

BEHAVIORAL ASSOCIATIONS OF SONG TYPES DURING AGGRESSIVE INTERACTIONS AMONG MALE YELLOW-RUMPED CACIQUES¹

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Abstract. Yellow-rumped Caciques (*Cacicus cela vitellinus*) in Panama had repertoires of around seven distinct song types that were shared among all male members of a breeding colony. During aggressive interactions among males, different song types were statistically associated with various behavioral contexts, including flying, beginning a song bout, supplanting, and following a pause in colony singing activity. Three general song classes contained structural analogs (song types sharing acoustic similarities) at twelve colonies. Both structural and functional properties of song types appeared to be widespread in the Isthmus of Panama.

Given a song type, the conditional probabilities of associated behaviors were usually low (0.05 to 0.50). Individual songs were better predictors of nonaggressive behavior, such as flight and starting song bouts, than supplanting behavior. Cacique song types are better interpreted as attention attracting devices rather than as signals of agonistic intentions.

Key words: Song; repertoire; communication; information; behavioral association; agonistic interaction; Yellow-rumped Cacique; Panama.

INTRODUCTION

The application of games theory analysis to competitive interactions has raised questions about the role of cooperation in communication (Dawkins and Krebs 1978, Krebs and Dawkins 1983). For example, do animals cooperate in the exchange of information during aggressive interactions? It has been hypothesized that animal displays might convey information about resource holding power (RHP: size and fighting ability), but animals are not expected to signal their motivational levels or behavioral intentions about attack or retreat (Maynard Smith 1982). Reliable information about RHP is presumably signalled by displays that are costly to produce; bluffing about RHP would be too costly for an animal of insufficient size or strength (Maynard Smith and Parker 1976, Zahavi 1977, Clutton-Brock and Albon 1979). On the other hand, bluffing about behavioral intentions may be profitable but not costly. Inexpensive displays might tend toward typical intensity as receivers are selected to ignore information about intentions to attack or retreat (Dawkins and Krebs

1978). Signalling reliable information about behavioral intentions suggests a degree of cooperation not compatible with games theory reasoning. This approach has stimulated inquiry into what types of information are conveyed during aggressive interactions, and how reliably this information is communicated (Caryl 1979, Nelson 1983).

In its role of resource defense, bird song can be considered an agonistic display, and bouts of countersinging often initiate interactions between competing males. Because events in these early stages of interaction may determine whether encounters escalate to more aggressive levels, it is important to understand the process of communication during singing. Many songbirds have repertoires of more than one discrete song variant (Krebs and Kroodsma 1980, Kroodsma 1982). These variants are often considered to be equivalent in meaning. However, it is also possible that they communicate a variety of messages (Smith 1977). Because there is no obvious way that song variants might be related to RHP, it is pertinent to ask whether they convey information about behavioral intentions during aggressive interactions.

The purpose of this study was to ask three questions about the use of song type repertoires during aggressive interactions among male Yellow-rumped Caciques (*Cacicus cela vitellinus*).

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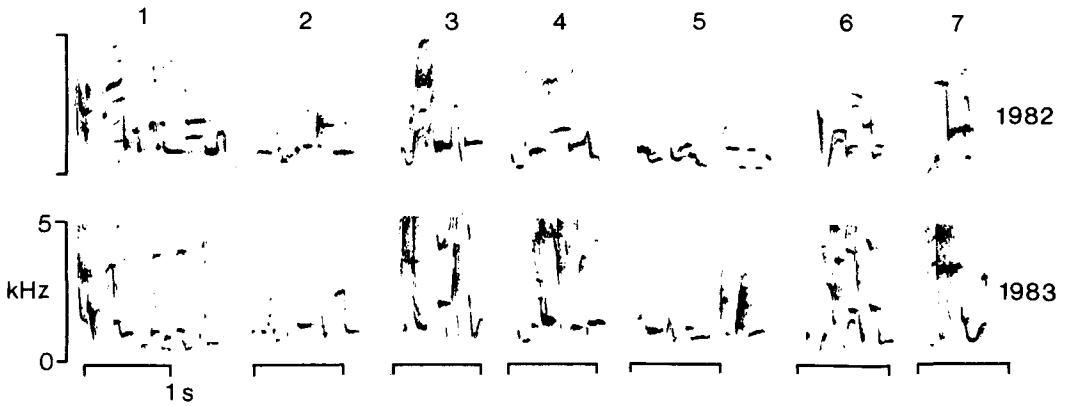


FIGURE 1. Yellow-rumped Cacique song types present at Lookout Colony in 1982 and 1983.

(1) Are song types associated with different behaviors of the singer? This reveals what information about the behavior of the singer may potentially be communicated by a song type (Smith 1977). (2) Are song types that are associated with a singer's behavior reliable indicators of that behavior? (3) Do song types potentially signal information about agonistic intentions?

Male Yellow-rumped Caciques gather to display in nesting colonies of up to 100 nests in a single tree. Female activity in the colony is centered around the nests, which they build in tight clusters (Robinson 1985a). Males compete to occupy preferred positions closest to the nests, but positions are not owned exclusively. They form a linear dominance hierarchy made evident by frequent supplanting interactions. Successful males mate polygynously, forming consortships with one or more females in a breeding season (Robinson 1986). Males have repertoires of five to seven song types, all of which are shared among members of a nesting colony (Feekes 1977, 1982; Trainer 1985). These song types, nearly indistinguishable among individuals at the same colony, are different from those sung at neighboring colonies a few kilometers away.

Aggressive interactions while countersinging are extremely frequent, usually involving supplanting of one male by another, but rarely resulting in a grappling fight (Trainer 1985). The risk of injury during fighting is probably high since caciques have strong feet and fatalities from fighting sometimes occur (Robinson 1985b). The organization of song types in a bout of singing is influenced by social interactions among males; the sequence of a male's song types is contingent

on what other males are singing, and song type use differs when males are singing in groups from when they are singing by themselves (Trainer 1985).

STUDY AREA AND METHODS

I tape recorded song samples at twelve cacique colonies along the isthmus of Panama, Republic of Panama. Eight of the colonies were concentrated near the Pacific entrance to the Panama Canal. Field work was conducted during three breeding seasons from 6 January to 21 May 1981, 13 January to 22 May 1982, and from 8 February to 21 April 1983.

Songs were recorded using either a Uher Report IC tape recorder or a Marantz PMD 340 cassette tape recorder with a Uher M 517 cardioid microphone or a Sennheiser ME 88 spot microphone. Songs were displayed on a Unigon Angioscan real-time audiospectrum analyzer, and the frequency vs. time display photographed with Plus-X 35 mm film. Although the frequency range of the songs was between 500 and 10,000 Hz, a 1.6 sec sample with frequencies between 0 and 5,000 Hz was displayed for maximum resolution of the highest amplitude notes in the songs.

Detailed observations on the behavioral context of song types during intermale interactions were collected at one colony, called Lookout Colony, during 1982 and 1983. At this colony, seven song types occurred in each of the 2 years of the study. A detailed study of gradual change in song structure (Trainer 1985) 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 (Fig. 1).

Caciques were captured in mist nets and banded with three colored polyvinylchloride (PVC) bands secured with PVC glue, and one numbered monel metal band. At Lookout Colony, I banded 40 females, 10 adult males, seven subadult males, and three juvenile males. Males were aged on the basis of plumage (Robinson 1985a, Trainer 1985). Focal animal samples (Altmann 1974) of banded and unbanded birds were recorded for about 4 hr every 2 to 9 days. The following observations were dictated into the microphone during real-time recording of singing interactions: identity of singers, their positions in the nest tree, perch changes, supplanting interactions, chases of females, courtship displays, and copulations. The sequences of songs and behavior recorded on tape were transcribed manually using an event recorder switch on a polygraph. Time intervals between songs or behavioral events were measured from the polygraph record with a precision of 0.2 sec.

To determine whether song types were used differentially in various behavioral situations, I tested whether song types were used more often than expected, given their frequency of occurrence at Lookout Colony when a certain behavior occurred. Hypotheses about which behaviors were associated with song types were derived from preliminary observations. I tested these hypotheses by comparing the relative incidences of song types associated with the behavior to the relative incidences in the entire song sample using a G-test for homogeneity. Specific associations were tested a posteriori with 95% confidence intervals (Goodman 1964). Differential use of song types in the following behavioral contexts was tested: during flight, at the start of a song bout, ≤ 30 sec before and after supplanting another male, and ≤ 30 sec before and after being supplanted.

A significant result of this statistical test indicates that when a certain song type is given, a positively associated behavior is more likely to occur than if another song type had been given. Because the frequencies of occurrence of behaviors are not considered, this test does not tell us whether one behavior is more likely to occur than another when a song type is given. For the same reason, the test does not tell us if the reliability with which a behavior is predicted by a song type is high or low. To estimate the reliability with

which a song type predicts a behavior, the conditional probability of the behavior given the song type was calculated for relevant associations.

A different approach was used to test the hypothesis that males tended to use certain song types after a pause in singing activity. For 30 songs of each type, I measured the following four intersong time intervals in seconds: the intervals between the song of interest and the songs immediately preceding and following given by the same male, and those given by a different male. A long interval for the preceding song indicates a pause in singing activity of the singer (same male) or of the colony (different male). The four intersong intervals were compared among song types using ANOVA.

RESULTS

The most distinct example of a song type used differentially was song type 5, the flight song. In both years, this song type was the only song delivered in flight. When a male sang this song while perched he often flew shortly afterward. Males used this song in various situations involving flight, including arrival in the nest tree, long distance flight over open habitat, flight into the surrounding forest in response to an alarm call, and flight while chasing females. This song type was not associated with pursuit or retreat during chasing or supplanting interactions among males. The probability for flight to occur simultaneously with or within 15 sec (a typical intersong interval) of song type 5 was 50%.

All song types were used to begin bouts, but some were used more often than expected by chance (Table 1). A male's song was considered to be the first of his song bout if he had not sung in the previous 60 sec. In both years song types 2 and 5 started bouts more often than expected. Song types 3, 4, and 7 were negatively associated with starting bouts in one or both years. Song type 5 was the flight song, and many bouts began as males flew into the nest tree. Of the utterances of song type 2, the type most likely to start a song bout, 27% actually occurred as the first song of a bout.

Song types associated with supplanting were different from those associated with being supplanted (Table 1). Song type 2 tended to occur both before and after supplanting, but tended not to occur after being supplanted. Song type 1 tended to occur both before and after being supplant-

TABLE 1. Proportion of each song type in the total song samples of 1982 and 1983, and the proportions^a used in various behavioral situations.

	Song type							G ^b
	1	2	3	4	5	6	7	
Total sample 1982	0.106	0.085	0.139	0.164	0.011	0.059	0.434	
Initiates song bout 1982	0.102	0.410+	0.130	0.026-	0.308+	0.061	0.051-	107.7
Total sample 1983	0.072	0.080	0.137	0.151	0.013	0.031	0.515	
Initiates song bout 1983	0.111	0.474+	0.044-	0.067-	0.192+	0.022	0.089-	296.3
Sung before supplanting	0.060	0.132+	0.192 ^c	0.115	0.033	0.033	0.434-	16.6
Sung after supplanting	0.116	0.134+	0.152	0.107	0.000	0.080+	0.411-	16.2
Sung before being supplanted	0.197+	0.099	0.105 ^c	0.138	0.013	0.020	0.428-	26.9
Sung after being supplanted	0.175+	0.035-	0.175	0.175	0.000	0.088	0.351-	15.9

^a The + or - sign indicates the direction in which proportions contrasted significantly ($P < 0.05$) with those in the total sample.

^b G-test for homogeneity, $P < 0.025$.

^c These two proportions contrasted significantly (95% confidence intervals).

ed. Song type 7 was negatively associated with all supplanting contexts. The probability of supplanting immediately after singing song type 2 was 5%, and the probability of being supplanted immediately after song type 1 was 6%.

There was no tendency of the singer or of other males to pause after certain song types; the mean time intervals between a given song type and the immediately following song given by both the same male and a different male did not differ significantly among the song types in 1983. On the other hand, the time intervals between a song type and the preceding songs by the same male and by a different male showed significant differences among song types (ANOVA, $F_{(6,203)} = 3.18$ and 6.51 respectively, $P < 0.005$; Table 2).

TABLE 2. Mean time interval between a song and the immediately preceding song by a different male and by the same male.

Song type	Mean time interval to preceding song by different male (sec) ^a		Mean time interval to preceding song by same male (sec) ^b	
	Mean	SD	Mean	SD
1	23.93 ^c	28.04	19.67	16.40
2	17.85	16.85	18.81	12.88
3	7.11	9.30	8.62 ^d	3.45
4	5.45	5.76	12.38	9.58
5	5.15	4.92	18.19	14.37
6	8.78	12.34	16.89	17.29
7	8.76	13.76	11.35	7.99

^a ANOVA, $F_{(6,203)} = 6.15$, $P < 0.0005$.

^b ANOVA, $F_{(6,203)} = 3.18$, $P < 0.005$.

^c Contrasted significantly with all other song types combined (95% confidence intervals).

^d Contrasted significantly with song types 1 and 2 combined (95% confidence intervals).

When the song of interest and the preceding song were sung by different males, the time intervals preceding song types 1 and 2 were high, although only the interval before song type 1 contrasted significantly with the other songs combined (95% confidence intervals). Thus song types 1 and to a lesser extent 2 tended to follow a pause in the singing of other males. No tendency was observed for a singer to use certain song types after a pause in his own singing; intervals preceding types 1 and 2 together contrasted significantly only with that of type 3.

SUMMARY OF USES AND PRESUMED FUNCTIONS OF SONG TYPES

Five out of seven song types at Lookout Colony were statistically associated with behaviors examined during social interactions among males, and appeared to have distinct functions. Song type 1 was used more often by males singing in groups than alone (Trainer 1985), and appeared to stimulate social interactions. It was used more often than other song types after a pause in singing by other males. This was usually the first song type heard after a brief lull in singing activity at the colony, and appeared to stimulate new activity. Often a singer gave one to four brief call notes, each answered alternately by another male, before singing song type 1 simultaneously with the respondent. This appeared to synchronize their singing prior to interacting. The initiating call notes may alert listeners, and increase their attention to the subsequent song (Richards 1981). By stimulating other males to sing, birds may

learn which individuals are present in the nest tree and willing to interact. Subordinate males often sang this song type from the periphery of the nest tree, sometimes stimulating a more dominant individual. This may account for the association of song type 1 with being supplanted (Table 1).

Song type 2 was sung more often and more repetitively by males when singing alone than when in groups (Trainer 1985). It tended to occur after a pause in singing at the colony. Song type 2 was used more often than any other song type as the first song of a song bout even though it ranked low in relative abundance. Song type 2 was used by males before supplanting others, but was avoided by males after being supplanted. This song type may be used by males, particularly dominant ones, to announce their presence in the nest tree.

Song type 3, unlike types 1 and 2, followed quickly after the singer's previous song, and was associated with social activity. It was used more often by males singing in groups than alone (Trainer 1985), and was used more often when supplanting other males than when being supplanted.

Song type 5 appeared to signal that a male was flying or about to fly. Males used this song in a variety of situations that involve flight, and often started a song bout after flying into the nest tree.

Song type 7 was almost always the most abundant song type in the repertoires of individual males, and it was repeated the greatest number of times before changing to a different song type (Trainer 1985). Bouts of this song type were usually spread evenly through a sequence of singing and often broke up otherwise continuous bouts of other song types. It was negatively associated with the start of song bouts and with supplanting interactions. It was used more often by males singing alone, a situation in which one would expect communication about behavioral intentions to be low, than when singing in groups. The high frequency of occurrence and lack of association with intermale social behavior suggests that this song type was an interstitial song of little value in predicting the behavior of the singer or influencing the response of male listeners.

Song types 4 and 6 were not positively associated with any of the behaviors I examined. These types, as well as song type 7, may be important in communication with females, although this was not tested in this study.

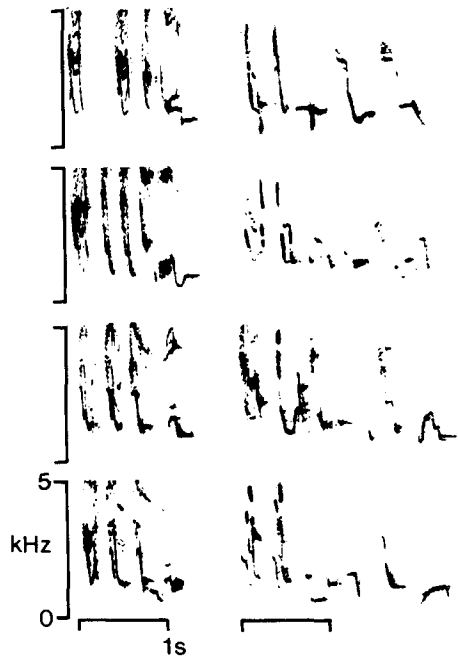


FIGURE 2. Representatives of song class A from eight Yellow-rumped Cacique colonies in the isthmus of Panama.

WIDESPREAD STRUCTURAL SONG CLASSES

Although song types at a given colony were distinct from those at others, some song types were structurally similar among colonies in general respects. These similarities were widespread throughout the isthmus of Panama, occurring at twelve colonies, some separated by as much as 60 km. I identified three structural classes, each containing usually one song type from each colony. Analogous song types from different colonies were audibly recognizable as belonging to the same class. Each class corresponded to a song type at Lookout Colony that appeared to have a special function, and some evidence indicates that song types in a class may function similarly at all colonies.

Class A (includes song type 1). These songs had the longest duration, usually about 1.5 sec long, but some reached 3.2 sec. Songs of this class were often preceded by one to four call notes, followed by a series of notes, each descending rapidly in pitch (Fig. 2). The tendency for a pair of males to alternate singing the call notes and to sing these songs simultaneously was observed at several colonies.

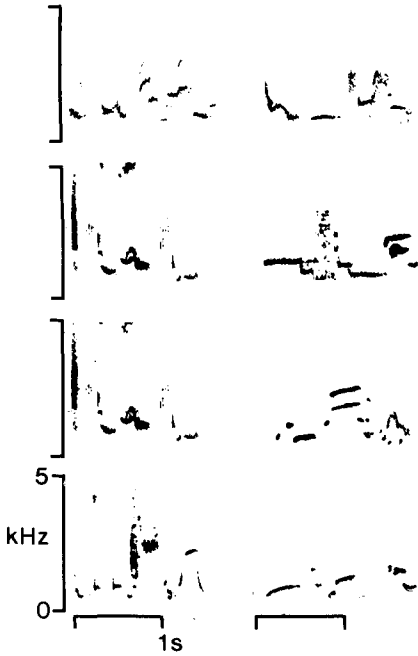


FIGURE 3. Representatives of song class B from eight Yellow-rumped Cacique Colonies.

Class B (includes song type 5). Songs of this class, easily recognized by ear, were low in amplitude, had no harsh elements, and had dominant frequencies not exceeding 2.5 kHz (Fig. 3). At every colony visited ($n = 12$) these song types were used in flight.

Class C (includes song type 7). These were among the briefest song types, lasting between 0.23 and 1.0 sec. Characteristically they contained a burst of harsh sound. A high amplitude note, which was often frequency modulated, occurred during or immediately after the harsh sound (Fig. 4). They were the most frequent song types at all colonies and may have functioned similarly to song type 7 at Lookout Colony.

DISCUSSION

Yellow-rumped Cacique song types are differentiated in their usage during intermale interactions; certain song types were more strongly associated statistically with various behaviors than other song types. Behavioral associations were usually not exclusive since each song type was observed in almost all behavioral contexts, but song types were given more often than expected by chance only in certain situations.

Three general song classes contained structural

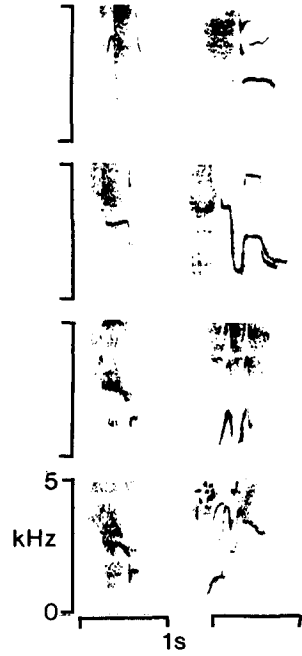


FIGURE 4. Representatives of song class C from eight Yellow-rumped Cacique colonies.

analogs at several colonies throughout the isthmus of Panama. Analogous members of a song class at different colonies were used in identical contexts. Song functions observed at Lookout Colony are probably widespread in Panama. Some evidence indicates that song classes may extend to other cacique populations as well. At each of five colonies along the Manu River in Peru, I recorded a song type recognizable in structure and function as song class A. This suggests that the functional properties of song types in cacique populations and their general structural features may be innate. Innate components of song repertoires may also occur in other species. A Village Indigobird (*Vidua chalybeata*) raised in isolation developed song types corresponding to structural and functional classes observed in wild populations (Payne 1979, pers. comm.). While the functions and general structure of cacique song types may be innate, the acoustic details of song types within a class appear to diverge through separate cultural evolution at different colonies (Trainer 1985).

Although song types were associated statistically with behaviors, the predictive power of individual utterances was generally low. For example, 50% of the utterances of song type 5 were

accompanied or followed by flight. Twenty-seven percent of the utterances of type 2 occurred as the first song of a bout. Only 5% of type 2 songs were given by males immediately before supplanting, and only 6% of type 1 songs were given by males before they were supplanted, even though these song types were significantly associated with these behaviors.

Most utterances of cacique song failed to stimulate action besides singing by other males. This result is not surprising in a situation in which communication is chronic, and most information is transferred only when a change in the status quo occurs. Signals used continuously and repetitively may have long range effects on the listeners' behavior (Schleidt 1973). For example, persistent singing in caciques may influence female mate choice and advertise a male's willingness to compete for preferred song perches. Song types may have advertising functions besides providing information about aggressive behavior.

Nevertheless, the possibility remains that information is communicated by singing organization at a higher level than individual song types. For example, song matching in which one male answers another with the same song type may be a mechanism of communicating relative dominance status if leaders and followers in song matching correspond to relative dominance ranks (Kroodsma 1979, Todt 1981). This information is available only after a bout of sufficient duration for males to detect song matching, and cannot be conveyed by a single song type. In caciques, like song types sung by different males tended to follow in sequence (Trainer 1985), a pattern that is expected if males match one another's songs. Likewise, motivation levels may be indicated by the rate of switching among song types in a bout of singing (Kramer et al. 1985, Simpson 1985). Caciques sing less repetitively when interacting with other males than when singing alone (Trainer 1985). Another possibility is that a male's probability of attack or retreat may change depending on the response of the listener (Simpson 1968; Hinde 1975, 1981). If these mechanisms are operating, then examining simple diads of song types and subsequent behavior might result in low observed statistical dependence.

Consistent with games theory, the reliability of predicting agonistic supplanting behavior was especially low in caciques. Other studies have revealed greater reliability in predicting agonistic behavior by nonvocal displays. For example, in

three species of tits, the highest probability of attack following a display ranged from 19 to 63%, and the highest probability of escape ranged from 70 to 91% (Stokes 1962). In Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) and Great Skuas (*Catharacta skua*) the maximum reliability of predicting attack was 45 and 55%, whereas that of predicting escape was around 80% (Dunham 1966, Andersson 1976). Nelson (1983) showed that variation in a graded vocalization by itself had little power to predict attack or escape. He suggested that the vocalization instead conveyed information about when an individual would attack or escape. Perhaps nonvocal displays derived from intention movements (Tinbergen 1964) are better predictors of agonistic behavior than vocal displays.

Cacique song types were more reliable indicators of nonaggressive behaviors such as flight and starting song bouts. These song types are better interpreted as attention attracting devices used to control the course of an interaction, rather than as signals to indicate the probability of attack or withdrawal. They may alert listeners to a change in an interaction and increase their attention. For example, song type 2 more reliably predicted the start of a bout than a supplanting act. This song type may attract attention to an individual when he joins a group of singing males. Similarly, the flight song may signal that a social interaction is about to be affected by a change in position. I have interpreted the function of song type 1 as a signal of readiness to interact and a stimulant for other males to respond. The call notes initiating song type 1 appear to be particularly effective at alerting listeners who often respond by joining in a simultaneous delivery of the song. The ability to draw attention to one's own singing may be especially important in a species such as the cacique in which several males sing at once.

Cooperation in the exchange of information may at times be compatible with the selfish interests of individuals in competitive situations. The attention getting function of song during aggressive interactions presents no paradox—singers benefit from the attention, and listeners benefit from information on the singer's location and readiness to interact.

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