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EFFECT OF MATE REMOVAL ON SINGING BEHAVIOR AND MOVEMENT PATTERNS OF FEMALE NORTHERN CARDINALS

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Abstract.—We temporarily removed the mates of four female Northern Cardinals (*Cardinalis cardinalis*) during the pre-nesting period in an attempt to clarify the functions of singing by females. Mate removal had no significant effect on singing rates, number of movements per hour, or distance moved per hour. The failure to increase singing rates after mate removal suggests that singing by female cardinals is not used to attract new mates and the absence of any change in movement patterns suggests that females may not actively seek new mates. When singing, female cardinals were usually accompanied by a singing male and, prior to and after mate removal, females often duetted with their mates. Female cardinals may sing and duet with mates to advertise the presence of a female and the mated status of a male. Duetting may also permit pairs to learn each other's songs. Such learning may represent a form of investment important in maintaining a pair bond and may also, later in the season, permit more efficient intrapair communication. *Received 26 Oct. 1995, accepted 10 Feb. 1996.*

Although singing by females is now well documented in several species of passerines (e.g., Arcese et al. 1988, Johnson and Kermott 1990, Baptista et al. 1993), the functions of such singing often remain unclear. Most suggested functions have been based largely on observations, and few investigators have used experimentation. When used, experimentation has been limited to playback experiments (e.g., Ritchison 1983, 1986; Arcese et al. 1988; Baptista et al. 1993). In contrast, investigators examining the singing behavior of male passerines have used a variety of experimental techniques, including mate removal experiments. In these studies, the singing behavior of males is observed prior to and after removal of mates. Typically, males increase singing rates after removal of their mates, suggesting that singing plays a role either in maintaining contact with mates or in attracting new mates (Wasserman 1977, Krebs et al. 1981, Cuthill and Hindmarsh 1985, Otter and Ratcliffe 1993).

Female Northern Cardinals (*Cardinalis cardinalis*) sing primarily during the period after males establish territories and before nesting begins (Ritchison 1986). Singing females usually are accompanied by singing mates (Lemon 1968, Ritchison 1986). Although these observations suggest that singing by female Northern Cardinals may be important in intrapair communication, perhaps playing some role in the formation of the pair bond (Ritchison 1986), additional information is needed. The objec-

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tive of our study was to use mate removal experiments in an attempt to clarify the functions of singing by female Northern Cardinals.

METHODS

We conducted this study during the pre-nesting periods (January through early May) of 1990, 1992, and 1993 at the Central Kentucky Wildlife Management Area located 17 km southeast of Richmond, Madison County, Kentucky. Male and female cardinals were captured in mist nets and individually marked with colored leg bands and plastic tape attached to the tail (Ritchison 1984). Beginning in March, marked cardinals were observed to determine the identity of pairs and the location and boundaries of territories. Paired females (N = 4) were subsequently re-captured and fitted with radio-transmitters. Removal experiments with these females began on 2 April and 20 April 1990, 19 April 1992, and 29 April 1993, respectively.

Experiments were divided into three periods: pre-removal, removal, and post-removal. Each period lasted two days and focal females were observed for three hours each day. All observations were made during the period from sunrise to 11:00. Pre-removal periods began no sooner than two days after females had been fitted with transmitters. After the pre-removal period, the female's mate was captured by luring him into a mist net using the playback of cardinal songs. During the two-day removal period, males were kept in the lab in a wire mesh cage and provided food and water. The post-removal period began with the release of the male.

The movements of focal females were monitored using a receiver (Telonic's TR-2) with a two-element antenna. The focal female's location was marked on a map of the study area every 15 min. All songs were recorded using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone or a Marantz recorder with a directional microphone. Observations and recordings of females were made from a distance of 20 m or more.

Recordings were analyzed using a Kay Elemetrics Sonagraph (Model 5500). For each observation period, we noted the number of songs and number of bouts, with a bout defined as a series of songs separated by intervals less than 30 sec. For each song, we determined the song type (see figures 1 and 2 in Ritchison 1988), number of syllables, and duration. Each bout was classified as either an accompanied bout or a non-accompanied bout, with an accompanied bout defined as a bout during which a conspecific male (either in the female's territory or in an adjacent territory) sang at some time during the bout. Bouts of female song during which their mates also sang were classified as duetting bouts.

Possible differences among periods for all variables were tested using repeated measures analysis of variance (SAS 1989). Repeated measures analysis provides a test for interactions (Beal and Khamis 1990), and we also examined possible interactions between individuals and periods. Tests for non-random use of song types were made using likelihood ratio chi-square tests (SAS 1989). All values are presented as means ± one standard error.

RESULTS

The singing rates of female cardinals did not vary significantly among test periods ($F = 1.34$, $P = 0.34$), with no significant interaction between individual and period ($F = 1.53$, $P = 0.21$). Females uttered an average of 20.6 ± 4.1 songs/h during the pre-removal period, 20.1 ± 6.5 songs/h during the removal period, and 22.7 ± 8.8 songs/h during the post-removal period.

Female cardinals exhibited no significant variation among periods in the number of syllables per song ($F = 1.93$, $P = 0.24$). We found a significant interaction between individual and period ($F = 2.47$, $P = 0.03$), however, no clear trend was apparent. Two females used songs with more syllables during the removal period, one female uttered songs with more syllables during the post-removal period (although this female sang only 11 songs during the pre-removal and removal periods), and the songs of the fourth female showed little variation in number of syllables per song among periods.

Female cardinals exhibited no significant variation among periods in song duration ($F = 0.6$, $P = 0.58$), with no significant interaction between individual and period ($F = 1.67$, $P = 0.14$). Also, we found no significant differences among periods in intersong intervals ($F = 0.21$, $P = 0.82$). There was a significant interaction between individual and period ($F = 4.7$, $P = 0.0003$), however, no clear trends were apparent. Three females exhibited little variation in intersong intervals among periods while intersong intervals for the fourth female were longer during the removal and post-removal periods than during the pre-removal period.

All four female cardinals exhibited significant variation (likelihood ratio tests, $P < 0.0001$) in the use of song types during the three periods. However, no consistent trends were found among the four females in the use of particular song types during particular periods.

During most bouts of song (N = 172 of 248 or 69.4%), female cardinals were accompanied by singing males, either their mate (duetting bouts) or another conspecific male. Females sang with their mates during 88 bouts and with other conspecific males during 84 bouts. During seven bouts, females sang with both their mate and an intruding male. Females were accompanied by males in 69 bouts during the pre-removal period, 46 during the removal period, and 57 during the post-removal period. The number of non-accompanied bouts declined from 45 during the pre-removal period to 18 during the removal period to 13 during the post-removal period.

Female cardinals showed no significant variation among periods either in number of movements per hour ($F = 1.57$, $P = 0.3$) or distance moved per hour ($F = 0.14$, $P = 0.63$). No significant interactions were noted for either movements per hour ($F = 0.36$, $P = 0.87$) or distance moved per hour ($F = 0.69$, $P = 0.63$). For all females and periods combined, the mean number of movements per hour was 4.07 ± 2.65 while the mean distance moved per hour was 109.5 ± 59.4 m. All four females remained on their respective territories after removal of their mates.

Trespassing by conspecific males occurred significantly more often during the removal period ($F = 19.6$, $P = 0.004$), with an average of 3.16 ± 1.02 intrusions per hour during the removal period, 0.46 ± 0.26 intrusions per hour during the pre-removal period, and 2.49 ± 1.11 intrusions per hour during the post-removal period. The number of singing bouts by intruding males in the territories of focal females varied significantly among periods (F = 28.8, P = 0.0018), with an average of 1.64 ± 0.35 bouts/h during the removal period, 0.09 ± 0.05 bouts/h during pre-removal, and 1.07 ± 0.42 bouts/h during post-removal. Focal females sang with intruding males an average of 0.6 ± 0.19 times/h during removal and 0.19 ± 0.04 times/h during post-removal, a significant difference (F = 12.6, P = 0.011). No singing with intruders occurred during the pre-removal period.

Three temporarily-removed males maintained their territories and their mates after being released. One male lost his territory and his mate to another male during the removal period and was unable to reclaim either after release.

DISCUSSION

Female Northern Cardinals in our study did not increase singing rates when mates were removed. In contrast, passerine males typically increase singing rates after removal of a mate (Wasserman 1977, Krebs et al. 1981, Cuthill and Hindmarsh 1985, Otter and Ratcliffe 1993). Increased song output following mate removal may indicate an attempt to re-establish contact with the absent mate or to attract a new mate (Krebs et al. 1981). Johnson and Kermott (1990) found that female House Wrens (*Troglodytes aedon*) sang primarily after losing contact with mates and these songs appeared to redirect a mate's attention to the singing female. Such behavior was not observed in our study, and this failure to increase singing rates after removal of mates suggests that singing by female cardinals is not used to establish or maintain contact with mates.

There is little evidence that passerine females sing to attract new mates. Baptista et al. (1993) reported that one widowed female White-crowned Sparrow (*Zonotrichiz leucophrys*) produced long bouts of loud song and suggested that she may have been advertising for a mate. Female Northern Cardinals did not increase song output after mate removal, and this suggests that singing by female cardinals is not used to attract new mates.

Female cardinals in our study exhibited no significant changes among periods in either number of movements or distance moved per hour. In contrast, Klatt and Ritchison (1994) found that female Eastern Screech-Owls (*Otus asio*) made significantly more movements and moved significantly greater distances after mate removal and suggested that such behavior would increase the chances either of re-establishing contact with a mate or attracting a new mate. The absence of any change in movement patterns after mate removal suggests that female cardinals may not actively seek either to re-establish contact with a mate or attract a new mate. Rather, females may use a more passive approach. The absence of a territorial male, as during the removal periods in our study, may indicate to other males the availability of a territory and, perhaps, of a female. Female cardinals may wait for neighboring or floater males to trespass, then seek to pair with the male that eventually obtains the territory.

Our results indicate that singing by female cardinals does not deter male intrusion into a female's territory. Male intrusion rates increased during the removal period even though females continued to sing. Female song may, however, deter trespassing by other females. If singing by females is directed primarily to conspecific females, then rates would not be expected to increase in the absence of the male. Thus, female cardinals may sing, and duet with mates, to advertise the presence of a female and, perhaps, the mated status of a male. In further support of this hypothesis, songs uttered by cardinals during duets are typically normal or high volume songs that can be heard in neighboring territories (pers. observ.). Such advertisement may be important in mate retention because unpaired females (floaters) are present in our cardinal population (Ritchison et al. 1994). Further, some male cardinals participate in extra-pair copulations (EPCs) (Ritchison et al. 1994). Female cardinals may reduce the likelihood that their mate will participate in EPCs by duetting with and advertising the mated status of their mate. Reduced participation in EPCs by mates may be beneficial to females because males that do not engage in EPCs (or engage in fewer EPCs) may provide more parental care (Westneat et al. 1990).

Singing by female Northern Cardinals may also permit pairs to learn each other's songs. Paired cardinals may sing from or near nests during the incubation and nestling periods, and Halkin (1990) proposed that female cardinals on the nest may match her mate's song type to inform the male that he need not visit (bring food to) the nest. For such communication to occur, paired cardinals must know the song type repertoires of their mates. Duetting prior to nesting may permit paired cardinals to become familiar with, and perhaps learn, song types in the repertoire of their mate. Lending support to this hypothesis, we found that male and female cardinals sometimes matched song types during duets (pers. obs.).

Matching song types during duets could also serve other functions. Learning a mate's song types may represent a form of investment that may be important in establishing and maintaining a pair bond (Wickler 1980). Thus, if male and female cardinals must learn the songs of their mates, then duetting may play a role in establishing and maintaining pair bonds.

In summary, our results suggest that female Northern Cardinals do not sing to re-establish contact with an absent mate or to attract a new mate. Rather, female cardinals sing (and duet with mates) to advertise the females' presence and the paired status of her mate. Duetting may also permit paired cardinals to learn other's songs. Such learning may represent a form of investment important in maintaining a pair bond (Wickler 1980) and may also, later in the season, permit more efficient communication in the vicinity of nests (Halkin 1990).

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