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THE EFFECT OF MATE REMOVAL ON THE VOCAL BEHAVIOR AND MOVEMENT PATTERNS OF MALE AND FEMALE EASTERN SCREECH-OWLS[1]

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Abstract. The effect of temporarily removing mates on the behavior of male and female Eastern Screech-Owls (*Otus asio*) was examined during the pre-breeding periods in 1990 and 1991. Male screech-owls increased singing rates and both males and females increased movement rates after removal of mates. Increased song output and movement appear to represent attempts either to re-establish contact with an absent mate or to attract a new mate. In support of the mate attraction hypothesis, five screech-owls apparently acquired new mates after mate removal. Male screech-owls sang more and moved more than females after mate removal, suggesting either that males place a higher priority on re-establishing contact with an absent mate or that males are more active in their attempts to attract new mates. Bounce songs were used more than whinny songs after mate removal, suggesting that bounce songs are more important in intersexual communication. Extended bounce songs were given more frequently after mates were released, and were typically uttered near potential nest cavities. These songs may be used to draw attention to suitable nesting cavities, a resource that may be important in mate choice.

Key words: Eastern Screech-Owl; mate removal; vocal behavior; Otus asio; *movement patterns.*

INTRODUCTION

The acquisition and retention of a mate is an essential aspect of reproduction in many species of birds. The strategies used to accomplish these goals vary among and within species as well as between sexes within a species. Among many passerines, for example, only males sing, and this singing appears to play an important role in mate attraction. Although the precise nature of that role remains unclear in many species, mate removal experiments have been conducted with several species in an attempt to clarify the function of singing in mate acquisition (Wasserman 1977, Krebs et al. 1981, Cuthill and Hindmarsh 1985). In these studies, the singing behavior of males was monitored prior to and after removal of a mate. The results of such studies do not provide conclusive evidence concerning song function (Kroodsma and Byers 1991), however, they provide insight into the function of different song types and at least indirect evidence concerning the general functions of male song.

The strategies of male and female passerines seeking to acquire or retain mates may also differ in another respect. Males appear to remain on their territories in the absence of their mate and attempt to re-establish contact with the absent mate or attract a new mate to that territory (Wasserman 1977, Krebs et al. 1981). Although, to our knowledge, no mate removal studies have been conducted with female passerines (i.e., the male of a pair is removed rather than the female), recent studies of female pairing strategies suggest that females might respond differently. Harper (1985) found that female European Robins (*Erithacus rubecula*) seeking mates were more likely to move to a male's territory than vice versa. In addition, translocated female Great Reed Warblers (*Acrocephalus arundinaceus*) seeking mates visited an average of 5.9 males and traveled an average of 2.94 km before pairing (Bensch and Hasselquist 1992). Although only suggestive, such results indicate that females seeking mates (or perhaps seeking to re-acquire an absent mate) might use a more active approach (more extra-territorial movements) than males.

Vocalizations that appear to be functionally equivalent to passerine song have been reported in several species of non-passerines, including

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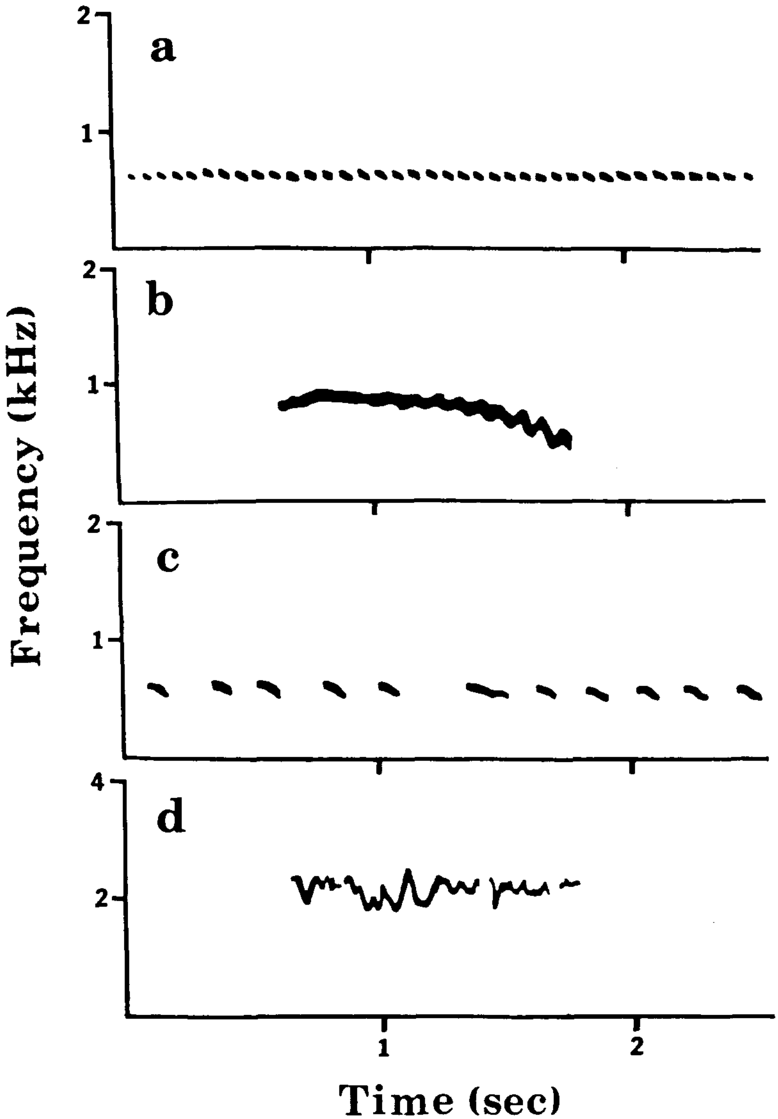

FIGURE 1. Vocalizations given by Eastern Screech-Owls during the mate removal experiments: (a) bounce song, (b) whinny song, (c) portion of an extended bounce song, and (d) squeal call.

owls (Bondrup-Nielsen 1984, Ritchison et al. 1988, Ganey 1990). For example, Eastern Screech-Owls (*Otus asio*) regularly use two song types, the bounce song and the whinny song (Fig. 1) (Cavanagh and Ritchison 1987, Ritchison et al. 1988). Unlike many passerine species, both male and female Eastern Screech-Owls utter these songs. However, female screech-owls appear to sing less than males (Ritchison et al. 1988). In addition to these two song types, the vocal repertoire of screech-owls includes two additional, but apparently rarely used, vocalizations: the extended bounce song and the squeal call (Klatt 1992). Although previous investigators have suggested possible functions for the bounce and whinny songs of Eastern Screech-Owls (Marshall 1967, Ritchison et al. 1988), the precise role that these songs play in mate acquisition or retention remains unclear. Further, almost nothing is known about the possible functions of extended bounce songs and squeal calls.

We used mate removal experiments to provide further insight into the possible functions of the songs (bounce, whinny, and extended bounce) and calls (squeal) of male and female Eastern Screech-Owls. Additionally, we sought to determine whether the vocal behavior and movement patterns of male and female screech-owls seeking to acquire or retain mates differed.

METHODS

This study was conducted at the Central Kentucky Wildlife Management Area located 17 km southeast of Richmond, Madison County, Kentucky. Screech-owls were captured beginning in October 1989 and fitted with a U.S. Fish and Wildlife Service aluminum band plus a five to six gram radio-transmitter (Wildlife Materials, Inc., Carbondale, IL). Once paired, male and female Eastern Screech-Owls typically roost near each other (Belthoff 1987, pers. observ.). Thus, nest boxes and natural cavities located near radio-tagged owls were checked regularly in an attempt to capture mates. Once both members of a presumed pair were radio-tagged, we continued to monitor their roost sites. If radio-tagged owls consistently roosted near each other (i.e., within 25 m or less), we assumed they were paired. Nine pairs of screech-owls were observed during the study. Paired status was confirmed for four pairs by observations made during the breeding season. Confirmation of status was not possible for five pairs because of the death of one member of the presumed pair prior to the breeding season. The sex of each member of a pair was determined by analyzing vocalizations (with those of females higher in frequency) and, if they survived, was confirmed by their behavior during the breeding season (mid-March through late July; Cavanagh and Ritchison 1987, Klatt 1992, Sproat 1992).

We conducted mate removal experiments during the pre-breeding periods in 1990 and 1991 (7 January to 13 March 1990 and 12 January to 21 March 1991). Experiments were conducted with six owls (both members of three pairs) in 1990 and with seven owls (both members of one pair plus one individual from each of five additional pairs) in 1991. When both members of a pair were studied, the experiment with the second owl began the night after completion of the experiment with the first owl (with the order of testing determined randomly). All experiments consisted of three periods: pre-removal, removal (capture and removal of mate), and replacement (release of mate). The removal and replacement of owls occurred during daylight hours, and "replaced" owls were placed in a nest box or natural cavity located within 10 m of the focal owl's roost site. During each period, the focal owl was monitored for at least six hours over at least two nights. Nightly observations were usually three hours in duration and began either at sunset or when the focal owl first moved from its roost. When inclement weather limited the duration of an observation period, observations were continued for a third night.

The location and movements of focal owls were monitored using a receiver (Model TR-2, Telonics, Inc., Mesa, AZ) with a two-element yagi antenna (Telonics, Inc.). Observation and recordings of focal owls were generally made from a distance of 40–75 m, i.e., sufficiently distant to minimize disturbance but close enough to obtain recordings. Recordings were made using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone and vocalizations were analyzed using a Kay Elemetrics Corp. DSP Sona-Graph (Model 5500).

During each observation period, we attempted to record all vocalizations given by the focal owl. We also recorded spoken notes concerning the behavior and movements of the focal bird and, if possible, the behavior and movements of conspecifics. Songs (bounce and whinny) given by focal owls were categorized as high volume, regular volume, or low volume. High volume songs were, in our judgement, audible at least 150 to 200 m away (i.e., into the next territory and possibly beyond). Regular volume song was not audible beyond 50 to 150 m, and low volume song was judged to be audible at distances of 50 m or less.

Tapes were analyzed to determine the number of each type of song or call given during each observation period. For bounce songs, we also determined intersong intervals, number of notes per song, song duration, tempo (number of notes per second), and frequency at maximum amplitude (FMA). FMA was determined on the Sona-Graph using a color enhancement function. We also measured the duration of all whinny songs.

The number of movements made by focal owls during each observation period was also noted, and the total distance moved during each observation period was calculated. The location of focal owls was monitored as continuously as possible, and all detected movements (no matter how small) were counted. The total distance

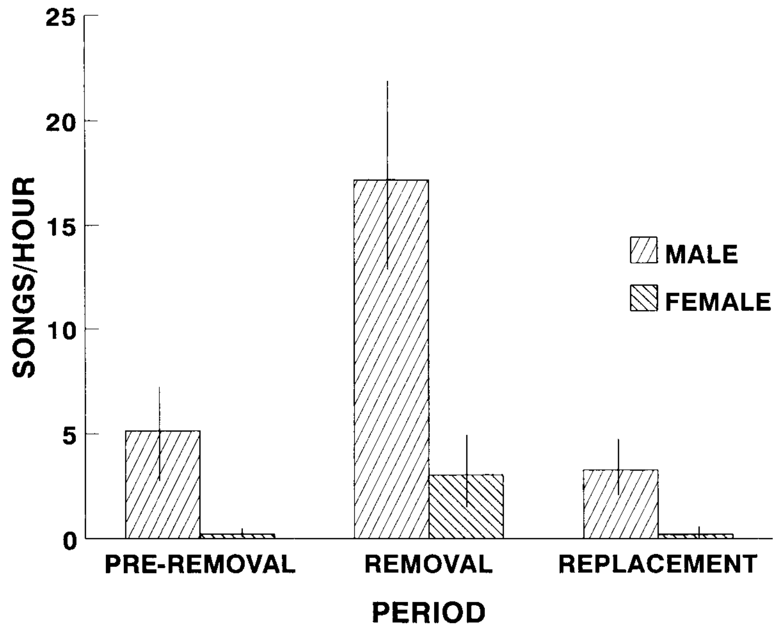

FIGURE 2. Number of bounce songs uttered per hour by male and female Eastern Screech-Owls during the three experimental periods.

moved was determined by plotting all locations on aerial photographs of the study area and then measuring the distance between successive locations.

Possible differences among individuals and across periods were examined using analysis of variance (ANOVA) applied to ranks (which is equivalent to a Kruskal-Wallis test) (SAS Institute 1989). If significant effects were detected, we performed Student-Newman-Keuls (SNK) tests to examine any difference between means. Combined effects of individual and period on the characteristics of bounce songs were tested with a two-way ANOVA (SAS Institute 1989). Wilcoxon tests were used for paired comparisons while chi-square tests were used to test for nonrandom distributions. Values are presented as means ± standard errors.

Two "natural" removals were also observed during the study (both in 1991). In each case, radio-tagged owls lost their mates to predators. These two owls were observed over seven nights and one night, respectively. Data from these two owls were not included in any of our statistical analyses.

RESULTS

SINGING RATES OF MALE AND FEMALE SCREECH-OWLS

Mate removal experiments. The singing rates of male screech-owls (n = 6) varied significantly among periods for both bounce songs ($F_{2,39}$ =

TABLE 1. Comparison of the characteristics of the bounce songs of male and female Eastern Screech-Owls.[a]

Characteristic	Males[b]	Females[c]	Wilcoxon z	Wilcoxon P
Intersong interval (sec)	21.57 ± 0.56	16.37 ± 1.35	3.37	0.007
Notes per song	58.40 ± 1.00	48.10 ± 2.57	3.99	0.001
Song duration (sec)	3.64 ± 0.05	3.36 ± 0.18	2.88	0.001
Notes per second	15.70 ± 0.06	14.27 ± 0.18	8.15	0.0001
FMA[d]	608.7 ± 1.2	741.9 ± 4.59	16.45	0.001

[a] Values are means ± standard errors.
[b] Values based on 766 songs from six males.
[c] Values based on 102 songs from six females.
[d] Frequency at maximum amplitude in Hertz.

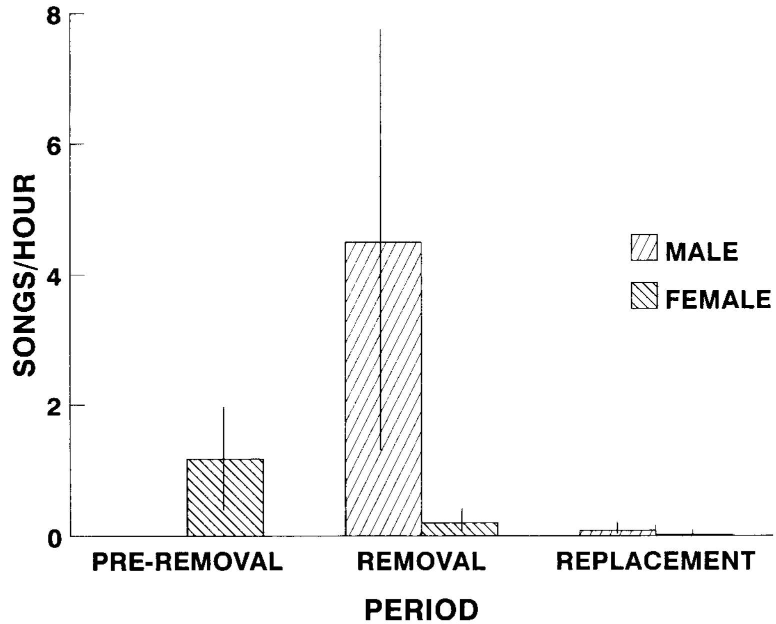

FIGURE 3. Number of whinny songs uttered per hour by male and female Eastern Screech-Owls during the three experimental periods.

4.56, $P = 0.017$) and whinny songs ($F_{2,39} = 3.32$, $P = 0.046$), with males singing significantly more (SNK, $P < 0.05$) during the removal period (Figs. 2, 3). Although female screech-owls ($n = 7$) also uttered more bounce songs during the removal period (Fig. 2), the differences were not significant ($P = 0.246$). Similarly, the number of whinny songs given by female screech-owls did not vary significantly ($P = 0.761$) among periods (Fig. 3).

Male screech-owls gave significantly more bounce songs (Wilcoxon tests, $P < 0.05$) than did females during all three periods (Fig. 2). Male and females screech-owls did not differ significantly (Wilcoxon tests, $P > 0.05$) in the number of whinny songs given during the three periods (Fig. 3).

Natural removals. Two radio-tagged screech-owls being monitored for possible use in the male removal experiments lost mates to predators. Observations of a male began on 31 January 1991, three days after the last sighting of his mate. During 19 hours of observation (3 hr per night for six nights plus 1 hr on the seventh night), this male gave 191 bounce songs and 97 whinny songs. Peak use of bounce songs occurred during the third and fourth nights (50 and 48 bounce songs, respectively) while peak use of whinny songs occurred during the sixth night (51 songs).

A female screech-owl was observed for four hours on 8 March 1991 (her mate was killed on 5 March). During the observation period the female gave 10 bounce songs and 152 whinny songs.

CHARACTERISTICS OF BOUNCE AND WHINNY SONGS

Sexual and individual variation. The bounce songs of male and female screech-owls differed significantly in all temporal and frequency characteristics (Table 1), with the songs of males longer in duration and lower in frequency. Within each sex, bounce songs exhibited significant interindividual variation (ANOVA, $P < 0.05$) in all temporal and frequency characteristics. Because of limited sample sizes, we did not compare the characteristics of the whinny songs of male and female screech-owls.

Variation among experimental periods. Male screech-owls uttered bounce songs during all three periods, and all characteristics of these songs (notes per song, notes per second, duration, intersong interval, and FMA) varied significantly among periods (two-way ANOVA, $P < 0.0001$). However, a significant interaction between individual and period was found for all variables (two-way ANOVA, $P < 0.0001$), with no consistent trends in the relationship between song characteristics and period.

Three male screech-owls uttered significantly more (χ^2 tests, $P < 0.05$) high volume bounce songs during the removal period. Another male uttered low volume songs during the pre-removal period and songs with regular volume during the removal period.

Female screech-owls also uttered bounce songs during all three periods, and all characteristics (notes per song, notes per second, duration, and FMA) except intersong interval (two-way ANOVA, $P = 0.095$) varied significantly among periods (two-way ANOVA, $P < 0.0016$). As with males, however, there was a significant interaction between individual and period for all variables (two-way ANOVAs, $P < 0.042$), and no consistent trends were apparent in the relationship between song characteristics and period.

Four females and four males uttered whinny songs during the mate removal experiments. However, most whinny songs were given during the removal period and, therefore, we were unable to test for differences in the characteristics of whinny songs uttered during the three periods.

OTHER VOCALIZATIONS GIVEN BY MALE AND FEMALE SCREECH-OWLS

Male ($n = 3$) and female ($n = 2$) Eastern Screech-Owls also gave extended bounce songs and squeal calls during our study. Extended bounce songs (Fig. 1c) consisted of a series of notes with relatively long internote intervals (see Klatt 1992 for a detailed description of these songs). Male screech-owls gave significantly more ($\chi^2 = 9.94$, df = 1, $P < 0.01$) extended bounce songs than did females. In addition, screech-owls gave significantly more ($\chi^2 = 28.41$, df = 2, $P < 0.001$) extended bounce songs during the replacement period ($n = 16$) than during either the pre-removal ($n = 1$) or removal ($n = 0$) periods.

Squeal calls consisted of one ($n = 4$), two ($n = 2$), or eight ($n = 1$) notes of varying duration that exhibited extensive frequency modulation (Fig. 1d; see Klatt 1992 for a detailed description). These calls were given by two males, two females, and three individuals of undetermined sex. Five squeal calls were given during the replacement period, and two were given during the pre-removal period.

MOVEMENT PATTERNS

During the pre-removal period, Eastern Screech-Owls averaged 2.64 ± 0.21 movements per hour and moved an average of 213.3 ± 24.6 meters per hour, with no significant differences (Wilcoxon tests, $P > 0.05$) between males ($n = 6$) and females ($n = 7$). During the removal period, males and females did not differ significantly ($z = 1.54$, $P = 0.122$) in the distance moved per hour, averaging 314.7 ± 28.1 meters per hour. However, males did make significantly more movements ($z = 2.19$, $P = 0.028$) per hour during the removal period, with males averaging 4.62 moves per hour and females 3.53 moves per hour. During the replacement period, screech-owls averaged 2.85 ± 0.19 movements per hour and moved an average of 196.1 ± 19.9 meters per hour, with no significant differences (Wilcoxon tests, $P > 0.05$) between males and females.

The movement patterns of male and female screech-owls varied significantly among periods. Both males ($F_{2,39} = 7.4$, $P = 0.0019$) and females ($F_{2,6} = 5.31$, $P = 0.0084$) made significantly more movements per hour during the removal period than during the pre-removal or replacement periods. Females also exhibited significant variation among periods in distance moved per hour ($F_{2,46} = 4.51$, $P = 0.0163$), with significantly greater movement during the removal period. Although males also moved greater distances during the removal period, the difference was not significant ($F_{2,39} = 2.98$, $P = 0.0624$).

TERRITORY FIDELITY AND THE ACQUISITION OF NEW MATES

All six males and six of seven females remained on their territories during and after mate removal. One female left her territory during the mate removal period and paired with a male in an adjacent territory. This male's previous mate was killed by a predator approximately three days prior to the focal female's movement into his territory.

At least five screech-owls (two males and three females) apparently acquired new mates during the removal period. Unbanded screech-owls were found roosting in cavities near those of three focal owls and, in addition, four focal owls (including two of the three found roosting near unbanded owls) engaged in duets with unidentified screech-owls.

DISCUSSION

SINGING RATES

Male Eastern Screech-Owls increased singing rates after removal of their mates and then reduced singing rates after release of their mates. Similar results have been reported in several species of passerines (Wasserman 1977, Krebs et al. 1981, Johnson 1983, Cuthill and Hindmarsh 1985). Krebs et al. (1981) presented three hypotheses to explain such changes in song output. First, an individual may compensate for the absence of a mate by putting more effort into territorial defense. This seems unlikely for two reasons. Eastern Screech-Owls exhibit pronounced seasonal variation in song output, with most singing during the period from July through September when juveniles are dispersing and little singing during the pre-breeding period (January through March) (Ritchison et al. 1988). Lundberg (1980) noted that the frequency of territorial advertising by Ural Owls (*Strix uralensis*) was low during the spring, probably because of this species' resident habits, strong pair-bonds, and well-established territories. Similarly, the low levels of singing by Eastern Screech-Owls during the pre-breeding period suggest a limited need for territorial advertising and also suggest that increased singing during the mate removal period in our study did not result from a need to compensate for the loss of a mate by putting more effort into territorial defense. Further, female Eastern Screech-Owls sing less than males (Ritchison et al. 1988, this study). This suggests that male screech-owls "compensating" for an absent mate would exhibit minimal increases in singing rates, while females would exhibit much greater increases in singing rates. This did not occur and, thus, our results do not support the hypothesis that increased singing rates represent an attempt to compensate for an absent mate.

Krebs et al. (1981) also suggested that song may be used to maintain contact with a mate and, therefore, song output increases when a mate is absent. During the period prior to nesting (January through March), paired screech-owls typically roost in adjacent cavities or in the same cavity (Belthoff 1987, pers. observ.). Further, during this same period, paired males and females contact each other (or at least come in close proximity) several times per night (pers. observ.). Such observations indicate that paired males and females maintain close contact prior to nesting and suggest that a screech-owl would soon (i.e., within a few hours) realize that its mate was absent. Although it seems unlikely that a screech-owl would persist in trying to re-establish contact with an absent mate for two or three nights (or for six nights during one of the natural removals), this remains a plausible interpretation.

Finally, increased song output may attract a new mate (Krebs et al. 1981). Our observation that five screech-owls apparently acquired new mates during the removal period is consistent with this hypothesis. In addition, one female left her territory during the removal period and paired with a male in an adjacent territory. Although not quantified, the singing rates of her new mate had been relatively high, perhaps because his previous mate had recently been killed by a predator.

Male screech-owls in our study sang significantly more than females during the mate removal period. Such results suggest that male screech-owls either expend greater effort to re-establish contact with an absent mate (perhaps because of the risk of cuckoldry) or use a more active approach than females to attract a new mate. If seeking a new mate, increased singing rates indicate that the male screech-owls actively advertise their unmated status to nearby females. In contrast, the lower singing rates of female screech-owls during the mate removal period suggest a less active approach. If male screech-owls play a greater role in maintaining territory boundaries, the absence of a male may signal the availability of a territory and, perhaps, a female. Thus, female screech-owls may wait for unmated males to trespass, then sing to advertise their location or participate in a duet.

Both male and female screech-owls used bounce songs more than whinny songs after removal of their mates and after release of their mates, suggesting that bounce songs are more important in intersexual communication (see also Marshall 1967, Gehlbach 1986). Ritchison et al. (1988) concluded that bounce songs were used in both aggressive (intrasexual) and non-aggressive (intersexual) contexts.

Previous work suggests that whinny songs serve an aggressive (territorial) function (Marshall 1967, Gehlbach 1986, Smith et al. 1987, Ritchison et al. 1988). However, we found that male screech-owls gave significantly more whinny songs after removal of their mates. In addition, both individuals (one male and one female) observed during the "natural" removals gave numerous whinny songs. Such results suggest that whinny songs may also be used in non-aggressive contexts. Ritchison et al. (1988) suggested that whinny songs may be used for long-range advertising. If so, our results suggest that whinny songs may not be used exclusively as long-range signals of territory ownership (intrasexual contexts) but may also be used as long-range signals by individuals trying to re-establish contact with an absent mate or attract a new mate (intersexual contexts).

CHARACTERISTICS OF BOUNCE AND WHINNY SONGS

Bounce songs (n = 616) given by screech-owls (n = 6 males and 5 females) during the mate removal period of our study (presumably serving to re-establish contact with a mate or attract a new mate) had a mean duration of 3.74 seconds and consisted of an average of 59.2 notes. In contrast, bounce songs given in response to playback (and, therefore, presumably serving an aggressive function) had a mean duration of 2.3 seconds and consisted of an average of 32.3 notes (Cavanagh and Ritchison 1987). Thus, our results support the hypothesis that the message conveyed by bounce songs is correlated with duration, with songs of increasing duration conveying decreasing levels of aggression (Klatt and Ritchison 1993).

Bounce songs were often given with greater volume during the mate removal period. Increased volume would increase transmission distance, which would be advantageous either when attempting to re-establish contact with a mate or attract a new mate.

Whinny songs given during the removal period of our study (n = 112 songs given by two males and one female) had a mean duration of 1.51 seconds. In contrast, whinny songs given in response to playback had a mean duration of 1.15 sec (Cavanagh and Ritchison 1987). Thus, as with bounce songs, longer whinny songs may convey decreasing levels of aggression.

OTHER VOCALIZATIONS GIVEN BY MALE AND FEMALE SCREECH-OWLS

Most extended bounce songs were given by male screech-owls during the replacement period and all were given when a mate was nearby and both individuals were near a cavity. Kelso (1938) described this song as the "wuh-wuh-wuh" call and reported that male screech-owls used these songs to advertise nest cavities. Similar behavior has been reported in other owls (Ligon 1968, Meehan 1980, Bondrup-Nielson 1984, Reynolds and Linkhart 1987). The presence of suitable nest cavities in a territory may be an important factor in mate choice by female owls (Carlsson 1991), and informing females about the presence of such cavities may be important in the establishment (or re-establishment) of pair bonds. Male screech-owls in our study may have advertised (or re-advertised) the presence of suitable cavities (and uttered extended bounce songs in the process) during the replacement period to remind mates that such cavities were available.

Squeal calls were given by both male and female screech-owls in our study, mainly during the replacement period. Although, to our knowledge, this call has not been described previously, similar calls have been reported in other owls (Haverschmidt 1946, Ligon 1968, Martin 1974). In these other species, such calls are given during copulation. Screech-owls may have been copulating during the replacement period to re-establish pair bonds or reduce the risk of cuckoldry (Birkhead and Møller 1992).

MOVEMENT PATTERNS

Male and female screech-owls in our study moved more frequently during the mate removal period and, in addition, females moved greater distances. Such behavior would increase the chances either of re-establishing contact with a mate or attracting a new mate.

Although female screech-owls in our study exhibited more movement during the removal period, most (six of seven) remained on their territories. This may be the best strategy in a resident species like the Eastern Screech-Owl where paired males and females maintain joint territories during the non-breeding season (Belthoff et al. 1993). The chances of a female screech-owl attracting a male (either a male from a nearby territory or, more likely, a "floater") to her territory would probably be better than the chances of locating an unpaired male in another territory.

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