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- LAURENCE C. BINFORD, 330 Grove Street, Glencoe, Illinois 60022. Received 20 Mar. 1989, accepted 20 April 1989.

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Why female Red-winged Blackbirds call at the nest.—Female Red-winged Blackbirds (*Agelaius phoeniceus*) often give a loud, three or more syllable "chit" call when arriving, sitting on, or departing their nests. These calls, distinguished as "Type I" by Beletsky (1983b), are conspicuous and draw attention to the caller and the location of her nest. Since predation is a major cause of egg and nestling mortality (Young 1964, Caccamise 1976), the calling by females is enigmatic. Beletsky and Orians (1985) tested the hypotheses that female calling signaled the male or signaled to other females, to coordinate group departures. Both hypotheses were rejected, and a third hypothesis, identifying females to their mates to maintain pairbonds, inform the male of reproductive status, and as a consequence, inhibit sexual harassment, was suggested. A subsequent study (Birks and Beletsky 1987) supported this hypothesis by showing that calling inhibited sexual harassment. However, Beletsky and

Orians (1985) established that females called more frequently when departing from a nest site than when arriving at it and that vocalization peaked in the incubation stage and then decreased: both of these patterns are unexplained by the sexual harassment hypothesis. If calling was to avoid harassment, calling should be more frequent at arrival, since the female is more likely to be unmated than one leaving a nest, and calling should peak during prenesting since this is when forced copulations could result in fertilization.

In this study we tested whether females call to signal their identity and nest area ownership by examining when and under what circumstances female Red-wings call, how their vocalizations change over the breeding cycle, and by comparing vocalization frequency between nest aggregations with high and low nest densities in eastern Washington State (EW) and nest aggregations with low nest densities in western Washington State (WW). Two hypotheses were tested: (1) that females call to identify residency and nest area ownership, and (2) that female calls inhibit male harassment.

Female Red-wings vocalize and display during aggressive interactions with each other (Nero 1956b, Beletsky 1983b, Hurly and Robertson 1984), and female aggression may affect settlement of other females (Hurly and Robertson 1985). If calling indicates identity and nest area ownership, we predicted that: (1) females should use the same call when arriving and departing and while sitting on their nests, and (2) calling should be more frequent on densely settled marshes than on marshes with few birds because large numbers of birds arriving and leaving would make visual identification difficult. Further, we predicted that if calling is an aggressive display or to counter male advertisement, calling should occur more often where intrusion by non-resident females is more common and should decrease as female settlement becomes less threatening to a females' fitness.

Study area and methods.—Red-winged Blackbirds were observed at Windmill Lake and Juvenile Lake in the Columbia National Wildlife Refuge (46°56'N, 119°10'W) Grant County, Southeastern Washington on 23, 24, and 30 April and 1 May 1988 for a total of six hours in the early morning and late afternoon. Five groups of birds were studied. Two groups were on isolated territories; each had one male, a preincubating female, and an incubating female. Three groups were part of a large Red-wing nest aggregation with contiguous territories; each of these three groups had one male and four to six preincubating or incubating females. Observations were made from cliffs overlooking the marshes. In WW, we watched birds over the entire breeding season at two ponds near the University of Washington (47°39'N, 122°18'W). From 26 April to 18 May 1988, we observed Red-wings from a 2-m ladder at pond I between 07:00 and 08:00 for a total of 18 h. The pond had two equal sized male territories, and each territory contained two females. A second pond with less vegetation had two territories of unequal size with one female in each. From 9 May to 7 June 1988, observers stood on the shore and watched for a total of 12 h between 07:00 and 08:00. The weather during observations was usually cold and cloudy in both EW and WW. We recorded departures, arrivals, and behavior of all females, the type of call, and the presence and behavior of the male, other females, and predators. The calls were: Type I, three to several "chits"; Type II, a growling "teer" (Beletsky 1983b); and one or two "chets" (Hurly and Robertson 1984). In WW we additionally noted when females called on their nests, whether the call answered the male or another female's vocalization (a call was considered an answer if given within two seconds of an initial vocalization), and if a predator was visible. All chases were noted.

Results.—Most Red-wings in EW nested in densely settled marshes with nest aggregations containing up to about 40 birds; WW birds nested in aggregations as large as six birds. Males in WW held territories more than three times larger than those in marshes in EW. Harem size was between 3 and 12 in EW and between 1 and 4 in WW (Orians 1980, this study). In EW there were more male-male interactions, male aggressive displays, and female-female

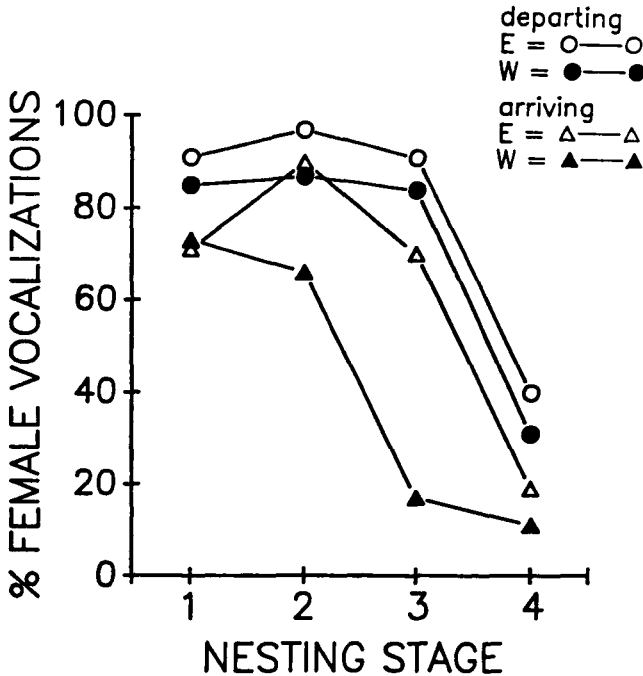


FIG. 1. The percentage of female red-wings vocalizing (Type I) when departing or arriving at their nests. The nesting stages are: 1 = preincubation, 2 = incubation, 3 = nestling and 4 = fledging. The EW (E) data is from Beletsky and Orians' (1985) study. The WW (W) data is from this study. The pattern of calling for both EW and WW is indicated along with whether the birds were departing or arriving. The number of observed vocal departures over the total observed departures for each stage in this study are: 1 = 18/21, 2 = 96/108, 3 = 100/119, 4 = 13/38. The observed vocal arrivals over the total observed arrivals for each stage in this study are: 1 = 15/20, 2 = 59/91, 3 = 21/118, 4 = 4/46.

and male-female chases than in WW. In WW males fed nestlings and continued feeding fledglings after the females had left the territories.

In both EW and WW, females were most aggressive when other females intruded on their mate's territory. At first, the resident female chased and called (Type I) at the new female when she entered any part of the male's territory. In WW, this distance gradually contracted to about 3 m as the new female built her nest. As intruders became more permanent residents, vocal bouts occurred across what appeared to be a border between their nest areas and lasted up to 15 sec. These interactions often included bill-up displays and wing spreads (see Orians and Christman 1968). Aggressive female activity was observed in both EW and WW and ceased when the intruder laid a clutch of eggs.

All females used Type I calls on and around their nests. In WW 51% of the calls made while females perched on their nests answered their mate's songs ($\bar{x} = 51\% \pm 21\%[SD]$, 8 days, $N = 265$); in the first minute after his return to the territory 70% of a male's songs were answered ($N = 40$) and 13% were answered after the first minute ($N = 62$). Females

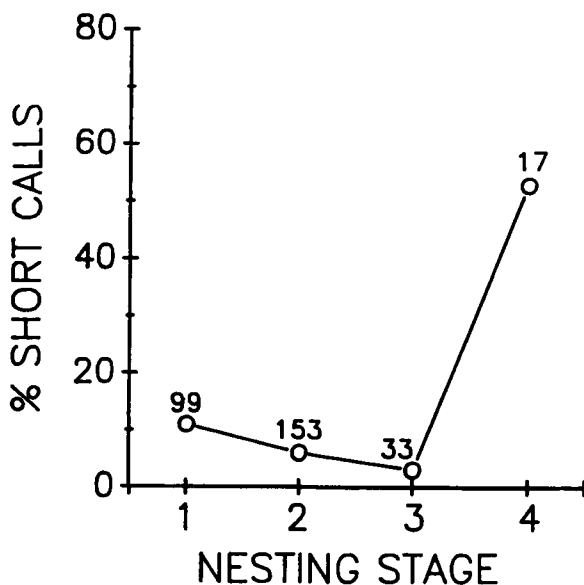


FIG. 2. The percent of short vocalizations, one or two chets, given by red-wing females in relation to nesting stage. Sample sizes indicating the total number of vocalizations given at each stage include both EW and WW data. Stages are: 1 = preincubation, 2 = incubation, 3 = nestling and 4 = fledgling.

were more likely to answer the male in the first minute after his return ($\chi^2 = 35$, $df = 1$, $P < 0.001$). Eleven percent of the females' calls made from the nest site answered other females' calls ($N = 222$). These were not correlated with arrivals of other females. During renesting, one female answered only 21% of male and 10% of other females' calls.

Type I and "chet" calls were given during arrivals and departures, but the frequencies changed over the nesting cycle (Figs. 1, 2). Females with nestlings often used Type I calls but occasionally called softly when returning to their nestlings. Females with fledglings rarely called (Fig. 1), and 53% (9/17) of these calls were chets (Fig. 2). Birds did not give Type II calls during observations. The arrival and departure calling of females at both ponds in WW during prenesting and incubation stages was similar and grouped for further analysis ($\chi^2 = 0.3$, $df = 1$, $P > 0.05$, Fig. 1). The frequency of arrival and departure calling was similar for the different territories in EW ($\chi^2 = 4.9$, $df = 2$, $P > 0.05$); for preincubating and incubating females these data are similar to the calling rates described in Beletsky and Orians (1985) for both arrivals ($\chi^2 = 0.46$, $df = 1$, $P > 0.05$) and departures ($\chi^2 = 0.04$, $df = 1$, $P > 0.05$). Female calling during preincubation and incubation in both our EW and WW sites was also similar for arrivals ($\chi^2 = 0.01$, $df = 1$, $P > 0.05$), and departures ($\chi^2 = 0.26$, $df = 1$, $P > 0.05$).

Although the frequency of departure calling in WW was comparable to that described by Beletsky and Orians (1985) ($\chi^2 = 0.06$, $df = 3$, $P > 0.05$), the percentage of arrivals accompanied by vocalization in WW was significantly lower than they described (Fig. 1), ($\chi^2 = 24.9$, $df = 3$, $P < 0.001$). Moreover, while Beletsky and Orians (1985) found that the frequency of calling at arrival and departure was similar within each of the four nesting

stages, we found that throughout the breeding cycle calling at departure is more common than calling at arrival in WW ($\chi^2 = 27.8$, $df = 3$, $P < 0.001$). Finally, in both EW and WW we found that the percent of vocal arrivals and vocal departures decreased over the nesting cycle ($\chi^2 = 246.3$, $\chi^2 = 57.91$, $df = 3$, $P < 0.001$).

The conditions under which calls were uttered and the consequences of calling varied. When a male was present in WW, females arriving at their nests called more than was expected; females called on 57 of 67 occasions when the male was present and on 12 of 19 when he was absent ($\chi^2 = 6.0$, $df = 1$, $P < 0.01$). In WW we observed only two short chases by males and both involved silently arriving non-resident females. In EW, the presence of the male apparently did not affect the frequency of calling on arrival; females called on 32 of 45 occasions with the male present and on 31 of 49 when he was absent ($\chi^2 = 0.84$, $df = 1$, $P > 0.05$). EW males were as likely to chase vocal arriving females (9/32 = 22% chased) as silent arriving females (4/13 = 24% chased), (Binomial Test, $P > 0.17$).

The presence of the male apparently did not affect the frequency of calling during departures in both WW (present: 84% [74/88] vocal vs absent: 77% [14/18] vocal) and EW (present: 89% [49/55] vocal vs absent: 93% [28/30] vocal), ($\chi^2 = 0.5$, $\chi^2 = 0.4$, $df = 1$, $P > 0.05$). In EW, males were less likely to chase females that called during departures (4/48 = 8% chased) than silent departing females, (3/7 = 43% chased), (Binomial Test, $P < 0.001$). Most male-female chases were short and were never observed to end in copulation. In WW, males were not observed chasing departing females.

Female intrusion was more common in EW where we saw 13 female-female chases in six hours. Only two of these intruding females were silent, suggesting that females were more likely to chase vocal females (Binomial Test, $P > 0.01$, $N = 15$). We saw females in WW chase females twice during 30 hours; in both cases, intruding females called. All female-female chases were short.

In WW, females' nest areas appeared highly dispersed, maximizing internest distance. When a new female settled, it was at an equal distance between other nests ($N = 4$).

Discussion.—Calling at all stages is more frequent in EW than WW (Fig. 1). Also, Red-wing densities in EW are greater than in WW. We believe resident females call to identify themselves because the higher activity makes visual identification difficult. By calling, a female quickly communicates her status as a resident before she violates the boundaries of other territories when moving on and off her own territory. Calling inhibited chases by males in EW, supporting the hypothesis that females call to suppress male harassment. Since chasing did not occur in WW, and calling is less frequent, we suspect identification is visual as well as vocal. Since Red-wing nest aggregations are less dense in WW, the advantage of calling for instant identity or ownership status should be lower in WW. Moreover, visual predators such as birds, are relatively less important in EW than in WW; consequently the risk of calling disclosing nests to predatory birds should be higher in WW than in EW. The higher calling frequencies in EW compared to WW is consistent with the idea that benefits of calling in EW are higher than in WW.

Females appear to occupy and defend space within the larger territory of their mates (Nero and Emlen 1951, Hurly and Robertson 1984). Females call to other females when defending their space and in aggressive interactions (Nero 1956a, b, Armstrong 1963, Beletsky 1983b, Hurly and Robertson 1984) and may attempt to prevent other females from settling nearby (Nero 1956a, b, Lenington 1980, Orians 1980, Hurly and Robertson 1985, Searcy 1986). Yet, Searcy (1988) found that female behavior did not appear to affect female settlement. Calling while on her nest, however, may communicate a female's ownership of an area to neighboring birds, and answering another resident's calls may acknowledge their residency. Such calling could help intruding females maximize internest distance and is consistent with the settlement pattern we observed.

The changes in calling frequency we observed over the nesting cycle (Fig. 1) provide insights into why females call. If female calling identifies residency and prevents other females from settling, calling should remain frequent until the female's clutch of eggs has hatched. At this point, the settlement of another female would not affect any male parental involvement in the raising of her young (Yasukawa and Searcy 1981, Beletsky and Orians 1985) as her young will have fledged by the time any new young hatch. Hurly and Robertson (1984) noted a decrease in aggressive and territorial behavior in females in the later part of the nesting cycle. The peak in vocalizations during the incubation stage and the subsequent decrease we observed during the nestling stage is consistent with the hypothesis that females call to both identify their ownership of an area and to discourage other females from settling.

Females also call to communicate with their territorial male (Beletsky 1983b). Female answering from the nest could be both a territorial response indicating ownership and occupancy to the male and a signal to prospecting females that a female is already present. The silent arrivals and departures during the male's absence in WW suggest there is no need to identify oneself and advertise ownership when the male is not present. In EW, however, where density is higher, neighboring males and females must also recognize a female as a resident, so females must call to alert neighbors as well. It is difficult to determine whether male and female chasing is sexual or aggressive behavior. The evidence, however, suggests chasing is territorial. Chasing did not lead to copulation attempts, and calls given by females as they arrived and departed their nests appeared to affect chasing under some circumstances and not under others. In sum, calling does appear to identify resident birds and prevent the harassment that a stranger elicits. Calling may also serve to assert nest area ownership, inhibit intrusion, increase spacing of nests, and delay settlement of other females. The relative importance of calling in each of these functions has yet to be determined. Our results suggest that females call to assert ownership of a nest site and to identify themselves to gain uncontested access to their space.

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MAUREEN P. SMALL AND P. DEE BOERSMA, *Inst. for Environmental Studies, FM-12 and Dept. Zoology, Univ. of Washington, Seattle, Washington 98195. Received 15 Sept. 1987, accepted 30 Aug. 1989.*

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Sarcosporidiosis observed more frequently in hybrids of Mallards and American Black Ducks.—American Black Duck (*Anas rubripes*) populations are declining (Kirby 1988). In part, this decline can be traced to the eastward range expansion of the Mallard (*A. platyrhynchos*) (Johnsgard 1961). Additionally, Mallard numbers in the eastern United States have increased through game farm releases (Heusmann 1974). Mallards and Black Ducks hybridize whenever they come into contact (Goodwin 1956, Johnsgard 1967, Heusmann 1974, Ankney et al. 1986), suggesting that these ducks are races of the same species. The lack of behavioral reproductive isolating mechanisms (Johnsgard 1960) is consistent with this interpretation. Black Duck hens, when courted by Black Duck and Mallard drakes, choose Mallards (Brodsky and Weatherhead 1984, Brodsky et al. 1988). Because hybrid drakes tend to exhibit Mallard drake plumage characteristics (e.g., some green on head, white-edged speculum) and because bright plumages among males of *Anas* species presumably evolved through sexual selection (Ankney et al. 1986, Heusmann 1974), it follows that hybrid drakes may be preferred by Black Duck hens over Black Duck drakes. If such preferences exist, then the hybrids pose a special problem for the integrity of the Black Duck phenotype because outcrossing often results in hybrid vigor. Black Duck × Mallard hybrid backcrosses are apparently as fertile as the parental types (Phillips 1915).

Fertility notwithstanding, disease or other factors could reduce hybrid fitness. Here we present retrospective observations that are consistent with this notion. We recorded the occurrence of sarcosporidiosis (a protozoan parasite) in 55 adult (older than 1 year) ducks collected by hunters on three New Jersey state game management areas (Great Bay Management Area, Tuckerton; Dix Management Area, Fairton; Fortescue Management Area, Fortescue) during the hunting seasons of 1986-1988. Juvenile ducks were excluded from