# MICHAEL AVERY AND LEWIS W. ORING

Song "dialects" have been described when certain aspects of a species' song exhibit little variation in one locality but vary demonstrably between localities. In species such as the Mistle Thrush (Turdus viscivorus; Isaac and Marler 1963), Rufous-collared Sparrow (Zonotrichia capensis; Nottebohm 1969, King 1972), and Song Sparrow (Melospiza melodia; Harris and Lemon 1972), individuals most often share certain phrases, syllables or parts of songs. In other species, individuals of a local, interbreeding population consistently share entire song patterns unique to their area. Male Short-toed Tree Creepers (Certhia brachydactyla; Thielcke 1961) and White-crowned Sparrows (Zonotrichia leucophrys; Marler and Tamura 1962, Milligan and Verner 1971, Baptista 1974, 1975, Baker 1975, Orejuela and Morton 1975) usually have but one song pattern while individual male Chaffinches (Fringilla coelebs; Marler 1952), Cardinals (Cardinalis cardinalis; Lemon 1966, 1967), Bewick's Wrens (Thryomanes bewickii; Kroodsma 1974) and House Finches (Carpodacus mexicanus; Mundinger 1975) have repertoires of two or more song types.

In Bobolinks (*Dolichonyx oryzivorus*), males within a local "population" or deme, frequently share entire song types unique to their locality. Normally, each male possesses only two highly stereotyped song patterns, each composed of 25 to 50 figures. In view of the great complexity and length of Bobolink song, and the extensive, localized song sharing, this species typifies the concept of song dialect in its most restricted sense. Study of its song is of interest because of the lack of descriptive data available on icterid dialects and because of the general paucity of knowledge regarding dialects of grassland birds.

### **METHODS**

We recorded songs of male Bobolinks from seven locations in North Dakota and Minnesota (fig. 1) in May and June 1973. Recordings were made at Twin Lakes on 20 and 31 May 1973; all other sites were visited only once in 1973. In 1974, the Jamestown and Lake Itasca PO populations were again recorded. At each site, we recorded at least ten songs from each singing male. We make no distinction between

flight and perch songs because sound spectrograms of songs recorded from the Itasca area prior to the start of our study show that figures and phrases are the same in both although figures occasionally are added or deleted (Avery or Oring, unpubl.). Because birds were not individually marked, great care was taken to record each bird in only one singing bout. We recorded only one morning at each locality; thus portions of repertoires of some birds probably were not obtained. Two song patterns were recorded for 41 of the 62 birds. More extensive recording undoubtedly would have yielded second song patterns for many or all of the other 21 males. Recordings were made with a Sennheiser 805 ultra-unidirectional microphone and Nagra IV D tape recorder at 3¾ ips. Sound spectrograms were made on Kay Electric Co. Sona-Graph model 6061-A, wide-band setting.

Each recorded song was timed at half speed with a stop watch. The two song patterns of individual birds were treated separately, and for each song pattern of every bird, a song of mean length was selected for spectrographic analysis. Spectrograms were photocopied and copies cut into individual figures. Similar figures were grouped together yielding a catalog of over 400 figure-types. Each original spectrogram was compared figure by figure with the catalog, and a list of figures was compiled for each song. Lists were examined to determine existence and distribution of recurring sequences of figures (= phrases). A list of 105 phrases was obtained. Several songs included no phrases that were found elsewhere. Comparisons were then made to determine intra- and inter-population differences in song repertoires using the phrase as the unit of comparison.

Intrapopulation analysis was made in the manner of Harris and Lemon (1972). For example, five phrases were common to the repertoires of birds 1 (6 phrase total repertoire) and 2 (7 phrase repertoire) of the River Road site. This yields a "similarity value" of (5+5)/(6+7) = 0.77 between the repertoires of these two birds. Individuals whose complete repertoires were recorded (i.e., two patterns) were included in this analysis, and the mean of the similarity values between pairs of birds was considered to be the within-population similarity value. Comparisons between populations were made by computing the similarity values between each pair of recording sites using the entire complement of phrases present at each.

We use the following terminology in this paper:

- Figure: a sound producing a single, complete, and distinct spectrographic impression (Bondesen and Davis 1966)
- Phrase: a sequence of figures comprising a distinct subunit of song pattern (Hartshorne 1973)
- Song Pattern: a particular sequence of phrases and minor variations thereof (Harris and Lemon 1972)
- Population: a group of Bobolinks resident in one field, interbreeding among themselves, and genetically isolated, for the most part, from the residents of other fields.



FIGURE 1. Map of recording localities in North Dakota and Minnesota. 1: Twin Lakes, 8 km N and 3 km E LaMoure, LaMoure Co.; 2: Jamestown, 6 km E and 3 km S of town, Stutsman Co.; 3: River Road, 5 km NW Grand Rapids, LaMoure Co.; 4: Chase Lake I, east shore, Stutsman Co.; 5: Chase Lake II, north shore, Stutsman Co.; 6: SW corner Itasca State Park, Clearwater Co.; 7: Lake Itasca PO, Clearwater Co.

### RESULTS

Similarity values within populations ranged from 0.87 on 31 May 1973 at Twin Lakes to 0 at SW Itasca, with a mean of 0.44 (table 1). At most sites, similarity values varied greatly for each two males compared, owing to the presence of males with song patterns entirely foreign to those of the rest of the population. All the birds at SW Itasca had unique song patterns.

The phrase complements of the seven populations recorded in 1973 showed very little similarity (table 2). Most populations were completely different from each other. Exceptions were the two Chase Lake populations, where similarity between populations was greater than similarity within populations at any place except Twin Lakes (table 1). The Chase Lake sites were approximately 1 km apart, and much interaction probably occurs between the two populations. However, despite the high degree of overlap in phrase types, in only one instance was a full song pattern shared by birds at these two sites.

A relatively high degree of similarity existed between populations at the two Chase Lake sites and at Jamestown 1973 (table 2). This was due primarily to a sequence of three phrases, 18–19–20, that occurred in songs of three of the four birds at both the Jamestown and Chase Lake I sites and in four of seven birds at Chase Lake II. These phrases did not occur elsewhere.

Phrases at the North Dakota and Minnesota sites (table 2) did not overlap. Only a slight similarity existed between the two Minnesota populations despite their proximity (about 25 km apart). No consistent relationship existed between the similarity values of pairs of fields and their proximity. The Twin Lakes and River Road sites are approximately 20 km apart and shared no phrases, yet a male at Chase Lake I sang a song nearly identical to some found at River Road over 80 km away (fig. 2). Song patterns were shared by individuals of two populations in only one other instance. A male at Jamestown 1974 had two song patterns characteristic of the Twin Lakes population in 1973.

Certain phrases are not positioned at random within song patterns. For example, the three-phrase sequence 18–19–20 ended four of the 13 songs in which it occurred and was in the final one quarter of the other nine songs. Phrase 13 occurred in seven songs on 20 and 31 May and in four and three songs, respectively, of the Jamestown population in

TABLE 1. Song characteristics of populations of Bobolinks.

| Field                  | No.<br>birds<br>recorded | No.<br>songs<br>recorded | No.<br>different<br>phrases | Total<br>no.<br>phrases | Within-<br>field<br>simi-<br>larity<br>value |
|------------------------|--------------------------|--------------------------|-----------------------------|-------------------------|--|
| 1. Twin Lakes 20 May   | 6                        | 11                       | 13                          | 49                      | 0.62   |
| 31 May                 | 9                        | 13                       | 11                          | 59                      | 0.87   |
| 2. Jamestown 1973      | 4                        | 8                        | 18                          | 42                      | 0.30   |
| 1974                   | 7                        | 11                       | 26                          | 51                      | 0.22   |
| 3. River Road          | 7                        | 13                       | 13                          | 44                      | 0.54   |
| 4. Chase Lake I        | 4                        | 8                        | 12                          | 32                      | 0.57   |
| 5. Chase Lake II       | 7                        | 10                       | 14                          | 45                      | 0.45   |
| 6. SW Itasca           | 6                        | 9                        | 15                          | 18                      | 0.00   |
| 7. Lake Itasca PO 1973 | 6                        | 10                       | 18                          | 29                      | 0.32   |
| 1974                   | 6                        | 10                       | 13                          | 32                      | 0.53   |
| Totals                 | 62                       | 103                      |                             |                         | $\bar{\mathbf{x}} = 0.44$                    |

|    |                   | 1    | 2    | 3    | 4    | 5 | 6    | 7 |
|----|-------------------|------|------|------|------|---|------|---|
| 1. | Twin Lakes 31 May | _    |      |      |      |   |      |   |
| 2. | Jamestown         | 0.07 | -    |      |      |   |      |   |
| з. | River Road        | 0    | 0    | _    |      |   |      |   |
| 4. | Chase Lake I      | 0    | 0.20 | 0.16 | _    |   |      |   |
| 5. | Chase Lake II     | 0    | 0.31 | 0    | 0.62 | - |      |   |
| 6. | SW Itasca         | 0    | 0    | 0    | 0    | 0 |      |   |
| 7. | Lake Itasca PO    | 0    | 0    | 0    | 0    | 0 | 0.12 | - |

TABLE 2. Similarity values between pairs of Bobolink populations in 1973.

1973 and 1974. In each instance, the phrase introduced the song.

Within populations, the non-random sequencing of phrases is evident. Figure 3 shows a flow chart of the phrases in songs of the six birds of the River Road field that shared phrases. The two basic song patterns are 44-45-46-47 and 49-50-47-48. Variations do exist, but the one-way arrows indicate a strict, non-random order to the song patterns. Other populations exhibited similar one-way flow in phrase sequences.

Recordings were made twice at three sites.

Six males were recorded at the Twin Lakes site on 20 May 1973. All except one shared the same two song patterns. Nine birds recorded there eleven days later shared the same two dominant song patterns recorded 20 May. The male with different song patterns was not heard.

We made recordings at the Jamestown and Lake Itasca PO sites in both 1973 and 1974. At each site, two song patterns found in 1973 also were present in 1974. The main song patterns at the Jamestown site were shared by two birds in both years. The remaining two



FIGURE 2. Sound spectrograms showing sharing of song pattern by male at Chase Lake I field (above) and at River Road (below).



FIGURE 3. Flow chart of phrases in song patterns of birds 1–6 of the River Road population. Numbers in boxes are phrase numbers; circled numbers and solid arrowheads indicate the number of songs starting or ending with that particular phrase; other numbers indicate that number of songs in the pathway; e.g., 3 songs began with phrase 44, and 7 ended with phrase 47.

birds in 1973 and four of the remaining five birds in 1974 had unique song patterns. That of one male in 1974 was like those of individuals at the Twin Lakes site in 1973. Three birds showed the dominant two song patterns at the Lake Itasca PO site in both 1973 and 1974. The remaining three birds in each year all had different song patterns. Thus, at both sites, only the dominant or most prevalent pair of song patterns was carried over from one year to the next. Possibly only the most successful 1973 males returned in 1974. The similarity values between 1973 and 1974 phrase repertoires were 0.41 for Jamestown and 0.39 for Lake Itasca PO.

### DISCUSSION

Evidence is rapidly accumulating that local sharing of songs or song parts is a common phenomenon (Thielcke 1969). Recently, a general model for dialect development in oscines has been proposed (Lemon 1975). Nevertheless, descriptions of dialects remain few and variable, precluding comprehensive

explanation of why dialects develop in some species or subspecies and not in others. Because of this inadequate theoretical base, it is essential to continue to describe dialect systems representing various phylogenetic groups and ecological types. Bobolinks are characterized by (1) loose, colonial nesting, (2) polygynous mating, (3) isolation of small inbred populations in stable fields, and (4) population shifts with changes in vegetative nature of fields. Bobolinks in Wisconsin use evenly distributed food resources, but the distribution of nest sites and song perches is patchy (Martin 1967, 1971). Females presumably select a territory on the basis of nest site quality. Song seems to function in malemale interactions, in male advertisement for females, and in stimulation and/or synchronization of female reproduction. Individual males sometimes may be identified on the basis of song but probably are identified most often by their membership in a particular population (based upon dialect) and position in the field. Martin (1974) found that an average of 63% of the male Bobolinks present in a Wisconsin field one year returned the next. The relatively long life span (Martin 1973) of this species contributes to the perpetuation of local dialects.

We heard essentially no singing by male Bobolinks in the Lake Itasca region after the hatching of eggs in late June and early July. Thus, it seems unlikely that Bobolink nestlings could acquire a song template. Songs may be learned on the South American wintering grounds, and males with similar song patterns may migrate north together and settle in the same fields, though this seems highly improbable. A more reasonable explanation of dialect formation and song acquisition in this species is that males breeding for the first time settle in a field near an older male and copy his repertoire. This is similar to the situation in the Chaffinch. Young Chaffinches may learn some features of their song in the first few days of life, but song details are not obtained until the first breeding season, through countersinging with other males. Thereafter the repertoire is fixed (Thorpe 1958).

The presence of male Bobolinks with song patterns different from prevailing ones may be due to movement as a result of habitat destruction. This species frequently inhabits hay fields, and thus breeding grounds are destroyed regularly. The male in the 1974 Jamestown field who had song patterns found in the 1973 Twin Lakes field may represent just such dispersal. The Twin Lakes field was mowed in the summer of 1973, and the vegetation height in spring 1974 was much lower than the year before. No Bobolinks were there in late May 1974.

No evidence exists for or against dialectspecific assortative mating in the Bobolink. Indications are that this system does not function in the manner proposed for *Zonotrichia capensis* (Nottebohm 1969) because Bobolink dialects vary on a much more local scale than do breeding environments. Most populations are isolated from most others and probably have unique dialects. Also, it seems unlikely that Bobolink dialects evolved in response to regular utilization of marginal breeding habitat subject to rapid change as may have occurred in *Z. l. oriantha* (Orejuela and Morton 1975).

Dialects should develop when breeding assortatively with members of one's home population is advantageous and where song dialect is the most efficient means for recognizing population members. The most flexible way for population recognition to be incorporated

into song communication systems is through certain modes of learning. The advantages of assortative mating and behavioral mechanisms maintaining the system, such as dialect production and recognition, are maximized under certain circumstances, e.g., when local habitat variations are such that experienced mates vield a considerable advantage (Nottebohm 1969, Orejuela and Morton 1975). Similarly, maintenance of population integrity may be advantageous to individuals when members of a population must move to a new breeding site. Advantages of dialect-monitored assortative mating are minimized when (1)variation in nature and distribution of requisite resources is not correlated with locality. (2) widespread outbreeding or regularized dispersal due to certain aspects of the species' natural history occurs, or (3) overriding selective forces, e.g., for total silence or maximization of other song characteristics, operate.

In Bobolinks, when populations are disrupted by environmental factors, e.g., fire, mowing, flooding, etc., within or between breeding seasons, all individuals must find new breeding sites. It may be advantageous for members of a population to continue to interact with each other as this may enhance stabilization in a new breeding area. If the move is in mid-season, male-male relationships and pairs are already established. If a suitable breeding site is found, there may be time to breed only if stabilization is rapid. Even if the move is made at the start of the season, male fitness should be enhanced if rapid stabilization allows additional opportunities for attracting females. Minimizing delays due to population shifts will benefit females as well, by allowing breeding as close as possible to the optimum time or by allowing time for replacement clutches.

## SUMMARY

Songs of 62 male Bobolinks from five sites in southeastern North Dakota and two in northcentral Minnesota were recorded in 1973 and 1974. Spectrographic analysis disclosed a generally high degree of sharing of phrases and song patterns within populations. Very little similarity was noted between populations except at two sites less than 1 km apart. At two other sites, where recordings were made in successive years, only the two dominant song patterns present the first year were found during the second. It is theorized that a male Bobolink acquires his repertoire of two song patterns during his first breeding season by copying the songs of an older male. Such a dialect system enhances rapid stabilization of the breeding population and is adaptive when individuals must move due to changes in the breeding environment.

#### **ACKNOWLEDGMENTS**

We gratefully acknowledge the University of Minnesota Forestry and Biological Station and its Director, David Parmelee for providing facilities, equipment, and encouragement. Our thanks also go to J. Frank Cassell and the Department of Zoology, North Dakota State University, for the loan of recording equipment, and to Rikki Fowler for many discussions of Bobolink vocal behavior. James Mulligan made numerous valuable suggestions regarding the manuscript.

#### LITERATURE CITED

- BAKER, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows (Zonotrichia leuconhrus) Evolution 20:226-241
- trichia leucophrys). Evolution 29:226-241. BAPTISTA, L. F. 1974. The effects of songs of wintering White-crowned Sparrows on song development in sedentary populations of the species. Z. Tierpsychol. 34:147-171.
- BAPTISTA, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). Univ. California Publ. Zool. 105:1–52.
- BONDESEN, P., AND L. I. DAVIS. 1966. Sound analysis within biological acoustics. Nat. Jutlandica 12:235–239.
- HARRIS, M. A., AND R. E. LEMON. 1972. Songs of the Song Sparrow (*Melospiza melodia*): individual variation and dialects. Can. J. Zool. 50: 301-309.
- HARTSHORNE, C. 1973. Born to sing. Indiana University Press, Bloomington.
- ISAAC, D., AND P. MARLER. 1963. Ordering of sequences of singing behavior of Mistle Thrushes in relationship to timing. Anim. Behav. 11:179– 188.
- KING, J. R. 1972. Variation in the song of the Rufous-collared Sparrow, Zonotrichia capensis, in Northwestern Argentina. Z. Tierpsychol. 30:344– 374.
- KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. Z. Tierpsychol. 35:352–380.
- LEMON, R. E. 1966. Geographic variation in the song of Cardinals. Can. J. Zool. 44:413-428.

- LEMON, R. E. 1967. The response of Cardinals to songs of different dialects. Anim. Behav. 15: 538-545.
- LEMON, R. E. 1975. How birds develop song dialects. Condor 77:385-406.
- MARLER, P. 1952. Variation of the song of the Chaffinch, Fringilla coelebs. Ibis 94:458-472.
- MARLER, P., AND M. TAMURA. 1962. Song "dialects' in three populations of White-crowned Sparrows. Condor 64:368–377.
- MARTIN, S. G. 1967. Breeding biology of the Bobolink. M.S. thesis, Univ. Wisconsin, Madison.
- MARTIN, S. G. 1971. Polygyny in the Bobolink: habitat quality and the adaptive complex. Ph.D. diss., Oregon State University, Corvallis.
- MARTIN, S. G. 1973. Longevity surprise: the Bobolink. Bird-Banding 44:57-58.
- MARTIN, S. C. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. Am. Zool. 14:109-119.
- MILLIGAN, M. M., AND J. VERNER. 1971. Interpopulation song dialect discrimination by the White-crowned Sparrow. Condor 73:208–213.
- MUNDINGER, P. 1975. Song dialects and colonization in the House Finch, *Carpodacus mexicanus*, on the East coast. Condor 77:407-422.
- NOTTEBOHM, F. 1969. The song of the Chingolo, Zonotrichia capensis, in Argentina: description and evaluation of a system of dialects. Condor 71:299-315.
- OREJUELA, J. E., AND M. L. MORTON. 1975. Song dialects in several populations of Mountain White-crowned Sparrows (*Zonotrichia leucophrys* oriantha) in the Sierra Nevada. Condor 77:145– 153.
- THIELCKE, G. 1961. Stammegeschichte und geographische Variation des Gesanges unserer Baumlaufer (*Certhia familiaris* L. und *Certhia brachydactyla* Brehm). Z. Tierpsychol. 18:188–204.
- THIELCKE, G. 1969. Geographic variation in bird vocalization, p. 311-339. In R. A. Hinde [ed.], Bird vocalizations. Cambridge Univ. Press, Cambridge, England.
- THORPE, W. H. 1958. The learning of song patterns by birds, with special reference to the song of the Chaffinch (*Fringilla coelebs*). Ibis 100: 535-570.

Department of Zoology, North Dakota State University, Fargo, North Dakota 58102. Address of second author: Department of Biology, The University of North Dakota, Grand Forks 58202. Accepted for publication 22 June 1976.