

seabirds, and are likely to be most successful with species nesting in dense aggregations on the surface or in burrows.

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Food Supplement Effects on Breeding Time and Harem Size in the Red-winged Blackbird (*Agelaius phoeniceus*)

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Some bird species (e.g. *Parus major*, Källander 1974; *Corvus corone*, Yom-Tov 1974; *Falco tinnunculus*, Cavé 1968; and *Melospiza melodioides*, Smith et al. 1980) advance the onset of breeding in response to increased food resources during the pre-laying season, whereas others (e.g. *Pica pica*, Högstädt 1981) do not. Ewald and Rohwer (1982) report advancing the onset of

breeding in Red-winged Blackbirds (*Agelaius phoeniceus*) by feeding. Their study, however, used whole lakes as experimental units, as opposed to territories or groups of territories within lakes. Ponds differ in surrounding vegetation, topography, substrate and productivity (Orians 1980), factors that may affect upland foraging success during the early breeding season, and relative timing of insect emergence later in the season. These latter factors may affect timing of breeding. One could therefore argue that the advancement that Ewald and Rohwer observed was due to intrinsic differences between marshes rather than

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TABLE 1. Mean first-egg day of nests 1-4 on fed and unfed territories on the 2 marshes. Significance levels between nests of a given rank on a marsh were determined by one-tailed Mann Whitney *U* tests.

| | Nest rank | | | |
|-----------------|-----------|---------|--------|--------|
| | 1 | 2 | 3 | 4 |
| SKELETON | | | | |
| Fed (day) | 106.2 | 110.5 | 116.3 | 119.4 |
| SD | 7.0 | 7.6 | 4.5 | 7.0 |
| <i>n</i> | 6 | 6 | 6 | 5 |
| Unfed (day) | 116.3** | 118.7** | 126.2* | 130.0* |
| SD | 3.9 | 2.4 | 2.2 | 6.2 |
| <i>n</i> | 6 | 6 | 6 | 6 |
| INFINITY | | | | |
| Fed (day) | 103.8 | 107.8 | 111.5 | 113.8 |
| SD | 2.9 | 4.7 | 2.4 | 1.0 |
| <i>n</i> | 4 | 4 | 4 | 4 |
| Unfed (day) | 116.3* | 120.0* | 123.0* | 123.5* |
| SD | 3.9 | 3.9 | 2.3 | 2.4 |
| <i>n</i> | 4 | 4 | 4 | 4 |

* $P < 0.05$; ** $P < 0.01$.

differences due to experimental feeding. I examined the extent to which supplemental feeding affects timing of breeding in single marshes in order to assess the generality of Ewald and Rohwer's (1982) earlier results.

I studied two ponds along Winchester Wasteway in Grant County, Washington (47.1°N, 119.5°W). The ponds (referred to as Skeleton and Infinity) were 1.5 km apart and each shaped like a peanut. Each half of the ponds contained from 4-6 territories. I randomly allocated one-half of each pond to the feeding treatment and one-half to the control. Even though treatments were allocated to pond halves, not territories, I treated each territory as an experimental unit in the analysis. The extent of female movement across territory boundaries was such that females would go into neighboring territories but only rarely would venture into territories across the pond. Had I randomly allocated territories to the treatments, females from unfed territories would have fed on neighboring fed territories. This would have obscured the effect of feeding. On both ponds, a shallow area with no open water separated the fed and unfed territories. I did not use the territories in these buffer strips in the experiment.

I mapped territories on each pond by noting where male-male displays took place. I placed one feeder in the middle of each fed territory on 4 April 1981. I filled the feeders daily with sunflower seeds, a protein-rich food source (Grau and Almquist 1945), the same food used by Ewald and Rohwer (1982). Nests were checked every 3-4 days. Each nest was labeled inconspicuously with a green twist-tie and tag below the nest, the contents and condition recorded, and

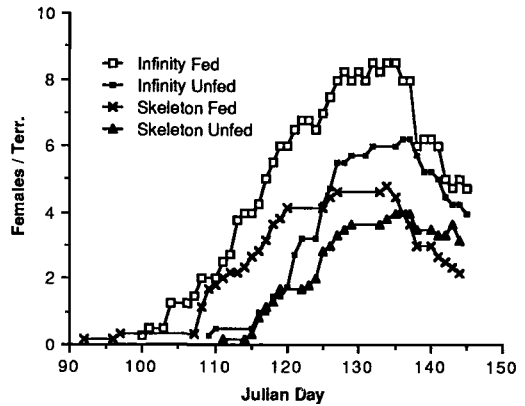


Fig. 1. The average number of females/territory for each marsh-treatment combination.

the territory noted. I estimated first egg day as follows: When a nest was discovered while eggs were being laid, first egg day was determined by subtracting the number of eggs in the nest, less one, from the Julian day on which the nest was found. If all eggs had been laid before I discovered the nest, I extrapolated first egg day from hatching date, or chick age, in the few cases where a nest was not discovered earlier. I allowed 12 days from clutch completion to hatching, and 13 days from hatching to fledging (Payne 1969). Harem size was calculated as the number of females nesting in a territory at any one time. Maximum harem size was the largest number of females that nested simultaneously in a territory during the duration of the experiment. I scored nest fate as: 1) all fledged, 2) over half the eggs fledged, 3) less than half the eggs fledged, and 4) none fledged. My last nest check was on 25 May 1981. The majority of nests are initiated before this time (Orians 1980).

Redwings used the feeders extensively. In nine 30-min intervals during the first half of May, there was at least 1 bird at the feeder, on average 9.9 min/30 min. The average stay on the feeder was 41 s. The mean arrival rate of birds at a feeder was 1 bird/2 min.

Supplemental feeding significantly advanced breeding on both lakes through the breeding season. Mean first-egg days for the first, second, third, and fourth nests per territory differed significantly for fed and unfed lake halves (Table 1). Because of small sample sizes after the fourth nest, I did not test differences for later nests. The magnitude of the difference remained the same.

I measured marsh effect by pooling first egg days for the first 40 nests on each marsh, regardless of whether they were on fed or unfed territories. Treatments were nested within marshes. There was no marsh effect ($F[1,76] = 0.05$, $P = 0.82$, see Fig. 1), but mean initiation dates on fed territories were signifi-

cantly earlier than on unfed territories ($F[2,76] = 8.07$, $P < 0.0007$).

Feeding increased maximum harem size on Infinity, but not Skeleton pond. On Skeleton there was a maximum of 5.2 ± 2.5 simultaneously nesting females on fed territories, and 4.7 ± 1.0 on unfed territories (Mann-Whitney $U = 19.5$, $P = 0.48$, see Fig. 1). On Infinity there was a maximum of 9.0 ± 1.6 females nesting simultaneously on fed territories but only 6.5 ± 0.6 females on unfed territories (Mann-Whitney $U = 15$, $P = 0.05$, see Fig. 1). However, there is no question that harem sizes were larger earlier in the season on supplemented territories (Fig. 1). The difference in harem size between fed and unfed territories remained relatively constant until mid-May (Julian Day 135) when all territories showed a simultaneous drop in the number of nests and the difference between fed and unfed territories was reduced (Infinity) or reversed (Skeleton) (Fig. 1).

I detected no temporal shift in the onset of breeding between the ponds but there were significantly more females per territory on unsupplemented territories on Infinity than on unsupplemented territories on Skeleton (Mann-Whitney $U = 23$, $P = 0.02$, $n_1 = 4$, $n_2 = 6$, see Fig. 1). On fed territories this difference was reduced (Mann-Whitney $U = 21$, $P = 0.10$, $n_1 = 6$, $n_2 = 4$). When all territories were pooled there were significantly greater maximum harem sizes on Infinity than on Skeleton (Mann-Whitney $U = 88$, $P < 0.002$, $n_1 = 12$, $n_2 = 8$).

There was no significant change in clutch size through the season in any of the marsh halves (treatments) except the unfed half of Skeleton (Spearman Rank = 0.50, $P < 0.005$, $n = 35$) where clutch size increased with season. When all nests were pooled there was no significant change in clutch size. Nests initiated earlier in the season fledged a greater proportion of young than later nests (Spearman Rank = 0.43, $P < 0.001$, $n = 61$). Almost all failure was due to predation.

I support Ewald and Rohwer's conclusion (1982) that food supplementation advances breeding and I show that marsh effects do not appear to explain the difference in breeding times between fed and unfed females. The number of females per territory differed between marshes. The major drawback of Ewald and Rohwer's (1982) experimental design which allocated whole marshes to treatments was that intrinsic differences between marshes rather than supplemental feeding could result in advanced breeding. I circumvented this problem by selecting single marshes. This is, however, likely to underestimate the effect of supplemental feeding on time of breeding because control females may advance their breeding somewhat in response to feeders on nearby territories. Females on food-supplemented territories probably have the greatest and most immediate access to feeders, but females forage off-territory, thus control females may derive some benefit from the feeders. The combined results of these studies demonstrates conclusively that

supplemental feeding advances breeding by at least 1-2 weeks in Red-winged Blackbirds in eastern Washington. Red-winged Blackbirds probably advance breeding rather than increase clutch size because later breeders suffer increased predation.

Ewald and Rohwer (1982) found that clutch size varied seasonally in only one of two years. I found a significant correlation of clutch size and season in only 1 of the 4 treatments that I examined. This suggests that the correlation between clutch size and time of season is, at best, weak and may be influenced by local conditions, as was suggested by Engstrom (1986).

My study corroborates one of the key predictions of the Verner-Orians resource-polygyny hypothesis (Verner 1964, Orians 1969): that a larger number of females should begin nesting earlier on the resource augmented territories. Harem sizes were greatest between treatments early in the season when food was most limiting and nests were most successful (Orians 1980, Ewald and Rohwer 1982). I observed a trend towards a higher maximum number of females nesting simultaneously on augmented territories which is not explicitly predicted by the Verner-Orians model. A number of ad hoc hypotheses can be erected to explain the failure to find consistent significant differences in maximum harem size between fed and unfed territories: 1) Insect emergence later in the season made the quality of control and treatment territories about equal; 2) Yellow-headed Blackbird (*X. xanthocephalus*) intrusion on the feeders beginning in early May reduced the the value of the feeders because they were emptied more quickly, and red-wings were excluded from feeding at them; 3) Females used factors other than food availability to choose the territory on which to settle; 4) The maximum number of simultaneously nesting females was an inadequate measure of harem size. The Verner-Orians model predicts that later arriving females will settle on poorer quality territories as the number of females on the best territories increases. Thus the mean date of the maximum number of females nesting simultaneously should be earlier on the fed territories than on the unfed territories. It is, but the maximum number of females nesting simultaneously may be the same because a maximum density of nesting females has been reached on all territories.

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