VOCAL DUELING AMONG MALE MARSH WRENS: EVIDENCE FOR RITUALIZED EXPRESSIONS OF DOMINANCE/SUBORDINANCE

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ABSTRACT.—Male Marsh Wrens[1] (*Cistothorus palustris*) sing with immediate variety (i.e. AB CDE . . .); they progress rapidly through their song repertoires and tend to countersing with the same song types. Intensive study of two hand-reared males in the laboratory now confirms that both the song types and the song sequences are learned. Furthermore, the leader/follower roles during countersinging duels are not determined at random. In this study, Bird 1 dominated Bird 2 in physical encounters; Bird 2 often followed (i.e. matched) the song type just sung by Bird 1, but Bird 1 matched the songs of Bird 2 only when the songs of the latter were electronically amplified. The leader/follower roles in countersinging may be ritualized expressions of dominance and subordinance, respectively, and could reveal to both males and females the relative vigor of the combatants. *Received 20 November 1978, accepted 26 March 1979.*

IMITATION plays an important role in the ontogeny of song in many songbird species (e.g. Nottebohm 1972, Kroodsma 1977), and if juveniles either remain at or return to the locality where songs were learned, interacting breeding males will possess similar songs. If a male has only one song type in his repertoire, temporal adjustments in song delivery may be used to achieve interference or avoidance (Wasserman 1977), but when males imitate several songs and develop sizeable repertoires of different song types, the potential for complexity of interactions during countersinging is escalated. Studies of Chaffinches (*Fringilla coelebs*), Great Tits (*Parus major*), Black-crested Titmice (*Parus bicolor*), Cardinals (*Cardinalis cardinalis*), Rufous-sided Towhees (*Pipilo erythrophthalmus*), etc., have revealed that neighboring males often respond to one another or to a tape recording (of a song from the local "dialect") with matching song types (Hinde 1958, Gompertz 1961, Lemon 1968a, b, Kroodsma 1971, respectively; see Falls and Krebs 1975 for an apparent exception to this pattern). Males of these species typically sing a song type several times before switching to another (i.e. AAAA . . . BBBB . . .), but the potential for vocal interactions is further heightened when successive songs are usually different (i.e. ABCDE . . .), as in the Marsh Wren (Verner 1975).

With such a rapid interchange of song types, the roles of leader and follower in the countersinging become immediately evident. Verner (1975: 295) speculated that this song-matching during countersinging reflected "the dominance/subordinance relationships between neighbors," but because of the complexity of both the song repertoire and the interactions in the field, he could not adequately document the relationship among males. Having studied this phenomenon in the laboratory with hand-reared birds, I can now (1) confirm that both the song types and favored sequences in this complex behavior are learned, (2) reveal that the roles of leader and follower in countersinging duels are not determined at random, and (3) support the hypothesis that such vocal dueling, together with loudness of delivery, is a reflection of size, age, and/or dominance/subordinance relationships and might be

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[1] See Kroodsma and Verner (1978) for encouraged change of common name from Long-billed Marsh Wren to Marsh Wren.
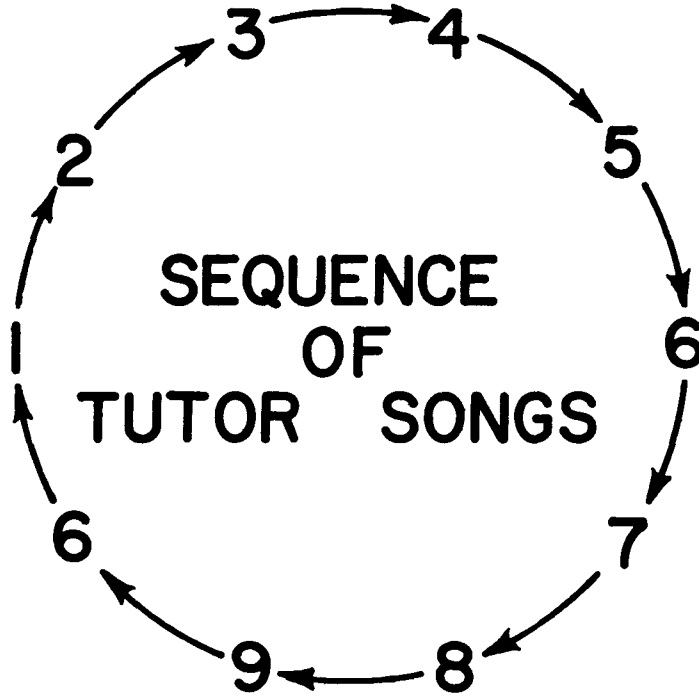
Fig. 1. The sequence of song types to which two Marsh Wren males were exposed between the ages of 15 and 65 days. The song type numbers correspond to those in Table 1. (Notice that song type 6 occurs twice.)

used by males or females in assessing vigor or potential fitness of possible rivals or mates.

METHODS

During June 1974 I collected from a New York marsh and raised by hand two 10-day-old Marsh Wren males. The two males were then housed in the same or nearby cages throughout the experiment. From day 15 to day 65 I tutored each male with nine different song types, which were presented in a cyclical fashion (Fig. 1) about 100 times daily. Subsong, analogous to babbling in human children, began at 20 days of age but ceased during November upon shortening daylengths; singing resumed and the adult songs were developed the next spring, as days again lengthened. Tape recording and spectrographic analysis of the singing revealed that each male had imitated the details of all nine song types that had been heard the previous July and August (Fig. 2).

During the experiment, each male was housed in a separate 27 × 28 × 52 cm wire cage on opposite sides of a small room. In order to determine how the two males were using their nine song types, I recorded in stereo the normal singing interactions of the birds on 11 days, from 1 March to 11 April, during their first spring. As with wild Marsh Wrens (Verner 1975), temporal patterning of singing did influence sequencing behaviors. With Bird 1, for example, the tendency to repeat a given song type increased as the intersong interval increased: a disproportionate number of transitions with time intervals of 10–15 s were between successive renditions of the same song type (χ^2, $P < 0.001$). Thus, sequences of song types sung by the two males were studied further only if 7.5 s or less intervened from the beginning of one song to the beginning of the next. This corresponds to a minimum of eight songs/minute.
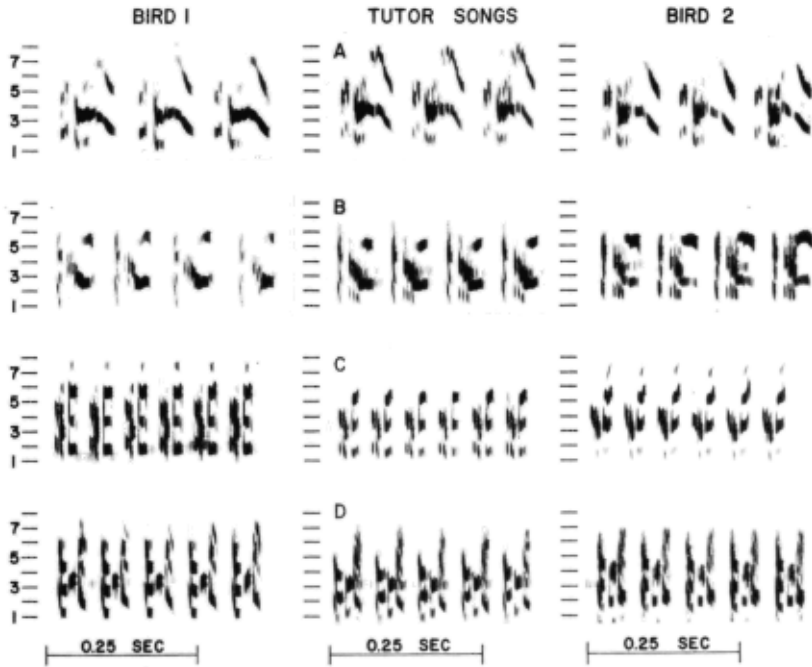
Fig. 2.   Representative trill syllables of four different song types that each of two Marsh Wren males learned from tutor tape songs presented via a loudspeaker. Axes are time and kHz. A typical marsh wren song lasts 1.5–2.0 s and consists of several introductory notes, a trill of repeated syllables, and several concluding notes. Because the trill is the major and most distinctive portion of the song, only it is presented here. The full song is displayed in Kroodsma (1978).

RESULTS

SONG SEQUENCING WITHIN THE INDIVIDUAL

Solo singing.—When either Bird 1 or Bird 2 sang without the immediate intervention of the other male, there was a significant tendency to sing the same sequence of song types as occurred on the tutor tape (see quadrants I and IV of Table 1, Fig. 3). Overall, out of 1,965 transitions from the two males, 565 were transitions that had been acquired from the tutor tape; this is 2.3 times the expected number of 246. Furthermore, the transition matrix for each male was asymmetrical; the mere association of song types on the tutor tape did not increase the likelihood of the male singing the reverse song sequences (e.g. the 2–3 transition was used frequently, but not 3–2, etc.), and observed entries for these reverse sequences were far less than expected for each male. Sequences of song types that were 4 or 5 transitions removed from one another in the tutor tape sequence (e.g. 4–9, see Fig. 1) were used even less by the two males; the observed/expected ratios were <1 (median = 0.46) for all 32 such possible transitions for the two males combined. Thus, the song-type sequences presented on the tutor tape during the first fall were learned and heavily favored during uninterrupted singing performances by each male the following spring.
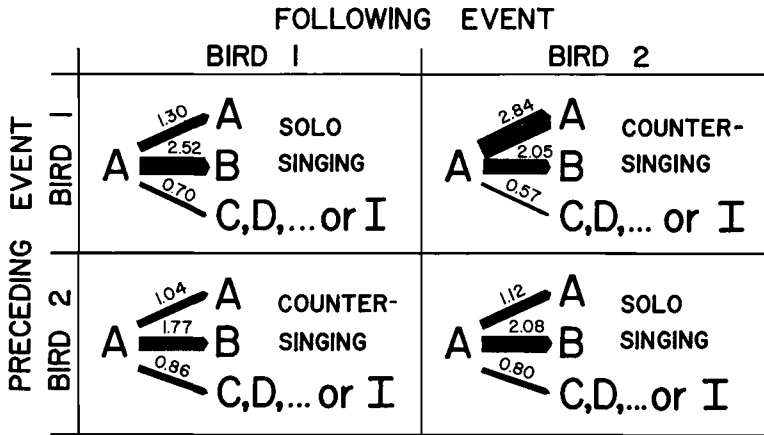
FOLLOWING EVENT

Fig. 3. Data summarized from the 18 × 18 transition matrix in Table 1. "A" represents any one of the nine song types in the repertoires of Birds 1 and 2, "B" then represents the next song type in the sequence of songs the males had acquired from the tutor songs (see Fig. 1), and "C" through "I" are the other song types in the repertoire. The relative width of the arrows depicts the observed/expected ratio for a given sequence of songs; the actual ratios occur above the arrows. For the sequence "A→C, D, . . . or I," the ratio is actually the average of all possible transitions (e.g. A→C, A→D, A→E, etc.). During "solo singing," both the preceding and following events illustrated in a quadrant are from the same male; in the "countersinging" quadrants, following events are responses by one of the males to the song types of the other male.

During uninterrupted singing, Bird 1 also tended to repeat a song type after he sang it, while Bird 2 did not. Overall, by comparing the index of predictive association for each of the 11 recording sessions (see Hays 1963), I found that the sequencing behavior of Bird 1 was more predictable than it was for Bird 2 (two-tailed Mann Whitney-U test, $P < 0.05$).

During countersinging.—The sequencing behaviors of the two males were influenced in different ways when they countersang with each other. Presumably in response to the more orderly and predictable behaviors of Bird 1, Bird 2 became *more* predictable in his song sequences: Bird 2 increased the observed/expected ratio of song type transitions that were acquired from the tutor tape (χ^2, $P < 0.001$; these data are not found in Table 1 or Fig. 3, for quadrants I and IV reveal patterns of uninterrupted singing, while quadrants II and III indicate responses to specific song types sung by the second bird—see below). Bird 2 did not, however, change the number of A–A transitions (χ^2, $P > 0.1$).

On the other hand, the sequencing behavior of Bird 1 became *less* predictable if Bird 2 interjected a song: Bird 1 decreased the observed/expected ratio of both the A–A transitions (χ^2, $P = 0.05$) and the song-type transitions acquired from the tutor tape (χ^2, $P < 0.001$). Thus, the responses of the two males to one another were assymetrical. Further clues as to the nature of this asymmetry are provided by examining how the males responded to the specific song types interjected by the second male.

RESPONSE TO SPECIFIC SONG TYPES OF THE
OTHER MALE DURING COUNTERSINGING

In response to specific song types interjected by the other bird, a male could reply with the same song type, advance to the next song type in the favored sequence, or

TABLE 1. A contingency table depicting the interactions between Bird 1 and Bird 2, two Marsh Wren males that were raised in captivity and that learned the same nine song types. Data are taken from 11 recording sessions during a 40-day period. Birds were tutored with the song type sequence depicted in Fig. 1, and * following a number in the table indicates a transition present on the tutor tape. A + following a number indicates song type matching by one of the two males. Row and column totals were used in calculating expected values for each cell (see Fig. 3).

| Preceding event		Following event																			
		Bird 1										Bird 2									
		1	2	3	4	5	6	7	8	9	Σ	1	2	3	4	5	6	7	8	9	Σ
Bird 1	1	23	40*	13	1	5	3	10	20	5	120	88+	64*	8	5	33	10	3	9	24	244
	2	16	36	31*	5	5	3	13	12	2	136	16	97+	20*	19	17	14	13	19	7	222
	3	14	4	27	46*	10	14	17	3	3	130	17	18	58+	67*	39	2	3	12	22	238
	4	4	11	7	4	26*	4	12	1	0	69	1	4	3	21+	49*	3	4	3	3	91
	5	5	9	20	2	9	15*	28	1	0	89	3	1	3	2	50+	21*	11	6	1	98
	6	30*	16	11	3	2	7	26*	7	6	108	31*	13	8	5	9	24+	18*	21	10	139
	7	10	14	10	4	11	18	32	44*	13	156	12	27	6	18	18	15	50+	27*	47	220
	8	22	5	10	0	1	8	17	13	15*	91	6	11	6	1	5	5	10	28+	52*	124
	9	4	14	0	0	1	32*	7	1	1	60	6	6	3	0	2	4*	4	3	30+	58
	Σ	128	149	129	65	72	107	162	102	45	959	180	241	115	138	222	98	116	128	196	1,434
Bird 2	1	28+	42*	46	8	12	9	11	41	8	205	13	29*	6	3	21	4	1	7	13	97
	2	61	28+	62*	14	3	11	32	12	5	228	28	43	23*	11	31	4	1	3	5	149
	3	11	7	11+	29*	13	9	16	4	3	103	9	3	5	23*	54	2	4	1	6	107
	4	25	29	9	17+	28*	9	20	4	1	142	3	16	2	12	54*	5	2	0	1	95
	5	34	31	40	14	26+	33*	35	10	4	227	20	16	32	34	32	46*	7	14	9	210
	6	29*	31	5	2	8	26+	11*	6	1	119	15*	13	0	1	22	19	13*	14	6	103
	7	10	6	8	2	6	14	14+	29*	13	102	7	2	1	1	9	13	8	11*	20	72
	8	18	6	30	5	11	18	17	7	21*	133	5	2	5	5	19	11	6	9	22*	84
	9	32	34	34	3	6	45*	30	4	9+	197	20	9	6	2	10	24*	5	6	6	88
	Σ	248	214	245	94	113	174	186	117	65	1,456	120	133	80	92	252	128	47	65	88	1,005
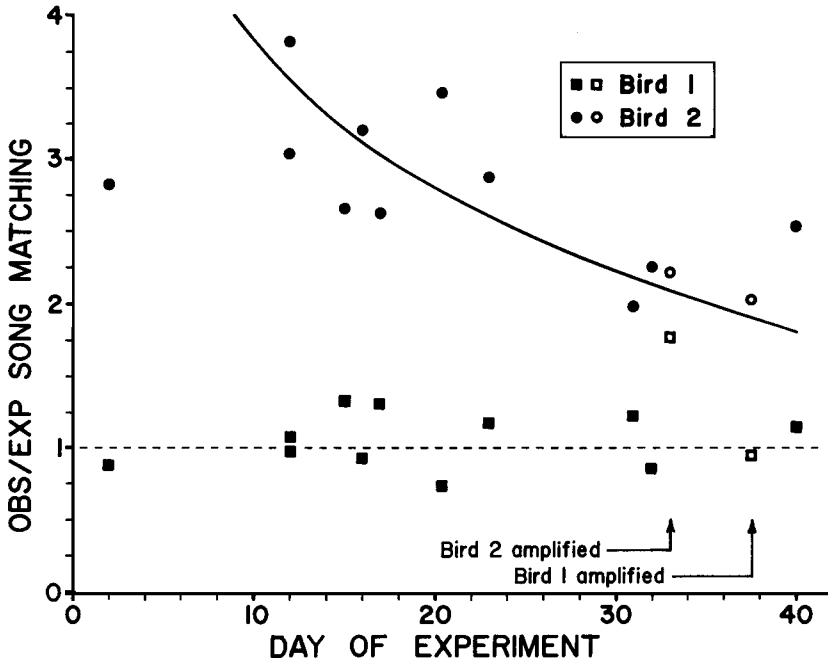
Fig. 4. A comparison of the observed/expected degree of song matching by Bird 1 and Bird 2 over a 40-day sampling period. The obs/exp ratio of 1 is expected by chance alone (dashed line). During two of the recording sessions, the songs of either Bird 1 (day 37) or Bird 2 (day 33) were amplified using microphone, amplifier, and speaker; these 2 days are represented by open squares or circles.

jump to any of the other songs available in the repertoire. When countersinging with Bird 1 (see Table 1 and Fig. 3, upper right quadrant), Bird 2 often advanced to the next song type in the favored sequence ($2.05\times$ the expected) but even more frequently replied with the song type that Bird 1 had just sung ($2.84\times$ the expected). Jumping to other points in the favored sequence occurred about half as often as expected by chance alone (obs/exp = 0.57).

A comparison of how Bird 1 responded to the song types of Bird 2 again emphasizes the asymmetry of the interactions. Bird 1 often advanced to the next song type in the favored sequence ($1.77\times$ expected), as did Bird 2. Bird 1, however, matched the song type that Bird 2 had just sung no more than would be expected by chance alone ($1.04\times$ expected). Rather, the probability of jumping to some other point in the singing sequence was greater for Bird 1 (obs/exp = 0.86) than it was for Bird 2 (obs/exp = 0.57; difference significant at $P < 0.05$, two-tailed Mann-Whitney U-test).

This last point is significant, for Bird 2 did often advance to the next song type in the sequence; if Bird 1 had ignored that advance and continued to sing in his favored sequence, he would then have been matching the song type that Bird 2 had just sung. That tended not to happen as often as expected; Bird 2 advanced to the next song type 2.05 times as often as expected, yet Bird 1 matched that song no more than expected by chance alone ($1.04\times$ expected). Overall, the responses of Bird 1 to Bird 2 were less predictable than vice versa (comparing the index of predictive association over the 11 recording sessions, $P < 0.002$, two-tailed Mann-

Whitney U-test). A major component of this unpredictability appears to consist of attempts by Bird 1 to avoid replying with the same song type that Bird 2 had just sung.

When combining the data from the 11 recording sessions over the 40-day period in one transition matrix, it is assumed that song patterning and matching are stable. There was a significant change, however, in the degree to which Bird 2 matched the songs of Bird 1 throughout this 40-day period. In Fig. 4 the observed/expected ratio of song-matching by Bird 1 and Bird 2 is plotted for each of the 13 sessions (11 natural + 2 experimental—see below) throughout the 40-day period. Bird 1 matched Bird 2 no more than expected by chance alone (except for day 33—see below); however, the degree to which Bird 2 matched Bird 1 was very high initially and decreased throughout the experiment (reciprocal transformation of obs/exp ratio, n = 13 sessions, $r = 0.69$, significantly different from 0 at $P < 0.01$).

In order to test whether the intensity of the signal could influence the extent of song-type matching, I amplified, via microphone, amplifier, and loudspeaker, the songs of Bird 2. On day 32 all equipment was in place, and on day 33 the amplifier was turned on. Bird 1 then matched the songs of Bird 2 more than during any other sampling period and significantly more than either the previous control day or all other recording sessions combined (two-tailed Mann-Whitney U-test, $n_1 = n_2 = 9$, comparing obs/exp ratios of diagonal cells for lower left quadrant of transition matrices for respective days; $P < 0.01$ in both cases). When the songs of Bird 1 were amplified in a similar experiment on day 37, Bird 2 did not significantly alter his singing behavior, but he did continue to match the songs sung by Bird 1.

DISCUSSION

Marsh Wrens in eastern Washington have large and nearly identical song-type repertoires (greater than 100 song types) and tend to sing their songs in highly stereotyped sequences. In fact, so stereotyped are the sequences that Verner (1975: 283) counted ". . . on six different occasions involving six different experimental subjects in the field . . . as many as nine consecutive correct matchings . . ." of the *next* song on a playback tape. Thus, the playback tape entrained the territorial male in the repertoire sequence, making the territorial male the ". . . leader in a counter-singing bout with the recorder."

Although a male of a species that typically sings with eventual variety (AAA . . . BBB . . .) may proceed through its repertoire in a semi-orderly fashion (e.g. see Lemon and Chatfield 1971), experimental studies have typically documented that a territorial male replies to a playback with the *same* or matching song type, not the next in the sequence. Several explanations could account for these observed differences. (1) They may reflect the focus of the investigators involved and the fact that discovering the sequential organization of "eventually versatile" songsters requires greater perserverence than it does for immediately versatile singers. On some occasions when birds do not match song types (e.g. 50–75% of time in Cardinals, Lemon 1968b), the leading male might actually be singing the next song type in the semi-orderly sequence of song-type bouts. (2) The differences undoubtedly reflect to some degree the escalated patterns of interaction than can occur in the *immediately* versatile Marsh Wren. The dominant feature of *eventually* versatile songsters is the seemingly endless repetition of a given song type (up to 100 repetitions in the Carolina Wren, *Thryothorus ludovicianus,* pers. obs.), while in the *immediately* ver-

satile species it is the contrast of the successive songs. It is quite possible that replies to interlopers (i.e. the playback tape recorder simulating an intruding male), which presumably are expressions of dominance or territorial possession, will be a reflection of that primary feature of the singing behavior, either the repetition of the same song type or the anticipation of the next. (3) Finally, the extended sequence of playback songs that Verner (1975) used, together with the smaller territory size of Marsh Wrens, may have evoked interactions that occur naturally among neighboring territorial males rather than those interactions that occur between a resident and an intruder.

But with either the immediate or eventual style of versatility in singing behavior, if countersinging of matching song types is to occur, there are both leader and follower roles. The major question then arises as to which interactant assumes which role. In this laboratory study, Bird 1 consistently assumed the role of leader. When singing solo, Bird 1 heavily favored the sequence of songs that had been learned the previous fall from the tutor tape; when Bird 2 intervened, the predictability of song sequences in Bird 1 actually declined. Overall, the data suggest that Bird 1 avoided matching Bird 2 by either advancing to the next song type or jumping to other points in the favored sequence.

On the other hand, Bird 2 actively matched the song types of Bird 1. When Bird 1 interjected a song type, the singing of Bird 2 became more predictable, largely as a result of his song-type matching during countersinging. During the hand-rearing period, Bird 2 had been quite sickly, and even though he survived, he never regained full vigor, and his songs were never quite as stable as were those of Bird 1. When the two birds were housed together or in the same cage with a single wire partition, Bird 2 was clearly subordinate, for aggressive attacks by Bird 1 were rarely (if ever) countered, and Bird 2 usually retreated to the opposite side of his cage space. Thus, in all respects, Bird 1 was physically dominant to Bird 2, and the alteration in countersinging during amplification of the song types of Bird 2 suggests further that the roles of leader and follower actually reflect the relative dominance of interactants. Aggressive tendencies or (apparent) size alone can be conveyed by the loudness or the frequency of a signal among some amphibians (for *Hyla,* G. M. Fellers pers. comm., and in *Bufo,* Davies and Halliday 1978), and with thrushes Dilger (1956) also demonstrated that loud song playback inhibited close approach by a territorial male, but lowered volumes again elicited approach (see also Morton 1977).

The relative dominance of interacting male Marsh Wrens could be expected to change in both time and space, and monitoring the interactions of known-age individuals throughout a breeding season should prove enlightening. If such vocal dueling can express dominance and subordinance, then one might predict that older established males would be dominant to first-year males or to other adult males that had just moved the center of their activity to a new courting center (see Verner 1965 for a discussion of the breeding biology of the Marsh Wren). Furthermore, one would predict that, all other things being equal, dominance and patterns of countersinging might change depending on the location of a male within his territory (Craig 1976, Brown 1963). Also, such relationships would not be stable but would change through time. Particularly intriguing here is the gradual reduction in the role of follower played by Bird 2 over the experimental period (Fig. 4). This pattern may reflect either declining subordinance in Bird 2 or the overall, gradual reduction in the frequency and probably the intensity of interactions over the experimental period.

The similarity in form and perhaps function between the vocal dueling by Marsh Wrens and the verbal dueling used by some segments of human societies is intriguing. Farb (1974) describes such human verbal dueling in the form of Eskimo song, West Indian calypso, or the insults exchanged by some Turkish or black ghetto youths (see also Labov 1972), the rapid verbal interchange being a means of developing vocal virtuosity and, perhaps even more important, serving as an intragroup competitive strategy that is an alternative to actual fighting. In the West Indies, for example, the game is played by adolescent males, and rhyme must be used during the rapid interchange of insults. The audience (usually other adolescent males) "incites both participants, cheering good hits and ridiculing bad ones." Fighting is abhored; rather, the loser of the verbal interchange will "sound out" another more vulnerable member of the group, and after several such interchanges a pecking order is eventually established (Farb 1974).

The roles of leader and follower are also evident in some frog choruses, though the roles involve the temporal delivery of a single call rather than the matching of different call types. Again, roles are not established at random, for certain males initiate more calling bouts than would be expected by chance alone. Furthermore, with the Pacific tree frog (*Hyla regilla*), Whitney and Krebs (1975) found that males that initiated calling bouts attracted a disproportionate number of the females. It is highly conceivable that the complex communication system that has evolved in some bird species may also function in a similar manner, conveying a wealth of information to both participants and listeners.

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