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NOTE ADDED IN PROOF

Recently, several complete elements of a probable new species of small duck have been identified from the Love Site, a late Clarendonian fossil locality in Alachua County, Florida (J. Becker pers. comm.). The carpometacarpus of this duck is smaller in length and more slender than, but not referable to, *A. schneideri*. This new species from an avifauna dated at 9 m.y. old, currently under study by J. Becker, indicates that a niche for a very small duck has existed in North America since the late Miocene.

Do Female Red-winged Blackbirds Limit Harem Size? I. A Removal Experiment

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Intrasexual aggression as a part of the reproductive strategy of female birds has been neglected until quite recently. Female-female aggression has been observed in several species of birds [Red-winged Blackbirds (*Agelaius phoeniceus*), Nero 1956, LaPrade and Graves 1982, Yasukawa and Searcy 1982; Brownheaded Cowbirds (*Molothrus ater*), Kevin Teather in prep.; Mountain Bluebirds (*Sialia currucoides*), Power and Doner 1980; Eastern Bluebirds (*Sialia sialis*), Gowaty 1981; Tree Swallows (*Tachycineta bicolor*), Leffelaar and Robertson in press; Tetraonidae, Scott 1942, Wiley 1973, Robel and Ballard 1974, Hannon 1983, 1984]. However, few studies have directly addressed the function and efficacy of female-female aggression.

LaPrade and Graves (1982) observed increased aggression by female Red-winged Blackbirds toward conspecific female models as the breeding season progressed and interpreted this in terms of parental investment theory (Trivers 1972, Dawkins and Carlisle 1976). They suggested that the females increased the level of defense of their offspring as the cost of replacing them increased. Yasukawa and Searcy (1982) presented evidence that female Red-wings attempted to monopolize male parental care by preventing additional females from joining the harem. Hurly and Robertson (1984) demonstrated that female Redwinged Blackbirds behaved territorially and suggested that this aggressive behavior was effective in deterring further recruitment into harems.

Here we present the results of a female removal experiment testing the effectiveness of female-female aggression in limiting harem size. We predicted that new female Red-winged Blackbirds would settle when aggressive resident females were removed, and that new nest initiations would occur more frequently in male territories where harem size was maintained at an artificially reduced level than in similar control territories. Support for our predictions would suggest that female-female aggression is an important factor limiting harem size.

This study was conducted at the Queen's University Biological Station north of Kingston, Ontario. The study site was Barb's Marsh, a 2-ha marsh dominated by willow (*Salix* spp.) and cattail (*Typha* spp.).

The front half of the marsh was searched for nests 3 times weekly from early May to the end of July 1981. Nests were marked by placing a numbered piece of flagging tape on vegetation approximately 1 m from the nest. Thirteen territories of males were mapped during the first three weeks of May. A random-number generator was used to select 7 experimental territories, leaving the remaining 6 as controls. Female removals occurred between 1800 and 2100 on 23 and 25 May and 6, 9, and 18 June 1981. On each of these days all females that could be associated with nests in the experimental territories were shot using a 12-gauge shotgun. Nests of incubating females were left as a test to ensure that the eggs were unattended on subsequent nest checks. If a removed female had nestlings, they were removed and killed in ether.

We attempted to remove all females nesting in the experimental territories. Some individuals (4) were very secretive and could not be shot without great disturbance of other females or some degree of uncertainty of identity; consequently, they were not removed. None of these females could have been responsible for new nest initiations. In general, an active nest was taken as an indication of a female on a male's territory. In two instances females that could not be associated with active nests were removed. These females vocalized and refused to leave the males' territories, so it was assumed that they either possessed nests that had not been found or were in the process of building nests. After the beginning of the remov-
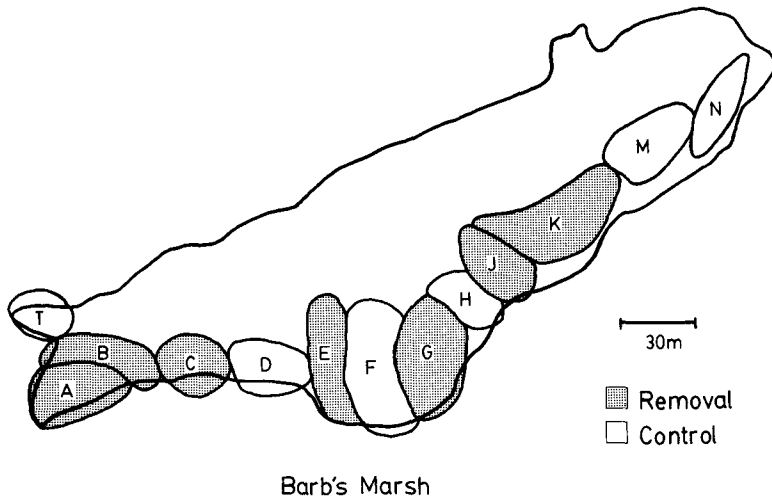
Fig. 1.   The distribution of experimental and control territories in Barb's Marsh, 1981.

als the number of new nest initiations in experimental territories was compared with the number in control territories.

The distribution of experimental and control territories is shown in Fig. 1. The sizes of control ($\bar{x} =$ 611 m² $\pm$ 107 SE) and experimental ($\bar{x} = 754$ m² $\pm$ 95 SE) territories did not differ significantly (Mann-Whitney U-test, $n = 13$, $P = 0.14$), nor did the initial harem sizes prior to removals [$\bar{x}$ (control) = 2.3 $\pm$ 0.56 SE females, $\bar{x}$ (experimental) = 2.0 $\pm$ 0.38 SE females, $P > 0.40$). Harem size was defined as the number of simultaneously active nests within a male's territory. In total 19 females (original residents and replacements) were removed from the experimental territories, the first 12 of these within a 48-h period.

Subsequent to the beginning of removals, new nests were initiated in all 7 of the experimental territories but in only 3 of the 6 control territories (G-test, $n =$ 13, $P = 0.023$; Sokal and Rohlf 1981). Table 1 presents the number of new nests initiated within each territory. The difference between experimental (11 new nests) and control (3 new nests) territories is significant (Mann-Whitney U-test, $n = 13$, $P < 0.01$). New nests were initiated in different sites from those used by the original residents, so it is unlikely that female recruitment was limited by the availability of nest sites *per se*.

The results indicate that the presence of nesting females within a male's territory inhibited further recruitment into the harem. Two important inferences can be drawn from this. First, newly arriving females seeking nest sites did not settle randomly within the marsh. Their choice of territories was negatively associated with the presence of resident females. Second, resident females did not actively recruit additional females, nor were new females attracted to settle in a territory by the presence of resident females. It appears that female Red-winged Blackbirds in our study site were behaving competitively rather than cooperatively [see Altmann et al. (1977) for a discussion of this]. Lenington (1980) studied the settling pattern of female Red-wings and concluded that they followed the competitive model rather than the cooperative model.

Although we have no direct measure of aggression in the females removed from this study site, we observed female-female chases and aggressive interactions and heard chit and teer vocalizations that are associated with female aggression, as observed in detail in our other study sites (Hurly 1982, Hurly and Robertson 1984; see also Nero 1956). We assumed that the females in this study site were, on average, as aggressive as those in the other sites.

The aggressive and territorial behavior exhibited by female Red-winged Blackbirds probably functions as more than the mere advertisement of occupancy (ideal free distribution, Fretwell and Lucas 1969). A sizable proportion of Red-wing populations nests in suboptimal habitat (Robertson 1972) and in so doing incur a reproductive cost. Territoriality in female Red-winged Blackbirds probably is an attempt by resident females to limit breeding density by restricting newly arriving females to poorer habitats. The result is similar to the ideal dominance distribution of Fretwell and Lucas (1969). This model, however, makes the unlikely assumption that all individuals are equal. There is considerable evidence that this is not the case in Red-wings (Searcy and Yasukawa 1983 and references therein, Hurly and Robertson in prep.) or in other species (e.g. Rohwer 1975, Watt et al. 1984) because individuals differ in fitness, dominance, and the ability to defend resources. Dominant females would be expected to settle in the better habitats, while subordinate (often younger) females arrive lat-

er (Crawford 1977) and either forsake breeding or settle in poor habitats. If aggression merely functioned to space females evenly within the territories of males, then harem size should be correlated with male territory size and quality. The original harem sizes in this study were not correlated with territory area (Spearman $r = -0.107$, $P \gg 0.2$, $n = 13$). In nearby study sites Weatherhead and Robertson (1977) found no correlation between harem size and territory size or quality.

The determinants of harem size usually are discussed within the context of the Polygyny Threshold Model (PTM; Verner and Willson 1966, Orians 1969). In the competitive version of the PTM (Altmann et al. 1977) it is assumed that each additional female entering a harem decreases the expected reproductive success of the harem members. The same assumption is made by Fretwell and Lucas (1969) in both of their models. According to the PTM, females choose the best available breeding situation (Wittenberger 1976) on the basis of male territory quality, male parental care, and male genetic quality (see Searcy and Yasukawa 1983 for a recent review), and thus harem size is dependent on female choice. Our results do not exclude the possibility that females merely avoid settling in male territories that already contain one or more females. The PTM predicts that they will settle elsewhere if better conditions exist. The model also predicts that joining an existing harem sometimes is the best choice of breeding situations. Considering the aggressive and territorial behavior of female Red-wings (Nero 1956; Holm 1973; Lenington 1980; LaPrade and Graves 1982; Yasukawa and Searcy 1982; Hurly and Robertson 1984, in prep.) and the fact that resident females can delay the nesting of new females (Yasukawa and Searcy 1981, Hurly and Robertson 1984), the evidence presented here suggests that aggression by resident females may place some constraints on harem size. Later-arriving females may not be free to choose the best breeding situations potentially available to them. Wittenberger and Tilson (1980) suggested that female aggression may be one of several factors limiting polygyny. Hannon (1984) presented evidence that female aggression tends to enforce a monogamous mating system in Willow Ptarmigan (*Lagopus lagopus*).

The source of the replacement females is unknown. In most territorial birds the removal of breeding males results in rapid replacement by nonbreeding or floater males, but earlier workers thought that there was no surplus of nonbreeding females (Hensley and Cope 1951, Stewart and Alderich 1951, Brown 1969). However, more recent studies have revealed the presence of surplus females that will replace lost breeders in various monogamous and polygamous species (Knapton and Krebs 1974, Power 1975, Smith 1978, Hannon and Zwickel 1979, Hannon 1983). The only published report investigating surplus females in Red-winged Blackbirds (Holcomb

TABLE 1. Harem size prior to removals, number of birds removed (including replacements removed), and the number of new nests initiated (indicating new females) in each territory subsequent to the start of removals.

Territory	Original harem size	Number of females removed	Number of new nests
Control			
D	1	0	0
F	1	0	1
H	4	0	0
M	4	0	1
N	2	0	0
T	2	0	1
Removal			
A	1	2	1
B	2	2	1
C	2	3	1
E	2	3	2
G	4	6	2
J	1	1	2
K	2	2	2

1974) found no evidence for a "notable surplus" of females, but the data were not specifically collected to test for this and may have been collected too late in the season to detect surplus females.

The replacement females could have originated from four sources. First, they may come from nonbreeders, resulting from seasonally limited breeding sites, that attempted to breed only when space was created for them by the removals. Second, from birds that would have bred elsewhere but attempted to settle when resident females were removed. Third, from failed breeders within the marsh that changed territories (and mates) for another breeding attempt. And finally, from failed breeders from other sites that moved into the study site for another breeding attempt.

We can reject the third hypothesis because marked females in nearby study sites never were seen to change territories (Hurly 1982, Hurly and Robertson 1984). While Picman (1981) demonstrated that an average of 16% of failed breeders changed territories, nest failures within the control territories potentially could account for a maximum of only 3 of the replacement females. We have no data pertinent to the first two explanations. Females usually had begun incubation when they were removed, so the presence of brood patches on those replacement females we collected does not indicate whether they already had attempted breeding elsewhere that season. This suggests that the term "surplus" can have more than one definition. A nonbreeder that will begin breeding given a suitable opening is certainly a surplus female, but a female currently breeding in suboptimal

habitat could be described as surplus to a more suitable site because it would move to the better site given the opportunity. Krebs (1971) observed this in Great Tits (*Parus major*). Robertson (1972) demonstrated that upland habitat is used by Red-wings but is suboptimal compared to marsh habitat.

Male Red-winged Blackbirds probably are willing to accept additional females into their harems because male reproductive success increases with harem size (Holm 1973, Weatherhead and Robertson 1977, Hurly 1982), and there probably is room for them in terms of available nest sites because replacement females never used old nest sites. However, resident females appear to deter further recruitment into a harem by limiting access to available breeding habitat through their aggressive and territorial behavior.

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