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Intraspecific Avoidance and Interspecific Overlap of Song Series in the Eastern Meadowlark

RICHARD W. KNAPTON

Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

Communication and transfer of information by song is best achieved by minimal interference from features of the habitat and from vocalizations of other animals. Song transmission in birds is influenced by environmental variables that result in sound degradation and attenuation (Morton 1975, Roberts et al. 1981, Cosens and Falls 1984). Acoustic interference also may occur if another individual of the same or a different species sings simultaneously. Avoidance of acoustic interference has been achieved in neighboring Bewick's Wrens (*Thryomanes bewickii*) and Wrentits (*Chamaea fasciata*) by using different diurnal singing cycles (Cody and Brown 1969, Fleischer et al. 1985) and in individuals of the same or different species singing asynchronously at the same time of day, with one individual singing immediately after another has stopped (Wasserman 1977, Gochfeld 1978 on the same species; Ficken et al. 1974, Popp et al. 1985 on assemblages of different species).

The studies on short-term temporal avoidance of interspecific acoustic interference by Ficken et al. (1974) and Popp et al. (1985) were conducted on bird pairs and communities in forests, a habitat in which sound attenuates quickly. I investigated temporal patterns of singing behavior of Eastern Meadowlarks (*Sturnella magna*), which occupy an open-country hab-

itat that is shared with several other species. I attempted to find if an Eastern Meadowlark avoided singing when its nearest neighbor was in song, and if there was interspecific avoidance of song overlap with other species of open-country birds. Clearly, if such avoidance of song overlap occurs, then rate of song delivery could be affected by the singing behavior of other species, and avoidance results because of overlap in song structure among different species.

I studied songs in old fields and abandoned vineyards in the Short Hills Provincial Park Reserve, Regional Municipality of Niagara, Ontario (43°00'N, 79°10'W). The old fields were dominated by various grasses and were bisected frequently by old fence lines, which were used as song perches. Abandoned vineyards had grasses and forbs growing among rows of old posts, wire, and dead cultivated grape stalks.

Eastern Meadowlarks were mist-netted and color-banded for individual recognition, primarily in March and April. Tape recordings were made in the open from concealed locations during the period 29 April to 26 May 1984 and 1985, between 0600 and 1000, with a Uher 4000 Report Monitor tape recorder and a Turner SE14 microphone. Spectrograms of songs were made on a Kay Electric 7029A Sonagraph.

Recording sessions of 10 different singing males

TABLE 1. Mean song lengths for individual Eastern Meadowlarks.

| Meadowlark no. | No. of songs | Recording length (min) | Mean song length (s) ^a | Percentage time spent in song |
|----------------|--------------|------------------------|-----------------------------------|-------------------------------|
| 1 | 404 | 106 | 1.31 ± 0.15 | 8.32 |
| 2 | 161 | 41 | 1.33 ± 0.17 | 8.70 |
| 3 | 400 | 152 | 1.15 ± 0.12 | 5.04 |
| 4 | 275 | 60 | 1.24 ± 0.16 | 9.47 |
| 5 | 180 | 41 | 1.29 ± 0.14 | 9.43 |
| 6 | 440 | 94 | 1.31 ± 0.22 | 10.22 |
| 7 | 320 | 98 | 1.26 ± 0.18 | 6.86 |
| 8 | 195 | 51 | 1.20 ± 0.18 | 7.65 |
| 9 | 293 | 62 | 1.18 ± 0.12 | 9.29 |
| 10 | 188 | 43 | 1.30 ± 0.18 | 9.47 |

^a Mean ± SD, calculated from 20 songs/meadowlark.

were used in each analysis. Each session was comprised of a target male while a territorial neighbor was also singing. The target male sang within his territory from perches close to the boundary of the neighboring male's territory. In each case, males were visible to each other and were usually less than 100 m apart. A minimum of 150 songs per target male was used for analysis (see Table 1). All males were paired and were in the nest-building or incubation stage of the breeding cycle.

Ten different recording sessions were used in the investigation of interspecific acoustical interference. Again, meadowlarks were the target species. Each session consisted of a meadowlark singing, up to a minimum of 200 songs per male, and up to 9 other species singing per recording session. Tapes were analyzed by listening to the tapes. Spectrograms were used to verify that interspecific overlap of singing had occurred between a meadowlark and another species.

For the investigation of intraspecific overlap, let m be the amount of time a neighboring bird sang and

\bar{m} equal the periods of silence. The probability of this bird being in song is:

$$p(m) = m/(m + \bar{m}) \\ = (\text{time spent singing})/(\text{total time}),$$

and, conversely, the probability of it being silent is:

$$p(\bar{m}) = \bar{m}/(m + \bar{m}).$$

If the target individual sang a total of s songs, and if these songs were delivered randomly during the observation period, then the predicted number of songs initiated while its neighbor was singing would be:

$$S_m = p(m)s,$$

and the predicted number of songs during periods of silence is:

$$S_{\bar{m}} = p(\bar{m})s.$$

The expected values S_m and $S_{\bar{m}}$ were compared with the observed values s_m and $s_{\bar{m}}$ using Chi-square tests (methods followed Ficken et al. 1974).

Rates of singing were determined by counting the number of songs per minute that a meadowlark sang. Song rates of a given male Eastern Meadowlark were compared between periods when another species was singing and when it was silent. Finally, frequency ranges were measured from spectrograms of each species. The ranges were compared with those of other species to determine the degree of overlap of frequency ranges.

Intraspecific acoustical interference.—The total recording period for the 10 target individuals was 748 min, and mean song lengths for the 10 males ranged from 1.15 to 1.33 s (Table 1). A given male did not sing the majority of its songs while its neighbor was already singing ($P < 0.001$ for each of the 10 males; Table 2). The mean percentage of songs started when a conspecific was singing was 1.8% (range 0–3.9%). Thus,

TABLE 2. Timing of Eastern Meadowlark songs relative to singing and silent periods of conspecifics.

| Meadowlark no. | Percentage time conspecific sang | No. of songs begun when conspecific | | | | χ^2 ^a |
|----------------|----------------------------------|-------------------------------------|----------------|------------------------|------------------------|-----------------------|
| | | Singing | | Silent | | |
| | | Exp. (S_m) | Obs. (s_m) | Exp. ($S_{\bar{m}}$) | Obs. ($s_{\bar{m}}$) | |
| 1 | 7.64 | 30.9 | 12 | 373.1 | 392 | 12.5 |
| 2 | 9.32 | 15.0 | 1 | 146.0 | 160 | 14.4 |
| 3 | 8.46 | 33.8 | 15 | 366.2 | 385 | 11.5 |
| 4 | 8.12 | 22.3 | 4 | 252.7 | 271 | 16.4 |
| 5 | 7.89 | 14.2 | 0 | 165.8 | 180 | 15.4 |
| 6 | 8.59 | 37.8 | 5 | 402.2 | 435 | 31.1 |
| 7 | 8.98 | 28.7 | 9 | 291.3 | 311 | 14.9 |
| 8 | 9.46 | 18.5 | 2 | 176.5 | 193 | 16.2 |
| 9 | 7.88 | 23.1 | 6 | 269.9 | 287 | 13.7 |
| 10 | 9.02 | 16.9 | 4 | 171.1 | 184 | 10.9 |

^a $P < 0.001$ in all cases.

TABLE 3. Timing of Eastern Meadowlark songs relative to singing and silent periods of different species neighbor.

| Meadowlark no. | Percentage time other species sang | No. of songs begun when heterospecific | | | | χ^2 ^a |
|-----------------------------|------------------------------------|--|----------------|----------------|----------------|-----------------------|
| | | Singing | | Silent | | |
| | | Exp. (S_m) | Obs. (s_m) | Exp. (S_m) | Obs. (s_m) | |
| Bobolink | | | | | | |
| 1 | 8.34 | 33.7 | 41 | 370.3 | 363 | 1.7 |
| 2 | 10.51 | 21.1 | 18 | 179.9 | 183 | 0.6 |
| 3 | 7.48 | 29.9 | 36 | 370.1 | 364 | 1.4 |
| 4 | 9.54 | 26.2 | 31 | 248.8 | 244 | 0.9 |
| 5 | 13.94 | 29.3 | 26 | 180.7 | 184 | 0.4 |
| 6 | 15.72 | 69.2 | 58 | 370.8 | 382 | 2.2 |
| 7 | 5.57 | 17.8 | 26 | 302.2 | 294 | 4.0* |
| 8 | 12.24 | 35.9 | 42 | 257.1 | 251 | 1.2 |
| 10 | 9.17 | 27.3 | 36 | 270.7 | 262 | 2.9 |
| Savannah Sparrow | | | | | | |
| 2 | 7.20 | 14.5 | 16 | 186.5 | 185 | 0.3 |
| 4 | 5.64 | 15.5 | 18 | 259.5 | 257 | 0.4 |
| 5 | 6.26 | 13.1 | 12 | 196.9 | 198 | 0.2 |
| 6 | 3.25 | 14.3 | 12 | 425.7 | 428 | 0.4 |
| 7 | 3.87 | 12.4 | 17 | 307.6 | 303 | 1.8 |
| 8 | 11.39 | 33.4 | 28 | 259.6 | 265 | 0.9 |
| 10 | 4.97 | 14.8 | 16 | 283.1 | 282 | 0.1 |
| Yellow Warbler | | | | | | |
| 1 | 2.67 | 10.8 | 9 | 393.2 | 395 | 0.3 |
| 7 | 3.45 | 11.0 | 15 | 309.0 | 305 | 1.5 |
| Common Yellowthroat | | | | | | |
| 5 | 5.29 | 11.1 | 9 | 198.9 | 201 | 0.5 |
| 7 | 1.50 | 4.8 | 8 | 315.2 | 312 | 2.2 |
| Willow Flycatcher | | | | | | |
| 7 | 0.95 | 3.0 | 1 | 317.0 | 319 | 1.4 |
| Upland Sandpiper | | | | | | |
| 3 | 2.72 | 10.9 | 9 | 389.1 | 391 | 0.3 |
| 7 | 0.87 | 2.8 | 1 | 317.2 | 319 | 1.2 |
| Red-winged Blackbird | | | | | | |
| 1 | 1.64 | 6.7 | 5 | 397.4 | 399 | 0.4 |
| 4 | 2.57 | 7.6 | 9 | 267.4 | 266 | 0.3 |
| 7 | 2.16 | 6.9 | 10 | 313.1 | 310 | 1.4 |
| Field Sparrow | | | | | | |
| 1 | 3.88 | 15.7 | 18 | 388.3 | 386 | 0.4 |
| 6 | 3.51 | 15.5 | 12 | 424.5 | 428 | 0.8 |
| 9 | 2.82 | 7.4 | 10 | 254.6 | 252 | 0.9 |
| Song Sparrow | | | | | | |
| 4 | 4.71 | 13.0 | 11 | 262.0 | 264 | 0.3 |
| 8 | 4.36 | 12.8 | 15 | 280.2 | 278 | 0.4 |
| 9 | 4.44 | 11.6 | 16 | 250.4 | 246 | 1.8 |

^a All χ^2 values, except the one marked by an asterisk, are nonsignificant at the 0.05 level; * = $P < 0.05$.

the hypothesis that an individual avoids singing while its neighbor is in song was supported.

Interspecific acoustical interference.—Thirty-two individuals of 9 species sang during the recording session of 779 min of the 10 meadowlarks. Eight of these other species were passerines: Bobolink (*Dolichonyx*

oryzivorus), Red-winged Blackbird (*Agelaius phoeniceus*), Savannah Sparrow (*Passerculus sandwichensis*), Song Sparrow (*Melospiza melodia*), Field Sparrow (*Spizella pusilla*), Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), and Willow Flycatcher (*Empidonax traillii*); one was a nonpas-

TABLE 4. Frequency ranges of Eastern Meadowlarks and 9 co-occurring species.

| | Frequency range (kHz) | |
|----------------------|-----------------------|-------------|
| | Minimum | Maximum |
| Bobolink | 1.37 ± 0.31 | 5.81 ± 0.16 |
| Savannah Sparrow | 3.96 ± 0.22 | 8.92 ± 0.13 |
| Yellow Warbler | 2.92 ± 0.13 | 7.22 ± 0.11 |
| Common Yellowthroat | 2.21 ± 0.03 | 5.63 ± 0.07 |
| Willow Flycatcher | 1.26 ± 0.08 | 5.93 ± 0.06 |
| Upland Sandpiper | 3.02 ± 0.06 | 4.43 ± 0.04 |
| Red-winged Blackbird | 1.22 ± 0.21 | 5.48 ± 0.09 |
| Field Sparrow | 2.55 ± 0.13 | 4.98 ± 0.01 |
| Song Sparrow | 1.82 ± 0.12 | 7.14 ± 0.18 |
| Eastern Meadowlark | 2.96 ± 0.26 | 6.85 ± 0.53 |

serine (Upland Sandpiper, *Bartramia longicauda*). Bobolinks and Savannah Sparrows sang during 9 and 7, respectively, of the meadowlark recording sessions. The remaining 7 species sang in 3 or less of the sessions.

There was no indication that a given meadowlark initiated most of its songs during the silent periods of any of the coexisting species (Table 3). Overlap occurred regularly with all nine species; in only one case (meadowlark 7 with a Bobolink) was there evidence of avoidance of acoustic interference.

Song rates and song structure.—Mean song rate when other species were singing was 3.90 ± 0.80 songs/min, and mean rate when other species were silent was 3.91 ± 0.84 ($t = 0.13$, not significant). Meadowlarks did not adjust their rates of singing when other species were in song.

The frequency range of meadowlarks was compared with those of the nine other species (Table 4). Meadowlark songs covered a broad frequency range, between 3 and 7 kHz. Between 3 and 5 kHz the frequency range of the songs overlapped all of the other species. Parts of the frequency ranges of songs of the two most commonly co-occurring species, Bobolink and Savannah Sparrow, fell outside the frequency bands of the meadowlark. The minimum frequency of Bobolink songs was considerably lower, and the maximum frequency of Savannah Sparrow songs higher than the corresponding levels of meadowlark songs (Table 4).

Individual male Eastern Meadowlarks appeared to actively avoid intraspecific acoustical interference by avoiding singing while neighboring males were in song, a situation similar to that in White-throated Sparrows (*Zonotrichia albicollis*; Wasserman 1977). In both species, sounds were not masked by acoustical interference from conspecifics, and hence information transfer is efficient and complete.

In contrast, Eastern Meadowlark males frequently and repeatedly overlapped the songs of all other species sampled on the study area. Two species, the

Bobolink and Savannah Sparrow, occurred often in the area in which meadowlarks were singing, but no significant evidence was obtained for acoustical avoidance (Table 3). The song rates of male meadowlarks did not differ when either of these two species were singing as opposed to when they were silent, further supporting the idea that meadowlark males pay little or no attention to songs of other species nearby. Because of this, it is highly unlikely that song rate, which could be influenced by the songs of other species, falls below some optimal level for the meadowlark.

Temporal acoustic interference could be avoided if vocalizations were at different frequencies (Littlejohn and Martin 1969). Meadowlark songs have been described as "clear slurred whistles," frequently descending the scale. A given song covers a wide frequency range, usually between 3 and 7 kHz. The lower end of the scale, between 3 and 5 kHz, overlaps the songs of all the other species. The songs of the Upland Sandpiper and Yellow Warbler were completely within the frequency range of the meadowlark's song. Despite such overlaps, there were no evident short-term adjustments of singing rate in any species. In the two most commonly co-occurring species, Bobolink and Savannah Sparrow, complete overlap did not occur. Part of the carrying frequency of the Bobolink's song falls below 3 kHz, and that of the Savannah Sparrow song above 7 kHz. Possibly enough information is conveyed in the unmasked parts of the songs of these species that short-term adjustments in temporal patterning of songs do not occur. It is not surprising that acoustic overlap was found in the case of the Bobolink, as songs of this species are long and given frequently. If individuals of other species were to adjust their song rates to periods of silence of Bobolinks, their rates would be very low.

Avoidance of acoustic overlap has been reported in woodland species (Ficken et al. 1974, Popp et al. 1985). I found no interspecific avoidance of acoustical interference in open-country species, in spite of extensive overlap in frequency ranges among nine species. The causes of differences between the two habitats are unclear.

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Sexing Monomorphic Birds by Vent Measurements

P. DEE BOERSMA^{1,2} AND EMILY M. DAVIES¹

¹Institute for Environmental Studies and ²Department of Zoology, University of Washington, Seattle, Washington 98195 USA

Sexing monomorphic birds in the field historically has presented serious difficulties to biologists. The technique of sexing birds by examination of minute differences in cloacae is well known among professional aviculturalists (Stromberg 1977) and has been proposed for wild birds (Mason 1938, Hochbaum 1942, Wolfson 1952, Samour et al. 1983). The distinguishing characteristics of cloacae differ among species, which affects the ease and reliability of discrimination (Stromberg 1977); many of these characteristics are also difficult, or impossible, to find under poor field conditions.

Early in the season female vents dilate to allow the passage of the disproportionately large egg. Serventy (1956) described a simple method to sex birds based on a comparative examination of birds' external cloacae, or vents. The studies of Cole (1913), Serventy (1956), and Richdale (1957) did not quantify the accuracy and reliability of the method, however, nor did they address its general applicability. Serventy (1956) and Richdale (1957) identified the limitations inherent in the technique: only females that had recently laid eggs, and their known mates, could be sexed by examining their vents.

We measured the vents of Fork-tailed Storm-Petrels (*Oceanodroma furcata*) on the Barren Islands, Alaska, in 1981-1983; American Coots (*Fulica americana*) at Turnbull National Wildlife Refuge, Washington, in 1982; and Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina, in 1983 and 1984. These species were selected incidentally during other research projects.

Birds were measured during their breeding seasons and, except for a sample of Fork-tailed Storm-Petrels mist-netted and laparotomized in 1981, only known

breeders were used. For all species two measurements of the vent were made with needle-nosed calipers; the transverse, or lateral, length; and the cranio-caudal width (Fig. 1).

We analyzed the data by discriminant analysis by SPSS, and by K-mean clustering by BMDP statistical packages. In addition, we tested our ability to sex birds correctly by using 40% of the sample to calculate the discriminant functions and the remaining 60% to assess the validity of sex determination.

We swabbed the birds' vents with 10% alcohol, which wet the surrounding feathers so the raised fleshy lips of the vents could be seen clearly and measured. The stimulation and cooling effect of the alcohol uniformly caused the birds to contract their sphincters. Females that had recently laid eggs could not contract their vents as small as males, so by stimulating contraction maximum differences in vent size between the sexes was measured.

To verify sex identification by vent measurements, we laparotomized 42 Fork-tailed Storm-Petrels mist-netted between 12 and 30 July 1981. In 1982 and 1983 we measured only known breeders captured in burrows. In 1982 we measured the vents of 182 birds; 158 were members of known pairs (79 pairs) in which both individuals were measured. In 1983 we measured 161 birds, 142 of which formed mated pairs (71 pairs). Because the results of the laparotomies corroborated what intuitively and deductively seemed true, we categorized the individual of a mated pair with the larger vent as female and the bird with the smaller vent as male. We were not present any year between May and mid-June when the majority of eggs were laid (Boersma et al. 1980). Because female vents regress in size after laying (Serventy 1956, pers. obs.),