

PLAYBACK OF CROWS OF MALE JAPANESE QUAIL ELICITS FEMALE PHONOTAXIS¹

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Abstract. We examined the response of male and female Japanese Quail (*Coturnix japonica*) to playback of crows recorded from unmated males and reversed crows (crows played backwards as a control noise), which were broadcast from opposite corners of a playback environment. Females showed a significant preference for the speaker broadcasting crows vs. the speaker broadcasting reversed crows, as measured by the number of time samples females were located within 1 m of the speakers and based upon the mean distance females maintained from the two speakers. Males showed no differential response to crows and reversed crows. Thus, female Japanese Quail, but not males, exhibit positive phonotaxis to the crows of males. Our data also suggest that the temporal pattern of crow syllables is an important factor eliciting female response.

Key words: *playback, phonotaxis, Japanese Quail, Coturnix japonica, crow vocalization.*

Male crowing is characteristic of the family Phasianidae and crows are perhaps the most salient vocalizations of the majority of species. Pioneering studies on Bobwhite Quail (*Colinus virginianus*) by Stokes (1967), on Japanese Quail (*Coturnix japonica*) by Potash (1974), and on California Quail (*Callipepla californica*) by Williams (1969) have suggested functions for a variety of vocalizations, including a mate attraction function for the crow of unmated males. However, female attraction to the crows of unmated males has not been experimentally demonstrated. Indeed, quantitative evidence for the function of any phasianid vocalization is limited to very few studies.

A recent study with domestic roosters (*Gallus gallus domesticus*; Leonard and Horn 1995) provided no evidence that crows attract females in this species, but did find that crowing is related to dominance. Dominant roosters crowed more often than subordinate roosters and crowed at a higher fundamental frequency. Dominant roosters also exhibited phonotaxis (approach) to speakers broadcasting crows of dominant, but not subordinate, males. Subordinate males and females exhibited no phonotactic response. Thus, although males of most species have a loud call (a crow or similar vocalization) that is often assumed to attract mates, an intersexual attraction function for these vocalizations has not yet been demonstrated.

The crow of male Japanese Quail is a loud, broad-

band, two-three syllable vocalization (Fig. 1). Males crow only during the breeding season (Wetherbee 1961) and the vocalization is dependent on circulating androgens (Beach and Inman 1965). In the wild, male Japanese Quail are spaced about 100 m apart and crow from slightly elevated ground. Japanese Quail are primarily monogamous during the breeding season and show a marked reduction in crowing upon pairing (Wetherbee 1961).

Potash (1974) distinguished between the crow of unmated male Japanese Quail (referred to here simply as the "crow") and that of males separated from their mates ("separation crow"). Crows are louder and less variable in intensity than separation crows. Crows usually are given singly, whereas separation crows are given in bouts of 2–12 crows each. Potash demonstrated that the separation crows are given primarily by males visually and/or acoustically isolated from their mates. Such a close relationship between the call of unmated males and the separation call also has been suggested by Stokes (1967) for California, Gambel's (*Callipepla gambelii*), and Bobwhite Quail.

Exposure to crows has been demonstrated to produce physiological responses in both male and female Japanese Quail. Exposure stimulates follicular development in females (Guyomarc'h and Guyomarc'h 1989), and increases sexual regression produced by decreasing photoperiod in males (Guyomarc'h and Guyomarc'h 1994), which was suggested as a potential response to dominance. However, overt behavioral responses to crows have not been documented.

Potash (1974) has suggested that crows may serve to space males and attract a mate. The proposal that the crow of unmated Japanese Quail serves to attract a mate is supported by the observation that crowing declines sharply after pairing in the wild (Wetherbee 1961) or after being housed with a female (Potash 1974). A similar observation has been made in the Bobwhite by Stokes (1967). However, experimental data using playback of crows are necessary to establish function (Catchpole 1982) and to determine whether the crow serves an intersexual function, an intrasexual function, or both. The cessation of a vocalization after pairing may simply be a result of an increased demand being placed on the male's time and energy resources. In the present investigation, playback was provided to both male and female Japanese Quail to determine their responses to the crows of unmated males.

METHODS

Crows of six adult, reproductively-active, male Japanese Quail were recorded in an anechoic room using

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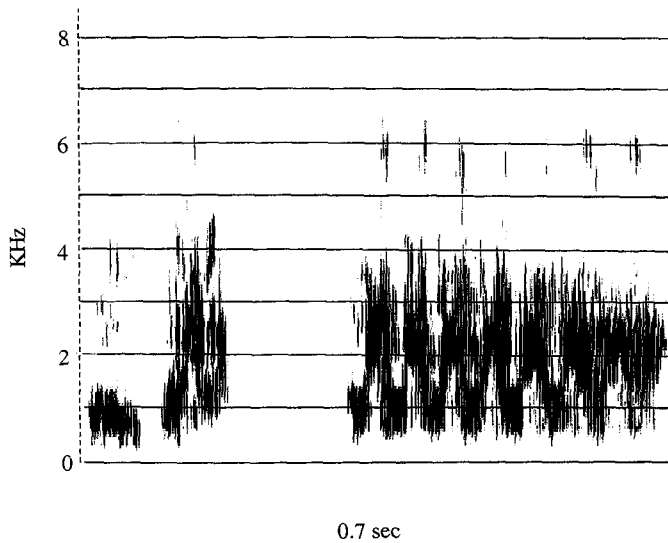


FIGURE 1. Sonogram of a typical crow of a male Japanese Quail.

a Marantz PMD-221 cassette recorder and a Realistic 33-984C unidirectional microphone. All males were sexually experienced, but had not had access to females for at least two weeks prior to recording. Tape-recorded crows were digitized using Soundedit software to prepare stimulus tapes for playback. Each stimulus tape consisted of one male's crow repeated every 20 sec; one tape was prepared for each of the six males' crows. Control tapes were generated by recording the same crows backwards on another tape at the same repetition rate.

We used reversed crows to control for the possible tendency of subjects to approach any noise of a frequency or intensity matching that of crows. Thus, only the response to species-typical crows of normal temporal patterning was examined in the present experiment. Responses based solely on intensity or frequency information (that is, independent of normal temporal patterning) were not assessed.

The playback environment was a 3.1×4.3 m room with an observation area at the rear separated from the room proper by a clear plastic curtain. Stalks of giant reed (*Phragmites communis*) approximately 1.2 m high were arranged in the room to create a grid of squares 0.3 m on a side. A thick layer of cedar chips covered the floor. Two speakers were placed in the room, one at each end of the 3.1 m wall opposite from the observation area. Food and water were provided ad libitum near the observation curtain.

The subjects were 26 reproductively-active Japanese Quail (13 males, 13 females). All subjects were sexually experienced birds that had no sexual access to other birds for at least 2 weeks prior to testing. Birds were housed on a long-day light:dark cycle (16L:8D) and provided with food and water ad libitum. Both male and female subjects were housed in the same room. Donor males which provided the recordings used for tests were not housed with the subjects and were unfamiliar to the subjects, thus subjects were pre-

sumably not familiar with their crows. Dominance status of donor males was unknown.

Subjects were tested singly. Each subject was placed in the playback room approximately 3 hr prior to testing and 8–10 hr after lights-on. No effort was made to restrain the birds prior to the onset of testing, thus allowing subjects to acclimate without human disturbance. Hence, subject location was random at the onset of playback. Testing began between 11 and 13 hr after lights on, a time period during which male mating (Ottinger et al. 1982) and female receptivity (Delville et al. 1986) are maximal in Japanese Quail. Playback was initiated 1 min prior to the beginning of data collection and consisted of reversed crows played from one speaker while normal crows, offset in time from the reversed crows, were played from the other speaker. The order of the first sound provided (i.e., crows vs. reversed crows) alternated between tests, and the location of crows and reversed crows alternated between speakers for separate tests. The delay between playback onset and data collection allowed the subject time to hear both crows and reversed crows and time to initiate a response. Playback was provided via two Marantz PMD-221 cassette recorders and two $15 \times 10 \times 10$ cm coaxial Soundesign speakers. Volume was set to 95 dB at 1 m, an intensity within the normal range for crows observed in our housing rooms. Thus, the playback simulated the presence of a crowing male located at the speaker.

Each of the six stimulus tapes was used for two male and two female birds, except for one that was used for three males and three females. Subjects were tested once, thus each subject was presented with one crow tape and the matched reversed crow tape. Data were collected for 20 min, and included the location of the bird in the grid, which was recorded every 30 sec (referred to here as "time samples"), and whether or not the subject bird contacted a speaker or crouched. The crouch is a solicitation for copulation and is distin-

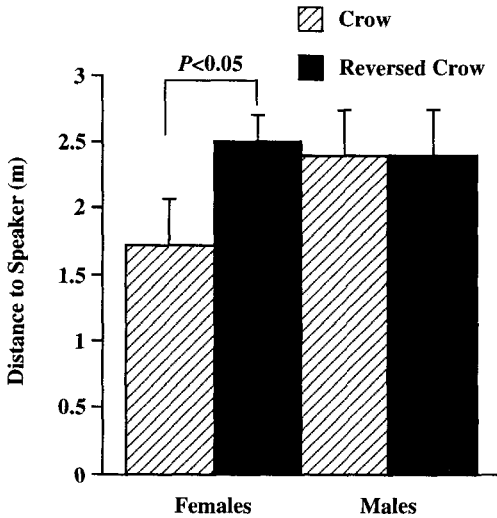


FIGURE 2. Mean \pm SE distances of female and male quail from speakers broadcasting normal and reversed crows.

gushed from simple sitting or dustbathing behavior by the low position of the head and extension of the neck (Schleidt et al. 1984).

For all data, means of samples were calculated for each subject. Group (male or female) means reported in the Results are thus means of individual means \pm SE. Data were analyzed using two-tailed paired *t*-tests.

RESULTS

Females maintained closer proximity to the speaker broadcasting crows vs. the speaker broadcasting reversed crows ($t_{12} = 2.41, P < 0.05$; Fig. 2). Males showed no differential response ($t_{12} = 0.24, P > 0.05$; Fig. 2).

Females also spent more time close to the crow speaker, as indicated by the percent of time samples in which the subject was within 1 m of the crow speaker or the reversed crow speaker ($t_{12} = 2.85, P < 0.05$; Fig. 3). Males again demonstrated no preference ($t_{12} = 0.22, P > 0.05$; Fig. 3). Percentage of time samples spent within 1 m of the crow speaker was greater for females than males, but not significantly so ($t_{24} = 1.93, P = 0.06$, independent *t*-test).

Five females crouched in response to playback and three made contact with the speaker broadcasting crows (either by pecking or jumping onto the speaker). Four of the females which crouched were within 1 m of the speaker broadcasting crows. One male was recorded as crouching (not within 1 m of either speaker) and one male contacted the speaker broadcasting crows. No contact by either sex was made with the speaker broadcasting reversed crows.

DISCUSSION

These results suggest an intersexual attraction function for the crow of male Japanese Quail. Females demonstrated a significant preference for crows over reversed crows, both in the proximity to speakers broad-

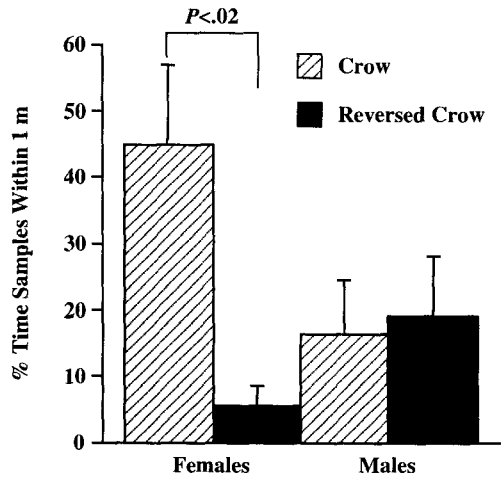


FIGURE 3. Mean \pm SE percent of time samples males and females were located within 1 m of speakers broadcasting crows and reversed crows.

casting crows and reversed crows and in the time spent within 1 m of those speakers. Males showed no differential response.

These data indicate that cues used by females in the recognition of, or in response to, male crows are disrupted by reversing the crows. Each of the two-three syllables in a Japanese Quail crow is structurally similar throughout (a "rattle" of fairly consistent intensity; Fig. 1) and sounds similar when reversed, but the first syllable is shorter and often less intense. Thus, amplitude modulation between syllables and temporal patterning may be cues used by females in their differential response to normal and reversed crows.

We designed the experiment to focus on phonotaxis and this study represents one of only a small number of studies showing approach by females of any avian species to conspecific male vocalizations (Searcy 1992). However, an increasing amount of research in songbirds has recently focused on female attraction, and the long-held hypothesis that male vocalizations serve to attract mates is now supported by a variety of data (Catchpole and Slater 1995). The solicitation displays by female Japanese Quail further underscore the sexual attractiveness of the male crow.

The results reported here cannot be taken as evidence that the crow does not also serve an intrasexual function as well. Daugherty (1977) demonstrated that male Japanese Quail can distinguish between familiar and strange males based on the intensity of their crows. In the present experiment, subject males were not housed in the same room as the crow "donors," and presumably were not familiar with their crows. However, the reversed crows were of the same intensity as the crows. If males use this intensity information for spacing, then the lack of difference in the males' distances to the speakers broadcasting reversed and forward crows would be expected. This topic deserves further research, because nothing is known about the

role of vocalizations in territory spacing and maintenance in Phasianidae.

Comparison of the present results with those obtained for the domestic rooster (Leonard and Horn 1995) indicates that crows serve different functions in these two species. Hens were not attracted to crows of domestic roosters, whereas female Japanese Quail approach crows of conspecific males. We did not examine the possibility that crows may function in dominance behavior. Therefore, comparisons of the use of crows in dominance behavior between male Japanese Quail and domestic roosters cannot be made at present.

The results of the present study indicate that if the crow does serve an agonistic function, the relevant acoustic cues, perhaps intensity or frequency information, are independent of the temporal structure of the call. The increased sexual regression of males exposed to crows while experiencing decreased photoperiod (Guyomarc'h and Guyomarc'h 1994) suggests that crowing may indeed function in dominance behavior, in addition to the mate attraction function demonstrated here.

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