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Breeding Strategies of Male Yellow-headed Blackbirds: Results of a Removal Experiment

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A male's behavior toward a female and her offspring should depend in part on the probability that he fathered the offspring. Alexander (1974: 331) and others have pointed out the correlation between high confidence of paternity and evolution of male parental investment; without confidence of paternity, males will show neutral behavior, at best, toward females and their offspring. In more extreme cases, males kill immature offspring of other males to gain or hasten reproductive access to the mother, as in lions (Schaller 1972) and other species of mammals, particularly primates (reviewed in Blaffer Hrdy 1979). However, infanticide associated with male reproductive strategies has never, to our knowledge, been reported among birds, in spite of at least one experiment appropriate to discover it (Power 1975).

By means of a removal experiment we investigated the effects of paternity confidence on male behavior toward females and offspring in the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). Yellowhead males defend marsh territories during the breeding season and are frequently polygynous. They also make numerous feeding trips for young and mob or attack some potential nest predators, particularly gulls and Long-billed Marsh Wrens (*Telmatodytes palustris*) (Willson 1966; pers. obs.).

We expected several differences in behavior between replacement males and control males. Assuming that males can distinguish between fostered nests and their own, the minimal response of replacement males should be a low investment in eggs and nestlings that were conceived prior to removals; in particular, the effectiveness of guarding should be reduced (resulting in differential rates of nest failure), and effort devoted to the feeding of young should either be reduced or transferred to nestlings conceived

after the removals. If renesting by females is possible, the maximal response of replacement males should be the destruction of eggs or nestlings soon after assuming control of the territory.

On 16 May 1976 and 14 May 1978, 8 and 13 resident males, respectively, were removed from their territories while some nests were still being initiated. In all cases, replacement males took over the territories within a few days after removal. In 1976, control and experimental territories were interspersed on three lakes. In 1978, control and removal territories were on separate lakes, but evidence suggests they were similar (if not conservatively biased) in failure rates exclusive of those associated with removals. Of the 31 nests on experimental territories 1 week after removal, only 4 failed in the following 2 weeks; on control territories, 11 of the 38 nests failed over that period ($\chi^2 = 2.58$, $0.10 < P < 0.20$). The study sites were in ponds or lakes along Frenchman Hills (1976) or Winchester Wasteway (1978) in Grant County, Washington.

Nest checks were performed the day of the removal or the day prior to removal at experimental sites and 0–3 days before the removal date at control sites. In 1976, nests were checked 6 and 13 days after the removal date; in 1978, checks were made at 3–6-day intervals for a month after removals. Only nests containing eggs or young are included in our analysis.

In addition, male feeding behavior was measured over a 6-day period in 1978. Birds were not banded, but none of the conclusions to follow is seriously affected by this problem.

In reporting our data below, we define statistical significance at $P \leq 0.05$, except where otherwise noted in the text.

Of a total of 27 nests on the removal territories for both years combined, 8 nests failed within the week following the removal, while only 2 of 35 nests on the control territories failed within the week following the removal. The difference in nest failure between removal and control territories was significant ($\chi^2 = 6.46$, $0.01 < P < 0.02$) for both years combined. In neither of the single-year data sets was this difference significant, however. Were these nest failures due to increased predation on nests unprotected by interested males, or to infanticide by replacement males?

In 1976, the pattern of failures in time suggests that infanticide was not involved. If infanticide had occurred, we would have expected to see a rash of failures shortly after the takeover, then a sharp decline in failure rate. The breeding season is relatively short, so a male would have to act soon to induce renesting. The failure rate on the 1976 removal territories, however, was as high the second week after replacement (4 of 10 nests) as it was the first (3 of 13 nests). By themselves, however, these data do not argue generally against infanticide in yellow-heads. Few nests (3 in the 21 control and experimental territories) were initiated in the 2 weeks after removal; due to the lateness of removals in this season, infanticide may have held no benefits to replacement males because of the low probability of renesting by females.

The data from 1978 are more conclusive. There was a rash of failures in the 3 days following removal; 5 of the 14 nests present on experimental territories failed in these 3 days, but only 1 of the 19 nests on control territories failed during this time. This difference is not statistically significant, but bisecting the experimental territories showed an interesting difference among them. The experimental marsh was a narrow peninsula of cattails extending east–west for about 80 m. Along the north side of the peninsula was the main body of the lake, the opposite shore being 150–200 m distant. On the south side, however, the peninsula was separated from the shore by a channel only about 10 m wide. This near shore, moreover, was occupied by at least one singing marsh wren at the time of the removals. Seven yellow-head nests were on the territories on the north edge of the peninsula, and 7 were on the south-edge territories; all 5 of the failures occurred on the south side ($P < 0.05$, Fisher's exact test, two-tailed). There is no satisfying way to account for this difference with an infanticide hypothesis; thus we reject infanticide as the explanation of the mortality following removals. By a similar argument, we can infer that the failures were not due to female abandonment, unless the females responded to the differential risk associated with the two sides of the marsh. For this season, the absence of infanticide cannot be attributed to a lack of opportunity for renesting; 38 new nests were found on 28 territories in the 2 weeks following the removals.

Excluding those failures occurring in the 3 days after removal, the failure rates on the north and south sides of the marsh were similar: through June 12, the last nest check date, 4 nests had failed on the north side and 4 on the south side; 13 had successfully fledged young on the north side and 5 on the south side ($P > 0.5$, Fisher's exact test). The most plausible hypothesis is that heavy predation, perhaps by the marsh wrens, occurred on the nearshore side of the marsh during the time that the nests were unprotected by territorial males. Support for this suggestion is provided by Patterson et al. (in press), who found that the rate of nest failures in yellow-heads declines when a female receives male assistance in feeding young, although the number of young fledged per successful nest is unaffected by male assistance. This implies

TABLE 1. Feeding rates of control and replacement males with chicks older than 4 days.

Control males		Replacement males	
Rate (feedings/h)	Sample time (min)	Rate (feedings/h)	Sample time (min)
2.25	80	1.50	80
1.69	142	0.34	175
0.83	227	0	177
0.73	165	0	177
0	75	0	90
0	75	0	90
		0	80
		0	80

that male attendance at nests significantly reduces predation. Whether the exceptional failure rate following our removals was due to the absence of a male on the territory or to more subtle forms of neglect or incompetence by the foster father is unknown.

Given that males do not seem to commit infanticide and that they do contribute to the survival of nestlings, we asked to what extent males were investing selectively in their own offspring. We expected males to attack predators indiscriminately, because clumping of nests probably prevents a male from determining which nest on his territory an approaching predator is likely to attack. Indiscriminate nest defense is supported by the similar (and low) rates of failure for "fathered" nests (2 of 15) and "adopted" nests (3 of 13) during the 2-week period following the first 6 days after removal (thereby excluding failures associated with the removals).

Which nestlings did males choose to feed? Unfortunately, nests were too close together to determine, from our vantage point, which were receiving male attention. Some data bear on the problem, however. Willson (1966) found that males did not feed chicks younger than 4 days old. In our sample, replacement males that were on territories with foster chicks over 4 days old (but without fathered chicks over 4 days old) fed nestlings at lower rates than did control males whose territories included chicks older than 4 days ($P = 0.071$, one-tailed Mann-Whitney U-test; Table 1). Age of chicks had no measurable effect on feeding rate in our data; among control males, a mild drop-off in feeding rates over the 6-day observation period probably followed weather patterns.

Tentatively accepting the difference in male feeding rates, we can propose three hypotheses to explain these data. First, replacement males may have discriminated against the offspring of removed males. Second, replacement males may have fed less, because they spent more time than controls attempting to attract settling females. In fact more new nests (counted somewhat arbitrarily as the number of nests with eggs on the last nest check of the season, 12 June—10 days after feeding observations terminated) were started late in the season on the experimental than on the control territories. If the frequency of new nests were proportional to the number of territories censused, then 6.4 new nests would be expected on the removal territories and 5.5 on the control territories. In fact, 10 nests were begun on the removal and 2 on the control territories; this is a significant difference ($\chi^2 = 4.03$, $0.025 < P < 0.05$). Third, replacement males may not have been sufficiently confident of territorial ownership to spend the time away from the territory that feeding trips require.

Our evidence suggests that males do not discriminate in allotting parental investment that is shareable. Feeding young is not shareable and is costly, however, and our results are consistent with the hypothesis that males discriminate in the feeding of young.

If males "know" their own offspring, why did replacement males not destroy nests with contents to induce at least some females to renest on their territories? One of numerous possible answers it that the behavior has not arisen in evolutionary time. This possibility cannot be tested in any one species but is rendered less plausible by interspecific comparisons. Many species have evolved the ability to discriminate against brood parasites by the selective destruction of parasitic eggs. Within the Icteridae and other families, both discriminators and nondiscriminators are found (Smith 1968; Rothstein 1975, 1977); this argues against the generality that infanticide, through egg destruction, could not arise in birds but admits the possibility that it has never arisen in yellow-heads.

Plausible adaptive hypotheses can be proposed to account for the absence of infanticide. It is possible that settling females in polygynous species such as yellow-heads use active nests as a signal of territory

quality; hence, males might tolerate foster nests as a means for attracting new females to the territory. This assumes that active nests do not offset their advertisement qualities by depleting territory resources.

Alternatively, females might desert the territory after nest failure, reducing within-breeding season gains to zero for the infanticidal males. Furthermore, males may weigh desertion probabilities against some future benefit, either a renesting later that season or a return to the same territory the next year, accompanied by a high probability of the male being able to reclaim that territory the following year. The limited data available suggest that within-season renesting is infrequent in yellow-heads (Fautin 1941; Willson 1966). Further, late season clutches may be of low value if winter survival depends on experience or some other function of fledging time (see Perrins 1970). In Great Tits (*Parus major*), both sexes normally show high year-to-year breeding site fidelity, but distances between successive annual breeding sites are higher if the first nesting attempt of the season fails (even if there is a successful renest) (Harvey et al. 1979). If female yellow-heads behave similarly, infanticide would not be profitable to male yellow-heads. There is evidence for persistent annual returns among male and female Red-winged Blackbirds (*Agelaius phoeniceus*) (Nero 1956 citing Beer and Tibbets 1950), but we are aware of no evidence of long-term pairing in yellow-heads. Equally, we are not aware that anyone has looked, so the future-mate hypothesis remains viable, if speculative.

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Growth of Nestling Rufous Hummingbirds

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Although the growth of some tropical hummingbirds has been studied (Dorst 1962, Oiseau 32: 95–126; Haverschmidt 1952, Wilson Bull. 64: 69–79), there has been apparently nothing reported on the growth in body weight of temperate-area hummingbirds. This note describes changes in the mass of two young nest-mate Rufous Hummingbirds (*Selasphorus rufus*) in the northern Rocky Mountains.

I studied a nest on the grounds of the University of Montana Biological Station, Flathead Lake,