ADJACENCY PATTERNS IN THE SONG-TYPE
DELIVERIES OF WESTERN MEADOWLARKS[1]

MARIA KLEMPERER AWEIDA

7184 Spring Court, Boulder, CO 80303

Male Western Meadowlarks (*Sturnella neglecta*) deliv-
er song repertoires of discrete, stereotypical song types,
each of which is repeated several times to form a bout
(Miller 1952, Falls and Krebs 1975). A bird, stringing
together these bouts, usually cycles through his whole
repertoire before he starts repeating song types (Fish
et al. 1962, Falls and Krebs 1975). Several investigators
have found preference patterns in such song-type se-
quences (Lemon and Chatfield 1971, Kroodsma 1975,
Verner 1975). Are such patterns based upon measur-
able parameters of the song types involved? Kroodsma
(1982) predicted that successive song types should dif-
fer more from one another than song-type pairs drawn
randomly from the repertoire. Whitney (1981), in his
study of singing patterns in the Varied Thrush (*Ixoreus
naevius*), found that the two song types in each rep-
ertoire judged most dissimilar on the basis of dominant
frequency and period of modulation were sung in
succession more often than expected by chance.
Kroodsma (1975) found that the song types of Rock
Wrens (*Salpinctes obsoletus*) that are frequently asso-
ciated in a singing session differ more in syllable length
and frequency range than do randomly selected song-
type pairs. Nelson (1973), studying the song-type de-
liveries of Western Meadowlarks, noted a sequential
pattern of upward and downward alternations based
on the pitch of the first sustained note in each new song
type in a series of bouts. However, other investigators
(Falls and Krebs 1975, Horn and Falls 1988) were
unable to confirm such a basis for patterning from their
observations of the same species. Verner (1975), in his
study of Marsh Wrens (*Cistothorus palustris*), also found
no tendency for adjacent song types to differ more from
one another than would be expected by chance.

The purpose of this study was to describe the se-
quencing of song types in the singing sessions of West-
ern Meadowlarks, in terms of factors that might influ-
ence selection of song type for each succeeding bout in
a series. I predicted that the choice of song type at the
point of each switch would be made to maximize the
internal variety of the session. This would conform to
the hypothesis set forth by Hartshorne (1956) that avi-
an singing behavior is geared towards stimulating and
maintaining the attention of the listener. The switching

of song types is in itself considered counter-habituating
(Kroodsma and Verner 1978, Krebs and Kroodsma
1980, Falls and d'Agincourt 1982). Do certain switches
maximize this effect?

METHODS

This study was based on recordings made in a 8-ha
meadow southeast of Boulder, Colorado, during the
years 1979–1987. The recording equipment used was
either a Sony TC-150 or Sony TCM-500 EV cassette
recorder, each with its own built-in microphone. Se-
lected for analysis from these recordings were the 12
birds for which the greatest number of song-type
switches were recorded. The number of uninterrupted
sequences of song-type bouts recorded ranged from six
to 92 for each bird, and the number of bouts ranged
from 59 to 431. Individual birds were identified through
their territories and repertoires, both of which remain
constant throughout a season (Falls 1985) and most of
which remain constant in succeeding years (Horn and
Falls 1988). The repertoire deliveries of two birds which
were considered returnees by these criteria were ana-
lyzed separately for each year, since the song-type ad-
jacency patterns within these deliveries differed slightly
from one year to the next. This can be expected if
repertoire organization is influenced by factors in ad-
dition to contrast maintenance, for example, the ten-
dency to match song types of other singers (Falls 1985)
or song types previously sung by the bird itself (Whit-
ney 1981).

For each repertoire, the number of times any two
song-type bouts were delivered adjacently was noted
and counted. Both sequence directions (song type A
preceding song type B, and song type B preceding song
type A) were examined to uncover any directional pref-
erences. These were rare.

Sonograms were prepared of each song type in the
repertoire of each bird, using a Kay Elemetrics 6061B
Sona-Graph with wide-band setting. Based upon the
prediction that song types with a certain degree of dif-
ference between them would be sung contiguously, a
difference index was developed to incorporate factors
identifiable on the sonograms. Such indexes have been
used in the past to measure the acoustical structure of
the songs of the Great Tit, *Parus major* (Falls et al.
1982), the Rock Wren (Kroodsma 1975), and the Marsh
Wren (Verner 1975). To contribute to a sensitive index,
a factor must show at least some variety from song to
song, and yet be basically the same for two renditions
of the same song by the same bird. Also, a factor should
not be unduly sensitive to sonogram quality. The fol-
lowing factors were used in the index:

TABLE 1. A comparison, by individual repertoire, of the difference scores of the three most common song-type pairs with those of the three least common ones.

Repertoire	Difference scores for most frequent pairs[a]	Difference scores for least frequent pairs[a]
1981 A	5,833	4,596
1983 C	9,779	8,270
1985 A	6,356	3,723
1985 C	3,163	3,664
1985 D	6,187	4,128
1986 A	3,943	2,945
1986 B	4,899	3,708
1986 C	4,970	3,790
1986 D	5,172	3,818
1987 A	5,853	6,260
1987 C	5,140	3,442
1987 D	5,483	3,602

[a] Figures were arrived at by totalling the difference scores of the three index factors.

(1) *Frequency range of songtype.* This was determined by measuring the distance (Hz) from the lowest portion of the lowest note to the highest portion of the highest note. A note was here defined as any uninterrupted pattern on the sonogram that was not wholly overlapped temporally by a longer note. This definition eliminated overtones and spike-like tones delivered simultaneously with basic song notes, which frequently appeared on some renditions and not others of the same song type by the same bird. Occasional notes on the sonogram that were much fainter than the others were not counted.

(2) *Mean frequency of song type.* This was taken as the mean between the frequency of the lowest portion of the lowest note and that of the highest portion of the highest note, using the definition of a note as given in factor (1).

(3) *Number of syllables in song type.* Syllables were defined as notes that exceeded an arbitrary length of 0.04 sec. Again, a note was defined as in factor (1) above.

The sonograms for each individual song type were measured for each of the three factors by three readers, independently of one another. Friedman's test (Sokal and Rohlf 1981) showed a high degree of concordance among the measurements of the readers ($P < 0.001$). The mean measures for the three readers were taken and these were then scaled so that the overall means for the three factors were the same. There is some evidence that birds attend to multiple components of song structure (Falls et al. 1988), but without knowledge of the saliency of any given component, scaling was considered the least arbitrary approach. Each possible song-type pair was assigned a difference score for each factor, determined by subtracting the lower measure from the higher. The association between these difference scores and the frequency of adjacency of each of the pairs was then examined.

RESULTS

Totalling the difference scores of the three most common song-type pairs in each of the 12 repertoires gave

TABLE 2. A comparison of the mean total difference scores ($n = 12$ repertoires) of the three most common song-type pairs with those of the three least common ones for each of the index factors.

	Three most common pairs	Three least common pairs
Difference in number of syllables	2,104	1,608
Difference in frequency range	2,113	1,685
Difference in mean frequency	1,347	1,036
Total	5,564	4,329

a mean score of 5,564, whereas the corresponding mean difference score for the least common song types was 4,329, the difference being statistically significant (one-tailed Mann-Whitney $U = 112$, $P < 0.025$). In all but two of the 12 repertoires (1985 C and 1987 A) the results were as predicted; the more common pairs had higher difference scores than the least common ones ($P < 0.017$, binomial probability; Table 1). The values for the three individual difference factors showed the same trend; in each case the total difference scores of the three most common pairs exceeded those of the three least common ones, though not to a significant extent (Mann-Whitney $U = 92$, $U = 93$, $U = 94$, $P > 0.10$ in each case; Table 2).

DISCUSSION

The results of this study suggest that Western Meadowlarks evince patterns of repertoire delivery based on contrast between adjacent song types. The most commonly associated song types differed more in number of syllables, frequency range, and mean frequency than did the least commonly associated ones. Although these preferences were not inflexible, neither were they random.

Any information conveyed to listeners by the use of repertoires depends upon stimulating and maintaining the attention of these listeners. Enhancing the effect of song-type switching by increasing contrasts would further this purpose. Kroodsma (1975) states that the singing of birds appears to be an exercise in contrasts and postulates that this could be maximized if frequently associated songs were very different from one another. My data do reveal a connection between sequence frequency and observable (by humans at least) differences between song types.

LITERATURE CITED

FALLS, J. B. 1985. Song matching in Western Meadowlarks. Can. J. Zool. 63:2520–2524.
FALLS, J. B., AND L. G. D'AGINCOURT. 1982. Why do meadowlarks switch song types? Can. J. Zool. 60: 3400–3408.

FALLS, J. B., A. HORN, AND T. E. DICKINSON. 1988. How Western Meadowlarks classify their songs: evidence from song matching. Anim. Behav. 36: 579–585.

FALLS, J. B., AND J. R. KREBS. 1975. Sequence of songs in repertoires of Western Meadowlarks (*Sturnella neglecta*). Can. J. Zool. 53:1165–1178.

FALLS, J. B., J. R. KREBS, AND P. K. McGREGOR. 1982. Song matching in the Great Tit (*Parus major*): the effect of similarity and familiarity. Anim. Behav. 30:997–1009.

FISH, W. R., K. NELSON, AND D. ISAAC. 1962. The temporal patterning of meadowlark song. Am. Zool. 2:409.

HARTSHORNE, C. 1956. The monotony threshold in singing birds. Auk 73:176–191.

HORN, A. G., AND B. F. FALLS. 1988. Repertoire and countersinging in Western Meadowlarks (*Sturnella neglecta*). Ethology 77:337–343.

KREBS, J. R., AND D. E. KROODSMA. 1980. Repertoires and geographical variation in bird song. Adv. Study Behav. 11:143–177.

KROODSMA, D. E. 1975. Song patterning in the Rock Wren. Condor 77:294–330.

KROODSMA, D. E. 1982. Song repertoires: problems in their definition and use, p. 125–146. *In* D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds. Vol. 2. Academic Press, New York.

KROODSMA, D. E., AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. Auk 95:703–716.

LEMON, R. E., AND C. CHATFIELD. 1971. Organization of song in Cardinals. Anim. Behav. 19:1–24.

MILLER, L. 1952. Songs of the Western Meadowlark. Wilson Bull. 64:106–107.

NELSON, K. 1973. Does the holistic study of behavior have a future?, p. 281–328. *In* P.P.G. Bateson and P. H. Klopfer [eds.], Perspectives in ethology. Plenum Press, New York.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Company, New York.

VERNER, J. 1975. Complex song repertoires of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14:263–330.

WHITNEY, C. L. 1981. Patterns of singing in the Varied Thrush II. A model of control. Z. Tierpsychol. 57:141–162.

HERITABILITY OF WING LENGTH AND WEIGHT IN EUROPEAN BEE-EATERS (*MEROPS APIASTER*)[1]

C. M. LESSELLS AND G. N. OVENDEN

Department of Animal Biology, University of Sheffield, Sheffield S10 2TN, United Kingdom

In recent years, an increasing number of studies have demonstrated the existence of significant heritable variation in morphological and other ecologically important traits in wild bird populations (van Noordwijk et al. 1980, Boag and van Noordwijk 1987). These heritability values have not only revealed the previously unexpected presence of considerable amounts of genetic variance, and hence the potential for populations to show microevolutionary change in response to selection (Boag and Grant 1981, van Noordwijk et al. 1981), but have also been used as a tool to estimate other variables of interest, such as the frequency of successful extra-pair copulation (Alatalo et al. 1984, Grant and Grant 1987, Møller 1987). Here we report

repeatability and heritability values for wing length and weight in the European Bee-Eater, *Merops apiaster*.

METHODS

Fully-grown bee-eaters were caught at the colony at Mas des Sarcelles (8 km south of Arles) in the Camargue region of southern France between mid-May and early August from 1983 to 1987. Birds were given a numbered aluminum band and were individually marked for field identification. Birds were reliably classified as 'juvenile' (born the previous calendar year) or 'adult' (born at least two calendar years ago) on the basis of plumage characteristics (Lessells and Krebs, unpubl.). Birds were also sexed in the hand on the basis of plumage characteristics; this technique was not completely reliable, but the sexes of most birds were confirmed from their breeding attempts. The wing length (flattened, straightened wing; Spencer 1984) was recorded to the nearest 1 mm, and weight was recorded to the nearest 0.1 g using a 100-g range Pesola balance. Chicks were banded from a third to a half of all nests each year, so parent-offspring relationships were known for these birds. Analyses were carried out using SAS