of the apparatus and falling to the floor. Later, even during the most vigorous responses, the birds rarely left the perch. A responding call from another bird often overcame the inhibition, however, and in spite of previous bad experiences in dashing against the lid, the bird was likely to fly up at once. The same performance was often repeated several times during the night. The sequence of increasingly intensive response should thus be extended as follows: flutter, call, fly-up, with increasing probability of the final step in the case of a return call from another bird.

These data suggest that in migration a ground-given call note may enhance the probability of nearby birds in appropriate physiological condition taking flight together. Furthermore, the calls of migrants passing overhead may induce birds in migratory condition to fly up. These possibilities will be examined in the following section with the interpretation of the evidence from the calls of naturally passing migrants.

Inmate character of the calls.—Three individuals taken as nestlings at Ithaca, New York, in June, 1960, were maintained in isolation from other Bobolinks. In mid-August two of these birds initiated night activity. Since these birds were quite tame, it was possible to sit beside the cages and observe the social effect of the calls. While no recordings were made at this time, the calls did not appear to my ear different from typical migration notes. It is possible that these individuals learned the notes as nestlings but it seems

more probable that the notes and the response to them are innate. As in the case of the adults, a strong mutual stimulatory effect was noted.

THE CALLS OF PASSING NIGHT MIGRANTS

The following data are based on my own field notes made while listening to night migrants at Ithaca, New York. Additional data are derived from a survey of the literature and from tape recordings of migrants passing over central Illinois obtained by Graber and Cochran (1959, 1960).

The possible triggering effect of calling migrants overhead.—Do the calls of overhead migrants induce grounded birds to fly up? Direct evidence on this point is lacking but even if a response to the calls were the rule, the probability of obtaining documentary evidence is low. Ball (1952), in his extensive study of migration on the Gaspé Peninsula, recorded only four instances of thrushes taking flight at night. In three of these cases the overhead situation at the time of departure is not indicated. Data are presented for thrush migration in general on two of these three nights. Other notes were heard on both nights. On the fourth occasion Ball indicates that no birds were aloft when the bird flew up. This bird called from the ground and took flight two minutes later, giving the typical flight note. The note was “instantly followed by a second note of slightly different pitch and quality, indicating that two thrushes had left the ground.” The second thrush had not vocalized from the ground and must have joined the first individual in response to the call note, an action perhaps conditioned by the preliminary ground note.

In response to my query concerning the possibility of inductive influence of flight calls by Coots (*Fulica americana*), a notably vociferous night migrant, Peter Ward (*in litt.*) offered the following appraisal: “It is hard to judge whether the calls of Coots in flight stimulate others to take flight. I have notes which indicate strongly that this may be the case. Often a single [bird] will circle and call, being answered by another from the water. Suddenly it becomes apparent that both voices are airborne and they then fade off across the marsh.”

This is the extent of the evidence I have been able to muster. Field observers can render an important service by carefully documenting observations of the actual departure of night migrants and the attendant conditions.

The flocking function of calls.—Before attempting to answer the question of whether or not call notes may serve a flocking function, we must first examine the question of whether or not calling passerines are in fact grouped during flight. On the basis of their extensive moon watching studies, Lowery and Newman (1955) suggest that compact flocks of night migrants are largely restricted to herons, geese, and shorebirds. This is not surprising since these species are preadapted in a sense to close flock flying at night by their typical tight daytime flocks. Other species generally are seen passing the face of the moon one by one. If they do flock, then, these additional species, including all the passerines with which we are primarily concerned here, do not form close flocks. Yet the moon watch personnel do report a pulsed pattern of migration for the smaller birds. Lowery and Newman (*op. cit.*:247) state that “for almost half a minute the moon may remain vacant. Then suddenly the observer is bombarded by a rapid fire of silhouettes. . . . these bursts . . . seldom suggest birds in flocks. Usually the paths crisscross, and the objects themselves display a variety of sizes, shapes, and qualities of focus, suggesting that many of them are not even at the same level.” While such observations give evidence that close flocks are not the rule, they seem to provide equally convincing proof that some sort of grouping does occur.

In discussing the interpretation of these data, Dr. Newman suggested to me that concentrations of this kind must not necessarily be social gatherings. Random concentrations might occur. He suggests that it is also possible that spatial gaps in distribution on the ground may be reflected by temporal gaps once the birds are on the wing. This interesting argument demonstrates the difficulty of interpreting the record of night migration and the numerous factors which must be considered. If the migrants were patchy on the ground, they would represent passing flocks later in spite of independent flight only if they departed simultaneously and flew on at the exact same rate and precise direction. If there were individual differences in either flight direction or rate of travel, flocks would persist only as a result of an active flocking mechanism. The matter of individual differences in celestially (or otherwise) determined flight direction is one which remains to be investigated. This is certainly a central question, a fundamental point upon which much of our interpretation must be based. Until such time as evidence is available, I prefer what seems to be the conservative interpretation, namely, that individual differences exist.

If nocturnal flocks are a reality, they are apparently more diffuse than typical daytime flocks, with both depth and horizontal dimension greatly expanded. But the only reasonable interpretation that can be made of the pulsed pattern is that it comes from aggregations. The observation that bursts are more frequent on the nights of massed movement is of exceptional interest. It lends some support to the contention that these massed migrations are formed at least in part by the effect of the calls of passing birds, inducing grounded birds to join the waves of migrants already aloft.

The aural record is more difficult to interpret. Even if we hear bursts of calling, there is no assurance that such pulses are more than bursts of calls in an evenly flowing migration. This interpretation is especially likely if we permit the introduction of the evidence from the studies of caged Bobolinks which indicate that these calls induce other calls. Ball (1952:57) felt that in thrushes "grouping does occur—probably as a general rule." His evidence is by no means convincing, however. The concentrations on the ground which he observed could have formed after landing, and pulsing of call notes could have been the result of social stimulation.

Only under exceptional circumstances such as a thin, broken cloud cover lighted by a full moon (Browne, 1953) or over the glow of flames (Stone, 1906) have observers actually seen night migrants. Yet at least occasionally the distance from observer to migrant is much less than the spacing between the individual birds. These observations would have little bearing on the question of the visibility of night migrants to one another if there were evidence that the visual acuity of night migrants exceeds the capacity of man. On this question there is no fully reliable information. Certainly some species, for example certain owls (Dice, 1945), have a lower threshold than man but the Starling (*Sturnus vulgaris*) and the American Robin (*Turdus migratorius*) seem to be considerably poorer than man in their visual acuity at low light intensities (Adler, 1960; Adler and Dalland, 1959). Perhaps on particularly bright moonlit nights there would be sufficient illumination to permit visual contact. However, the very nature of the diffuse passerine flocks, if they are indeed flocks, would seem to argue against the use of vision as the primary means of maintaining contact. If vision normally played a prominent role, a closer rather than a more diffuse flock structure would be anticipated under marginal night-lighting conditions.

Are the flocks of mixed species composition?—On a night of heavy migration a considerable variety of calls may be heard in most localities. In itself this is not surprising, for passerine and much of the non-passerine migration may be concentrated into a few

nights in the spring and fall when conditions are meteorologically best suited to movement. What is surprising, however, is that the aural record indicates that interspecific grouping seems to occur on these nights. The following notes were taken at Ithaca, New York, at a time when I entertained no hypothesis concerning migration other than it provided opportunity to record a great variety of species at one locality:

"May 28, 1952. Time, 2230 to 2245. Complete overcast. Small birds (sparrows and warblers?) 64; Olive-backed Thrush, 223; other thrushes, 5; other birds, 4. *The calls of the 64 small birds coincide with the concentration of thrush calls.* Each note was counted as a bird although some individuals were probably within earshot more than once."

Additional evidence comes from night recordings of Graber and Cochran (1959, 1960). The calls definitely come in spurts through the night. Other species such as Dickcissels (*Spiza americana*) are often heard with mixed flocks of thrushes.

All these observations are liable to the additional interpretation that social stimulation is producing bursts of calls in an even flow of migrants and that the effect is interspecific.

Stone (1906) actually witnessed a night migration over a flaming lumber yard in Philadelphia in the early spring and commented on the diffuse scatter of the birds. He reported no groups. While he was unable to identify the species involved with any certainty, some Slate-colored Juncos (*Junco hyemalis*) and Song Sparrows (*Melospiza melodia*) were killed by the blaze. Stone's observations are difficult to analyze because of the possibility that birds were attracted to the light of the fire, but the uniform line of flight that he observed suggests that the species he was watching were not previously grouped. It hardly seems necessary to point out that in many circumstances interspecific flocking will have little value. Different flight lines and different winter quarters might make such groupings disadvantageous except in the case of completely disoriented individuals. As we become more familiar with the identity of the night callers, it will be interesting to see if these interspecific flocks show adaptive groupings of species with directionally similar goals.

SONAGRAPH ANALYSIS

The sonagraph analysis of the captive Bobolinks reinforces some of the conclusions already derived from field observation and behavior analysis. The sonagrams presented in figure 2 were made at natural speed with a wide band filter. Portions of sonagrams containing usable calls were clipped and figure 2 represents a composite record of these notes. The original recordings were made by placing a microphone near the cages of calling birds. The following discussion is based largely on the assumption that the call notes given by these caged birds are directly comparable with the calls of free-flying migrants since the preceding analysis of the behavior of captives when giving these calls suggests that this is a reasonable assumption.

Relation of night calls to daytime calls.—During the day Bobolinks give a typical flight call. To the ear these calls sound the same as the night calls, and a comparison of sonagrams (fig. 2) of calls by caged birds during the day with those given at night supports the contention that they are essentially the same. If the night calls are the same or nearly the same as the daytime flight calls, their function is more easily understood. Analysis of flight and social calls (see Marler, 1956a, 1956b, 1959) may apply equally to night calls. If this same comparison is valid for other species, the question arises as to why so many of the night calls of migrants are unfamiliar to experienced ornithologists quite familiar with the usual vocal repertoire of the species involved. The answer may stem from the fact that many species do not regularly flock except in migration.

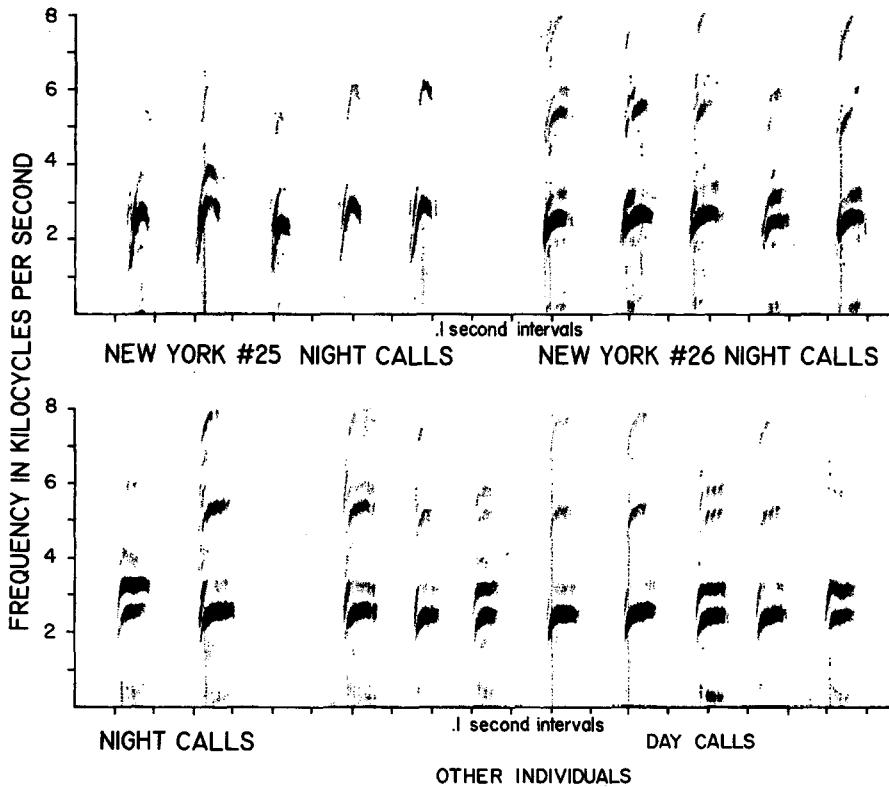


Fig. 2. Calls given by captive Bobolinks exhibiting migration behavior at night and activity during the day. The top line shows five notes given by each of two individuals, hand-reared nest mates, from Ithaca, New York. The second line shows two night call notes from two additional individuals and a series of call notes from several individuals given during the day.

There is thus no opportunity for the field ornithologist to become familiar with the aggregation notes of birds such as the Ovenbird (*Seiurus aurocapillus*) or Olive-backed Thrush (*Hylocichla ustulata*) in the course of usual field work. On the other hand, the calls of the Bobolink, flocking regularly at premigratory and transient sites, have often been identified (Brewster, 1886; Chapman, 1909). Tyler (1916:138) comments: "The call note of the Bobolink is diagnostic: it is used by day as well as by night." Identification of the night call note with the diurnal flock note lends further support to the contention that these night calls serve a flocking function.

Individual differences in notes.—It was possible to recognize several of the captive Bobolinks by their call notes. Sonagraph analysis of the call notes of the two hand-reared individuals (fig. 2, top row), reveals striking individual differences. That such differences can be demonstrated is important to considerations of the manner in which these notes may be used in flocking.

The physical structure of the call notes.—As Marler (1959) has pointed out, some avian vocalizations may be subject to quite divergent selective forces. Thus, species specificity and individual recognizability are incompatible to a degree, one requirement favoring specific homogeneity of performance, the other heterogeneity. The same principle may apply to night call notes. While I emphasized earlier the remarkable inter-specific composition of some night flocks, we should not overlook the fact that, based

on the aural record, a great many night groups seem to be composed entirely or largely of a single species. Species recognition undoubtedly plays an important role in maintaining these groups and would, therefore, be a factor influencing the evolution of the characteristics of call notes. The other factors which, on the basis of previous discussion, may be expected to be involved in the evolution of these notes are susceptibility to individual recognition and location. In flight and at night, predation pressures probably play a minimum role in shaping the characteristics of the note.

The night calls of many birds are species specific as demonstrated by our ability to distinguish them, but further discussion must be waived pending the accumulation of a sufficient body of sonagram records of known species origin. It may be instructive to point out, however, that selective pressures for species specificity may influence the evolutionary solution to the other aspects of the problem, individual recognition and location. In part the adaptations evolved to meet these qualifications will be contingent on adaptations to species specificity. If ability to locate were the only general requirement, many species might evolve very similar notes differing only according to the physical dimension of the species (see Marler, 1955). But with species specificity and individuality probable factors, we may expect a number of independent solutions having similar over-all physical effects achieved in different ways.

Ability to locate will be facilitated by a wide frequency distribution of energy, abrupt beginnings and endings, and discontinuities. While the first two requirements are fulfilled by Bobolink call notes, the notes seem to lack discontinuities. This suggests that the transmission of directional information may depend to a great degree upon the calls of the flock or the repetition of the call by individuals rather than on a single note.

DISCUSSION

The premise that the night calls do in fact convey directional information is implicit in the assumption that the night calls are the mechanism of nocturnal flock maintenance. Directional information might be derived in one of several ways.

One possibility is that the responder determines only the location of the caller. The only response that would lead to a closer grouping under this circumstance would be to fly toward the point where calls were last heard and continue this course until another call is heard, then correct the course again. If the listener can determine the direction of flight of the caller, much more appropriate and less energy consuming corrections can be made. The listener can then either maintain the original course or make a correction to intercept or narrow the distance between the two birds.

This determination would be possible by (1) determining direction of flight from the single call note of another bird, (2) determining direction of flight from subsequent call notes given by the same individual, or (3) determining the flight direction of the flock. The latter method would be most effective to a bird well separated from a flock. In this situation the calls of the birds in the flock would provide a nearly continuous flow of information, sufficiently broken to provide excellent location cues.

Concerning the potential ability of an isolated bird to determine the direction of flight of a passing bird we have no evidence. One possible approach to this problem might be to test the directional response of caged birds to the call notes of overhead migrants. A negative result would not be too meaningful, however, since we have already shown that the call notes, in addition to maintaining groups, may trigger grounded birds to fly up, and the initial movement might be quite non-directional, or if directional, based on cues other than the call.

If direction of flight of other birds is determined from the calling of a single individual, the directional determination would be greatly facilitated by repetition of the

call note. In a flock, however, additional calls from an individual would be usable only if individual recognition were possible. This determination could be made either by note characteristics or a species specific interval between calls. Ball (1952) provides evidence indicating the possibility of individual recognition based on his own ability to recognize individuals. The sonagraph evidence for captive Bobolinks lends further support to the contention that individuals may be readily identified by characteristics of their call notes. The interval between calls, if characteristic, would provide excellent cues for individual recognition and thus the determination of direction of flight. Practically no information about call intervals has been reported, but Ball states that the intervals do vary. He says (1952:54) that they are "usually . . . rather uniform for a given bird, but may be increased or shortened. For example, a hermit thrush flying a straight course down a wide valley piped at intervals of 13, 13, and 12 seconds. Then as it curved more and more sharply toward a hillside upon which it was about to alight, the intervals were reduced to 9 and 6 seconds." The point thus remains unsettled and further discussion must await further evidence.

Frequency of calling is probably also influenced by the social environment. In the Chaffinch (*Fringilla coelebs*) the frequency of social calls bears an inverse relationship to flock size (Marler, 1956a) and the same is true of the Bushtit, *Psaltriparus minimus* (Miller, 1921). If the same were true of migration calls at night, then a lone individual would tend to call more frequently than one in a flock, behavior advantageous in forming a flock of optimal size but concealing the difference between light and heavy migration to the listener.

Flight calls play a prominent role in the behavior of birds at the start of overseas movements. This is probably associated with the additional advantages of flock structure in overseas migration. In their migration many land birds demonstrate reluctance to cross wide bodies of water, a behavior that is most evident on the part of solitary birds. This behavior pattern probably accounts for a large part of "coasting behavior," that is, the tendency of a number of species to follow coastlines (Lowery and Newman, 1955). In the case of the Bobolink most, if not all, of the fall migrants must span 400 miles or more of the open Caribbean (Chapman, 1890). Yet single individuals of the same species are reluctant to cross lesser bodies of water (Stone, 1937). A single individual may initiate a flight, then turn back and delay crossing until additional numbers of the same species arrive. Lack and Lack (1953) have documented additional instances of the reluctance of passerines to cross bodies of water alone. Ball (1952) notes that this may be the case even when the opposite shore is clearly discernible, and he cites additional examples of the paths of calling birds indicating that the reluctance to cross open water persists at night. Such a behavior pattern might be adaptive in many ways. Just as the flock may be an adaptive mechanism for detecting predators, so it may also be effective in detecting limited or obscure landmarks. In addition, birds using innately recognizable celestial cues may still profit from experience. If the celestially based course is subject to learning, birds may adjust their courses from season to season according to experience. Young birds or even less experienced adults might well profit from the experience of seasoned travellers even though they can individually determine an approximately appropriate course from the sky. In effect, a bird would maintain contact with the flock as long as the course of the flock is in general agreement with its own celestial or topographical determination of appropriate direction.

It is also possible that some species, in particular those travelling long distances or required to strike a comparatively small goal, may find the celestial orientation mechanism insufficiently accurate to pinpoint the goal. If this were true, we should anticipate strong selective pressures for flocking mechanisms in species travelling long distances, crossing large bodies of water, or required to locate limited favorable habitats.

Comparisons within some groups suggest that there may be some merit to the argument. Among the American buteos, for example, the species with the longest migration, the Swainson (*Buteo swainsoni*) and Broad-winged hawks (*Buteo platypterus*), are prominent flocking species in migration, whereas the Red-tailed Hawk (*Buteo jamaicensis*) and other forms moving back and forth across the North American continent are less apt to be grouped in migration. The whole waterfowl order, largely migratory, must accurately locate comparatively limited stopping places in passage and equally restricted winter quarters. It is thus no surprise that Hochbaum (1955) was able to demonstrate so many correlations of migratory pathways with learned behavior that is dependent on flocking mechanisms for its transmission from generation to generation.

ACKNOWLEDGMENTS

Dr. Robert J. Newman kindly studied an early draft of the manuscript and offered numerous suggestions. Frank Bellrose and Dr. E. G. Franz Sauer provided additional stimulating comment. Dr. Peter Marler permitted the use of sonagraph equipment and commented on the manuscript. I am especially indebted to Dr. and Mrs. Robert Gammell of Kenmare, North Dakota, for supplying Bobolinks upon which this study is largely based. This research is an outgrowth of work on celestial orientation supported by the United States Air Force through the Air Force Office of Scientific Research of the Air Research and Development Command, under contract No. AF49(638)-825.

SUMMARY

Many species of birds migrating at night have characteristic call notes. Species which regularly form flocks during the day have a night migration note apparently indistinguishable from the daytime call note. Other species seem to have a night note so different from the day note that it is often difficult to identify the caller.

The most intensive night restlessness of captive caged Bobolinks is reflected by fluttering. Associated with this fluttering is a call note which is apparently the same as the call of migrants. If this call is recorded and played back to caged birds it amplifies the response of birds already showing migratory restlessness and may induce weakly responding birds to greater responsiveness. Birds which have not been responding regularly, and may thus be assumed not to be in physiological migratory condition, usually ignore the stimulus.

With the input of additional calls to strongly responding birds the response is often to fly up even though the bird has previously learned that such action will result in crashing into the lid of the apparatus. The suggestion is made that this behavior, extended to natural migration, may mean that the calls of migrants aloft induce grounded birds to fly up. This suggestion is in part supported by observations and analysis of the temporal pattern of migration.

Some species of passerines and some nonpasserines seem to maintain flocks during night migration. These flocks are very open in comparison with flocks of birds noted during daylight and it is suggested that for many species contact is maintained largely by the call note.

The night flocks of passerines are often composed of mixed species.

Possible ways in which the call notes may serve to provide sufficient orienting cues for flock maintenance are discussed. While the sonagraph analysis shows that each note has characteristics that may enhance its location, more effective corrections for direction would be possible by either hearing the same individual a second time or by using the calls from a flock.

Consistent individual differences in structure of notes suggest the feasibility of corrections based on hearing subsequent notes from the same individual.

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California Academy of Sciences, San Francisco, California, March 19, 1962.