

EFFECT OF SYMPATRY ON MEADOWLARK VOCALIZATIONS

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When the ranges of two similar species partially overlap, differences between the two species are usually greater in the areas of overlap than where they are separate. This is character displacement as described by Brown and Wilson (1956). Lack (1971) cited many examples of character displacement in such features as morphology, habitat, and feeding behavior.

Contrary to the theory of character displacement, Rohwer (1973) suggested that, under certain conditions, interspecific territoriality and convergence in display characters can be expected in an interacting species pair. In his study of the two species of meadowlark (*Sturnella*) he found convergence in characters used in posturing displays. He also noted a loss of information content in vocalizations when territorial males of one species were exposed to the primary song of the other species. This resulted in increased fighting as a compensation for the ineffectiveness of song for maintaining territorial possession.

Cody (1969) stated that similarities are often less pronounced or even absent where two species are allopatric and that sympatry is necessary for retention of any similarities. He proposed that songs, specifically in the case of the two meadowlarks, show convergence in the zone of sympatry in response to selection for interspecific territoriality.

Moynihan (1968) predicted that related species which are sympatric will usually be more similar in overall appearance than equally closely related species of similar habits which are allopatric. Frequent contacts between individuals of sympatric species result in closer resemblances between them to facilitate social reactions.

The Eastern Meadowlark (*Sturnella magna*) and the Western Meadowlark (*S. neglecta*) have overlapping breeding ranges from the southwest United States northward to Ontario. *S. magna* extends into the range of *S. neglecta* along the low river valleys of the plains. During breeding, the males of the two species maintain interspecific territories in the area of overlap (Lanyon 1957). In allopatric areas each species has a distinctive song, audibly and spectrographically different from that of the other species. Differences occur in timing, frequency, and homogeneity of the component elements (Lanyon 1957). Cody's (1969) theory of convergence and Moynihan's (1968) prediction of similarity suggest that the distinctive components of the two species' songs would be more alike in areas of sympatry, where interspecific territoriality is critical, than in allopatric zones. My study investigated the possibility of convergence of primary song in the sympatric zone of the two species of *Sturnella*.

This study was conducted in Nebraska and Iowa, which contain a broad zone of overlapping breeding ranges for the two meadowlarks. I recorded three or four primary songs of individual males of each species in their allopatric and sympatric areas. Field observations were made before recording to assure purity of non-overlapping populations and to determine sympatry as defined by Rohwer (1972b). In the area of sympatry, I identified birds by call notes and the presence of certain distinguishing elements within the primary song as suggested by Lanyon (1957). All recordings were made with a Uher 4000 Report-L tape recorder at 18.05 mm per sec with an Electro-Voice 644 dynamic microphone. Visual records of a representative song of each male were produced on a Kay Electric Company 6061-B Sound Spectrograph. Measurements were made of total duration, component duration, and the average and range of component frequencies following Lanyon (1957).

Statistical tests were made using a one-way analysis of variance and least significant difference (table 1). Average frequency and low frequency show significant differences ($P < .01$) between species but no significant difference within the species' populations. High frequency and component length also show significant differences ($P < .05$) between species but also indicate slight differences within the species' populations that may indicate character divergence [see sympatric *magna*-high frequency ($P < .2$) and sympatric *neglecta* and sympatric *magna*-component length ($P < .1$ and $P < .05$)]. The integrity of each species' song suggests that no convergence of song components has occurred in the zone of overlap.

These results show that selection has opposed the establishment of a single song type in the area of sympatry. If songs were used only in territory establishment and maintenance, they would be expected to converge. This is especially true because the primary song is learned and rapid change should be possible (Lanyon 1957, 1966, Rohwer 1972a). The integrity of each song implies that song may be of great importance in functions other than delimiting territories. Lanyon (1957) established that song is of importance in initial mate attraction in meadowlarks. Selection to prevent interspecific matings apparently opposes convergence in the distinctive songs of these two species. This selection is strong enough that the results of increased fighting due to information loss (Rohwer 1973) must be largely outweighed.

Cody's (1969) suggestion of convergence in the song of *Sturnella* was based on his field observations of a "hybrid" song type in which it was difficult to determine the species of the singing bird. He felt that this was the result of convergence of the two songs since interbreeding between the species has been found to be rare (Lanyon 1957, 1966, Szij 1966). Rohwer (1972a) stated that he found very few songs in the area of sympatry that were difficult

TABLE 1. Means and standard deviations of measurements.*

POPULATION	Sample size	Mean frequency	Component duration	High frequency	Low frequency
Sympatric <i>magna</i>	6	58.34 ± 4.52	17.51 ± 3.70	73.50 ± 9.16	47.17 ± 4.17
Sympatric <i>neglecta</i>	7	33.32 ± 6.95	13.11 ± 2.70	48.38 ± 16.75	21.25 ± 2.55
Allopatric <i>neglecta</i>	6	36.95 ± 6.41	11.04 ± 2.00	51.50 ± 4.23	20.17 ± 8.04
Allopatric <i>magna</i>	5	54.40 ± 3.18	13.47 ± 3.35	63.80 ± 3.56	46.00 ± 2.74
Least significant difference		10.22 ($P < .01$)	3.86 ($P < .05$)	14.46 ($P < .05$)	8.58 ($P < .01$)

* All measurements in mm: 1mm = 7.6msec or 77Hz.

to type as either *S. neglecta* or *S. magna*. My own field observations support Rohwer, and available audiospectrographic analyses offer additional credence to the rarity of intermediate song.

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NONRANDOM ORIENTATION OF ENTRANCE HOLES TO WOODPECKER NESTS IN ASPEN TREES

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Lawrence (1967) discussed the nonrandom orientation of nest entrance holes in Yellow-bellied Sapsuckers (*Sphyrapicus varius*), Common Flickers (*Colaptes auratus*), Hairy Woodpeckers (*Dendrocopos villosus*), and Downy Woodpeckers (*D. pubescens*) in central Ontario. She found that 43% of 89 nest openings faced eastward, 22% westward, 54% southward, and 10% northward. Other workers have found similar results (e.g., Pynnönen 1939 in Lawrence 1967, Blume 1961, and Dennis 1969). Dennis (1971) found that 73.5% of 362 nest entrance holes of Red-cockaded Woodpeckers (*Dendrocopos borealis*) in northeastern South Carolina faced westward and only 10% eastward. He suggested that the westerly orientation resulted from an attempt to expose resinous surfaces (resin diggings) near the opening to the longest periods possible of daylight sunshine and warmth. Presumably, this exposure would enhance the protective effect that Dennis had postulated. Two desert birds, the Cactus Wren (*Campylorhynchus brunneicapillus*) and the Verdin (*Auriparus flaviceps*), respond to seasonal changes in their thermal environment by changing the orientation of nest entrances. For the first brood in the spring, entrances of Cactus Wren nests face away from the cold winds; during the hot summer months, nest entrances are oriented toward the predominant afternoon breezes, which keep them from becoming too hot (Ricklefs and Hainsworth 1969). Austin (1974) discovered that the orientation of Verdin nests is important in fledging success. Nests oriented in the predominant direction for the season were more successful than those oriented in less commonly used directions. Nest orientation may be similarly important in the other species discussed above.

In the vicinity of the Rocky Mountain Biological Laboratory, Gothic, Colorado, Yellow-bellied Sapsuckers and Common Flickers excavate nest cavities in aspen trees. During the summer of 1973, I located 25 trees containing a total of 42 nests (36 sapsucker, 6 flicker). Twelve of these nests were active (10 sapsucker, 2 flicker) and the remainder were at least one year old. For each nest I recorded entrance-hole diameter, height of hole from the ground, diameter at breast height (dbh) of the tree containing the nest, and compass direction of the hole, measured to the nearest 5 degrees. Although winter roosting holes may have been included in the data, it appeared that all were nest holes. All but one were apparently completed nests; the exception was either a nest in construction or a "trial hole."

I found no significant difference in height of holes or in mean dbh of trees selected by the two species. Differences in sizes of entrance holes were used to identify which species constructed unoccupied nests. Entrance holes of sapsucker nests were usually about

TABLE 1. The number of nests and mean directions.

	No. of nests	Mean direction	s ^a	r ^b
All nests	42	186°	68.1°	0.2936
Sapsucker nests	36	170°	71.6°	0.2189
Flicker nests	6	182°	40.3°	0.7532
Sapsucker nests, west side of valley	3	52°	18.7°	0.9466
Sapsucker nests, east side of valley	33	175°	68.3°	0.2890

^a "s" is a measure of dispersion, the mean angular deviation, calculated for a circular distribution. It has properties similar to the standard deviation (Batschelet 1965).

^b "r" is another measure of dispersion, the concentration about the mean direction, from which "s" is calculated. Its values range from 0 to 1; the higher the concentration, the closer is "r" to the value 1 (Batschelet 1965).