

# SINGING ORGANIZATION DURING AGGRESSIVE INTERACTIONS AMONG MALE YELLOW-RUMPED CACIQUES<sup>1</sup>

JILL M. TRAINER<sup>2</sup>

*Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, MI 48109*

**Abstract.** Singing organization during aggressive supplanting interactions was compared among color-banded male Yellow-rumped Caciques (*Cacicus cela vitellinus*) at one breeding colony in Panama. All male colony members shared seven song types, which, when ranked from most to least frequent, occurred in similar relative abundances in their repertoires. Males had similar patterns of song sequencing, which were consistent across 2 years. During countersinging, caciques tended to follow other males' songs with the same type. Song bouts of birds singing in the presence of other singing males contained different proportions of song types, were more diverse, and were less repetitive than those of males singing solo. Social interactions among males and behavioral associations of cacique song types were important factors in determining these patterns of singing organization. The possible functions of these patterns are discussed.

**Key words:** Song; repertoire; singing organization; song sequences; transition matrix; agonistic interaction; Yellow-rumped Cacique; Panama.

## INTRODUCTION

Like many species of songbirds that have repertoires of more than one song type, Yellow-rumped Caciques (*Cacicus cela vitellinus*) have complex patterns of singing organization. Although singing organization has been described in several species (Isaac and Marler 1963, Lemon 1971, Lemon and Chatfield 1973, Falls and Krebs 1975, Catchpole 1976, Verner 1976, Dobson and Lemon 1979, Payne 1979, Whitney 1985), the significance of the observed patterns is not well understood. Proposed functions of song repertoires may apply also to singing organization. For example, songs in a bout of singing may be organized to increase the effectiveness of advertisement, by preventing territorial neighbors from habituating to song (Dobson and Lemon 1975, Lemon et al. 1981), increasing the apparent density of territorial males (Krebs 1977), or stimulating reproductive activity in females (Kroodsmma 1976). In this study I examined an alternative suggestion that singing organization is influenced by immediate social interactions. This hypothesis predicts that the singing organization of individuals will change depending on the social context. For example, the rate of switching between the song types of Song Sparrows (*Melospiza*

*melodia*) increased with greater intensity of agonistic stimulation (Kramer and Lemon 1983, Kramer et al. 1985). Observing color-banded Yellow-rumped Caciques during aggressive interactions, I examined the organizational properties of singing, including the relative incidences of song types, patterns of song sequencing, rate of singing, repetitiveness, and song diversity.

Caciques made good subjects for this study because male members of nesting colonies interacted frequently. The polygynous males gathered in trees of 10 to 100 nests to countersing with one another and consort with females (Trainer 1985, Robinson 1986). Males at a colony formed a stable linear dominance hierarchy, maintained by continual supplanting among males. One context of song appeared to be aggressive because countersinging males often engaged in supplanting interactions in which the dominant individual displaced the subordinate. Rarely, such an interaction resulted in a chase or grappling fight.

Caciques sang repertoires of five to seven distinct song types, which were shared among all male members of a colony and differed from those of other colonies a few kilometers away (Trainer, in press). In a previous paper, I showed that at one colony, four out of seven song types were statistically associated with different behaviors; when a given behavior occurred, males were more likely to sing an associated song type than expected by its frequency of occurrence (Trainer 1987). I concluded that utterances of

<sup>1</sup> Received 16 January 1988. Final acceptance 13 April 1988.

<sup>2</sup> Present address: Department of Biology, University of Missouri, St. Louis, MO 63121.

single songs potentially communicate information used to control the course of aggressive interactions. Focusing above the level of single utterances, I here describe patterns of singing organization in the song bouts of individual males.

Unlike studies describing species-typical patterns of singing, I avoided pooling samples from more than one male where sample sizes permitted. This approach, although it requires large samples for each male, has two advantages. First, it allowed me to examine the consistency among males in patterns of singing organization. Second, it allowed me to demonstrate that differences in singing organization based on social context are due to changes in the behavior of individuals rather than the presence of different individuals. I asked three questions about singing organization in naturally interacting individual birds. (1) Is there consistency among males in the relative incidences of song types and song-sequencing patterns? Agreement among males in song sequencing is seldom examined, yet this is important for understanding the functional significance of these patterns. (2) Are the song sequences of individual males influenced by what other males are singing? (3) Does the organization of an individual's singing change with the social context?

## METHODS

I conducted this study at Lookout colony on Howard Air Force Base near the Pacific entrance to the Panama Canal. Caciques in Panama breed during the dry season from February to June and nest in the same trees year after year. I collected observations at Lookout colony for two breeding seasons from 13 January to 22 May 1982, and from 8 February to 21 April 1983.

Ten adult male caciques were captured in mist nets and banded with three colored polyvinylchloride (PVC) bands secured with PVC glue, and one numbered monel metal band. I aged males on the basis of plumage and eye color (Robinson 1985, Trainer 1985). Only the behavior of adult males is described because immature males do not sing in the nest tree.

I tape recorded songs using either a Uher Report IC tape recorder or a Marantz PMD 340 cassette tape recorder with a Uher M 517 cardioid microphone that recorded the singing of several males simultaneously. By allowing the tape recorder to run continuously, I collected focal animal and sequence samples (Altmann 1974)

of banded birds from 07:00 to 11:00 every 2 to 9 days. Samples ranging from 103 to 1,843 songs were recorded from each of seven marked males in 1982 and six marked males in 1983. The sequences of recorded song types, which were identified by ear, were transcribed manually using an event recorder switch on a polygraph.

Seven song types occurred at Lookout colony in each of the 2 years of the study. A detailed study of gradual change in song structure (Trainer, in press) revealed that each song type in 1983 appeared to be derived from a song type present the previous year. Corresponding song types from each year are designated with the same number. Audiospectrograms of these songs have been published previously (Trainer 1987).

In the following analysis procedures, a song bout is defined as an uninterrupted recording of at least 10 songs, each separated by no more than 60 sec.

## ANALYSIS OF SONG TRANSITION MATRICES

For each color-banded male, all song bouts were combined to produce a song transition matrix. The two rarest song types from each year were eliminated from the analysis so that only the transitions with expected values greater than one were considered. These omitted songs comprised 6% and 4% of the total songs recorded from marked males in 1982 and 1983 respectively. Four marked males in each year had a sufficient number of recorded songs to allow a test of their song sequences for first-order dependencies (i.e., fewer than 20% of the cells had expected values  $< 5$ ). This test assumes stationarity, i.e., constancy over time in the relative incidences of song types (Slater 1973). Using a *G*-test for heterogeneity, I verified the condition of stationarity in the song sequences of these eight males by comparing the relative incidences of song types in five consecutive samples of 100 to 200 songs ( $G < 36.42$ ,  $df = 24$ ,  $P > 0.05$ ). Some samples recorded late in the breeding season contained different relative incidences of song types from earlier samples, and were not included in the analysis.

I tested for independence among first-order song transitions using chi-square analysis, calculating expected values from marginal totals of the song transition matrices (Chatfield and Lemon 1970). A significant result occurs when songs are sung in a nonrandom sequence with respect to the immediately preceding song type.

A pattern of singing in which birds tend to repeat the same song type one or more times before switching to a different song type usually results in a highly significant first-order dependency among songs. A more interesting question, therefore, is whether runs of unlike song types are sequenced nonrandomly. In a second chi-square test for sequential dependencies among runs of unlike song types, I omitted song transitions between like song types, i.e., along the diagonal (Lemon and Chatfield 1971) (Table 1). Because expected values from such incomplete matrices cannot be calculated from marginal totals, I computed them by numerical iteration (Goodman 1968).

Based on the latter analysis, I tested whether males shared patterns of song sequencing by comparing among males those song transitions which contributed most to significant sequential dependencies. Among the matrices of four males in each year, I compared those transitions in which the departure in the observed from the expected values exceeded the following threshold criterion. For each transition, the entire matrix was collapsed around the transition to form a  $2 \times 2$  matrix, combining frequencies from other song types (Slater 1973). If the chi-square statistic computed from the resulting matrix exceeded the 5% critical value ( $df = 1$ ), I considered the transition to show a major departure from the expected value. Using this method, around 5% of the cells in each matrix would show a major departure by chance alone. However, this criterion provided a standard useful in comparing the important transitions in the matrices of different males.

#### ANALYSIS OF INTERMALE SONG TRANSITIONS

For each of four marked males in 1983 I constructed two matrices of intermale song transitions, excluding the two rarest song types. One matrix contained the frequencies with which a given male's song types were followed immediately (with no intervening songs) by another male's song. Often the subject male uttered several songs consecutively without intervening songs of other males, but I included in the analysis only those songs followed immediately by another male. The second matrix contained the transitions between songs of any male followed by those of the subject male. Small sample sizes precluded testing the intermale transitions of pairs of marked males.

TABLE 1. Major song transitions<sup>a</sup> in song sequences of four marked Yellow-rumped Caciques in 1982.

Preceding song type	Following song type				
	1	2	3	4	7
1		1+ 3+ 4+			3- 4-
2			1+ 2+ 3+ 4+	4-	1-
3					
4	2+	1-	1- 2- 4-		1+ 3+ 4+
7	2-				

<sup>a</sup> The numbers in the song transition cells indicate individual males for which the departure in the observed from the expected frequencies exceeded a threshold criterion in the direction indicated by the sign. Marked males are indicated by numbers as follows: 1—ORW, 2—WRY, 3—WYG, 4—WRB.

#### ANALYSIS OF SOLO AND GROUP SINGING BEHAVIOR

For each of eight color-banded males, I compared several characteristics of singing behavior in two behavioral contexts: (1) solo—a male singing near the nest clumps with no other singing males present, and (2) group—the same male in the presence of other singing males. I compared the average song rate (songs/min) of a male's solo song bouts with the average song rate of his group bouts. For the following parameters a male's song bouts were pooled within each context: Shannon-Wiener song diversity =  $\log_2 N - 1 \div N(\sum n_i \log_2 n_i)$  where  $N$  = the number of songs in the samples and  $n_i$  = the number of utterances of a song type (Krebs 1978); overall song repetition index (average number of times a song of any type was sung before changing to a different type); the repetition index of each song type (average number of times a given song type is sung before changing); and the relative incidence of each song type. I tested for differences in these parameters between solo and group singing using two-tailed Wilcoxon's signed-rank tests.

#### RESULTS

##### CONSISTENCY IN SINGING ORGANIZATION

Combining a male's song bouts over the entire breeding season, I found that the relative incidences of song types differed significantly among males in each year ( $G$ -test for heterogeneity, 1982:

TABLE 2. Proportion and relative abundance rank of each song type in the repertoires of Yellow-rumped Cacique males.

Male	Song type						
	1	2	3	4	5	6	7
1982							
ORW	0.075 (5)	0.123 (4)	0.130 (3)	0.137 (2)	0.009 (6)	0.004 (7)	0.522 (1)
WRV	0.123 (5)	0.065 (6)	0.195 (3)	0.212 (2)	0.015 (7)	0.150 (4)	0.241 (1)
WYG	0.144 (4)	0.062 (5)	0.213 (3)	0.233 (2)	0.001 (7)	0.045 (6)	0.301 (1)
WRB	0.103 (4)	0.060 (6)	0.104 (3)	0.138 (2)	0.013 (7)	0.075 (5)	0.507 (1)
OGW	0.252 (1)	0.068 (6)	0.223 (3)	0.126 (4)	0.010 (7)	0.087 (5)	0.233 (2)
WBG	0.113 (2)	0.063 (6)	0.072 (5)	0.201 (2)	0.023 (7)	0.104 (4)	0.424 (1)
WRW	0.148 (2)	0.087 (5)	0.148 (3)	0.096 (4)	0.009 (7)	0.043 (6)	0.470 (1)
1983							
OGG	0.063 (5)	0.130 (4)	0.170 (2)	0.144 (3)	0.025 (7)	0.043 (6)	0.424 (1)
WRW	0.085 (4)	0.080 (5)	0.142 (3)	0.154 (2)	0.011 (7)	0.034 (6)	0.495 (1)
WRV	0.087 (4)	0.065 (5)	0.208 (2)	0.110 (3)	0.009 (7)	0.043 (6)	0.477 (1)
WYG	0.052 (5)	0.060 (4)	0.099 (3)	0.153 (2)	0.011 (7)	0.009 (6)	0.615 (1)
WRB	0.069 (4)	0.045 (5)	0.111 (3)	0.111 (2)	0.009 (7)	0.019 (6)	0.636 (1)
WBG	0.093 (5)	0.103 (4)	0.115 (3)	0.151 (2)	0.006 (7)	0.035 (6)	0.497 (1)

$G = 313.97$ ,  $df = 36$ ,  $n = 7$ ,  $P < 0.005$ ; 1983:  $G = 511.48$ ,  $df = 30$ ,  $n = 6$ ,  $P < 0.005$ ; Table 2). A posteriori tests did not reveal groups of homogeneous song samples including more than two males. However, when the proportions of song types were ranked from most to least abundant within the repertoire of each male (Table 2), concordance of abundance ranks among males within a year was significant; males exhibited similar ranking of song types (1982: Kendall's coefficient of concordance  $W = 0.82$ ,  $F_{(5.7, 34.3)} = 27.7$ ,  $P < 0.001$ ; 1983:  $W = 0.95$ ,  $F_{(4.7, 23.4)} = 95$ ,  $P < 0.001$ ).

Chi-square analysis of song matrices that included the transitions between like song types revealed significant dependence among the songs of all males tested ( $\chi^2 = 266$  to 1,489,  $df = 16$ ,  $P < 0.005$ ). Large frequencies in cells along the diagonal of the matrices indicated that males tended to sing song types more than once before switching to a different song type.

The transitions between unlike song types were nonrandom in all eight samples ( $\chi^2 = 25$  to 124,  $df = 11$ ,  $P < 0.01$ ). Several transition frequencies showed major departures from their expected values (the departures exceeded the threshold criterion). In 1982 four major transitions were shared among three or more males (Table 1). These males sang song transitions 1-2, 2-3, and 4-7 more often than expected by chance and transition 4-3 less often. A few transitions involving negatively associated song types were unique to one individual. In 1983 three transi-

tions were shared among three or more males (Table 3). These males showed a positive tendency to sing transitions 2-3, 7-4 and a negative tendency to sing 4-3. Four other transitions were shared among two males and four were unique to one male.

Four out of five significant positive and negative transitions that were shared by two or more males persisted from one year to the next. One additional positive shared transition appeared in

TABLE 3. Major song transitions<sup>a</sup> in song sequences of four marked Yellow-rumped Caciques in 1983.

Preceding song type	Following song type				
	1	2	3	4	7
1		1+ 4+		3+	3-
2			1+ 2+ 3+ 4+	1- 3-	1- 4-
3				4-	
4	2+ 3+		1- 2- 3-		1+ 3+
7	2-	1-		1+ 2+ 4+	

<sup>a</sup> The numbers in the song transition cells indicate individual males for which the departure in the observed from the expected frequencies exceeded a threshold criterion in the direction indicated by the sign. Marked males are indicated by numbers as follows: 1-OGG, 2-WRV, 3-WYG, 4-WRW.

TABLE 4. Major intermale song transitions<sup>a</sup> of Yellow-rumped Caciques in 1983.

Preceding song type	Following song type				
	1	2	3	4	7
1	1+	1+		2+	1-
	2+	2+			2-
	3+	3+			3-
2		1+			1-
		2+			2-
		3+			
		4+			
3			1+	1-	2+
			2+	2-	3-
			3+	3-	
			4+	4-	
4		4+	2-	2+	
			3-	3+	
			4-	4+	
7	2-	1-		3+	1+
		2-			3+
		3-			

<sup>a</sup> The numbers in the song transition cells indicate individual males for which the departure in the observed from the expected frequencies exceeded a threshold criterion in the direction indicated by the sign. Marked males are indicated by numbers as follows: 1—OGG, 2—WRY, 3—WYG, 4—WRW.

1983. Two individuals were present in both years and their significant transitions were similar over the 2 years. All but one transition appearing in 1982 persisted in 1983. Two new positive and two new negative transitions appeared in 1983. For these transitions the departure of the expected from the observed frequencies in 1982 was in the same direction as those the following year. Some of these transitions may have failed to reach significance in 1982 due to the smaller sample sizes.

#### INTERMALE SONG TRANSITIONS

Intermale song transitions were nonrandom for the four males tested, either when a male sang the preceding song, or when the male sang the following song, or both ( $df = 16$ ,  $P < 0.05$ ). Table 4 shows the transitions in which the observed frequencies deviated from the expected in one or both of the matrices of each male. The major positive song associations were along the diagonal, indicating that males tended to match each other's songs. The only other positive trend was for song type 2 to follow type 1. Four negatively associated transitions, 1-7, 3-4, 4-3, and 7-2 appeared in the matrices of at least three males.

TABLE 5. Differences in relative incidences and repetition indices between males singing solo and in groups.

Song type <sup>a</sup>	Relative incidence			Repetition index		
	Solo	Group	$P^b$	Solo	Group	$P^b$
1	0.052	0.091	0.004	1.22	1.35	ns
2	0.113	0.068	0.027	2.25	1.68	0.027
3	0.077	0.106	0.004	1.42	1.63	ns
4	0.130	0.146	ns	2.00	1.98	ns
5	0.023	0.011	ns	0.89	0.91	ns
6	0.090	0.100	ns	1.46	1.63	ns
7	0.533	0.474	0.020	4.21	3.11	0.004

<sup>a</sup> Samples for song types in 1983 were combined with those of song types in 1982 from which they appeared to be derived.

<sup>b</sup> Two-tailed Wilcoxon's signed-rank test,  $n = 8$  males.

For three out of four males, the intermale transitions between runs of different song types were not independent. In these matrices the association among bouts of different song types corresponded to the major song associations observed in the song sequences of individual males (Tables 1 and 3), except that for two males song type 1 tended to follow 4 and 4 tended to follow 2.

#### SOLO AND GROUP SINGING BEHAVIOR

The average song rate of males singing solo did not differ from when they sang in groups. Song diversity was higher when males sang in groups than when they sang alone (two-tailed Wilcoxon's signed-rank test,  $\bar{x} \pm SD = 2.18 \pm 0.248$  in groups,  $\bar{x} \pm SD = 1.94 \pm 0.356$  solo,  $T_s = 3$ ,  $P < 0.020$ ). The overall repetition index was lower when males sang in groups (two-tailed Wilcoxon's signed-rank test,  $\bar{x} \pm SD = 2.31 \pm 0.380$  in groups,  $\bar{x} \pm SD = 2.72 \pm 0.486$  solo,  $T_s = 0$ ,  $P < 0.004$ ).

The relative incidences of song types 1 and 3 were higher when males sang in groups, whereas the relative incidences of song types 2 and 7 were higher when males sang alone (Table 5). Song types 2 and 7 had higher repetition rates solo than in groups.

#### DISCUSSION

Patterns of singing organization were not peculiar to individuals; males showed similarly ranked relative incidences of song types and patterns of song sequencing. Furthermore, song transition patterns were similar from one year to the next. The absence of some significant transitions in 1982 was probably due to the larger sample sizes collected in 1983. These results suggest the existence of consistent rules governing song sequences of males at a colony.

The association of different song types with similar behaviors may be one important rule in determining sequential dependencies between these song types. In a previous study I found that when a given behavior occurred, males were more likely to sing certain associated song types than expected by their overall frequency of occurrence (Trainer 1987). These song types were associated with flight, starting song bouts, supplanting, and low colony singing activity. Song types associated with the same behaviors tended to occur sequentially in a bout of singing. For example, song types 2 and 3 were both used before supplanting other males, and types 1 and 2 were used before and after supplanting interactions and when the song rate at a colony was low. These song diads were positively associated in song sequences. Similar results were found in a study of singing organization in Village Indigo-birds, *Vidua chalybeata* (Payne 1979). Song types associated with aggressive behavior occurred together, and song types associated with sexual behavior occurred together. In caciques and indigo-birds, behavioral associations of song types may partly explain sequential dependencies among song types.

Several people have suggested that internal mechanisms intrinsic to an individual control the sequence of song types in a male's singing (Lemon and Chatfield 1971, Slater 1983, Whitney 1985). For example, the production of a song type by a male may inhibit or facilitate his subsequent production of certain other song types. While these mechanisms may exist in caciques, my study provides some evidence for external controls of song sequencing. Because a male's behavior is influenced by the environment, and his songs are associated with behaviors, his song sequences are to some extent controlled externally.

Social interactions were also important in influencing singing organization. Individuals tended to match the song types of others in a bout of singing. One possible explanation for this is that males find themselves in similar behavioral situations in which they use the same song types. It seems unlikely, however, that this could completely explain song matching, because the rate of switching between song types appears to be greater than that required by changes in the behavioral context. Males typically sing five different song types in only 90 sec; this frequency of switching exceeds the frequency of switching

among behaviors associated with song—flight, starting song bouts, and supplanting (Trainer 1987). Therefore, what a male sings was contingent on what other individuals were singing.

Other evidence of the influence of social interactions was that singing organization of individuals depended on whether they sang solo or in a group; song diversity was higher and singing less repetitive when males sang in groups. The prevalence and high repetition index of two song types in solo singing helped to explain these differences.

Behavioral associations of song types may account for the differences in song content of solo and group singing. For example, song type 1, which appears to stimulate other males to sing (Trainer 1987), occurred more often when males sang in groups. Song type 2, which was associated with starting song bouts, occurred more often alone. Song type 7, which was negatively associated with all social situations I examined, occurred more often when males were singing solo.

Demonstrating that social interactions influence singing organization and that the singing of individuals changes with social context is a first step in determining the functional significance of singing organization in communication during social interactions. Both social interactions and behavioral associations of song types appeared to be important determinants of singing organization in caciques. Several suggestions have been made as to the functions of the patterns I examined.

Stereotyped sequences of song types may serve as messages just as individual song types do. I did not test this possibility in caciques by observing behavioral associations of song sequences. However, sequences of songs were not stereotyped, although some transitions occurred more often than expected by chance. These transitions sometimes represented song types associated with similar behaviors.

Two functions of song matching have been suggested. First, a male may match the songs of another to attract the attention of a particular individual (Lemon 1968). This ability may be especially important in caciques because usually several males simultaneously sing in a nest tree. Second, a male may match another to signal his relative dominance status (Kroodsma 1979, Smith and Norman 1979, Todt 1981). This possibility could be tested in caciques by recording large samples of countersinging in diads of males

with known relative dominance status, and testing whether the intermale transitions showed greater dependence of the subordinate individual's songs on those of the dominant than the reverse.

Low repetition and high diversity in singing may signal high motivation or aggression. The low repetition index in group singing caciques corresponds to a higher rate of switching between song types. Thus, these results are consistent with those from other species in which high switching rates were related to greater agonistic stimulation (Kramer et al. 1985, Simpson 1985).

These possible functions of singing organization are best explored further by observing the responses of individuals to different patterns of singing. For example, captive Eurasian Blackbirds (*Turdus merula*) showed the greatest response to playback songs that matched and overlapped temporally with the subject's songs (Todd 1981). This approach may uncover the possibly rich source of information in singing organization.

#### ACKNOWLEDGMENTS

I am indebted to Tom C. Will for assistance with fieldwork. The use of equipment and facilities was generously provided by William Conner, Nathan Gale, J. W. Hardy (Florida State Museum), Neal G. Smith, and R. Haven Wiley. This research benefitted from discussion with and advice from Robert B. Payne, Peter R. Grant, W. John Smith, and Scott K. Robinson. I am grateful to Thomas R. Meagher for advice on the statistical analysis, and to Kathleen Groschupf, Marcy Lawton, and Mary Victoria McDonald for their comments on this manuscript. Funds for this research were provided by the Smithsonian Tropical Research Institute, American Museum of Natural History, Sigma Xi, the American Ornithologists' Union, Wilson Ornithological Society, Northeastern Bird Banding Association, and by the Rackham Graduate School and the Museum of Zoology, University of Michigan.

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