

COMMENTARIES

Male Parental Investment and Female Competence in Yellow-headed Blackbirds

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Gori (1988) hypothesized that, in species with biparental care, selection favored individuals who assess the parental ability, or competence, of their mates and adjust their own investment levels to maximize the return on their investment. He argued that in polygynous species, males should assist those mates whose broods offer the highest return on investment as measured by the increase in the number or quality of young. He attempted to test this hypothesis experimentally in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). Although we feel that Gori's hypothesis is interesting and deserves further attention, we are not satisfied that his experiments adequately tested the hypothesis. Specifically, we question his control for the presence of other broods on a male's territory, and we question his measurements of paternal investment.

Gori defined competent females as those capable of rearing 3 or 4 young to day 6 of the nestling period. Females that raised only 2 young to this point were considered incompetent. Gori assumed that all nestling mortality resulted from starvation caused by parental incompetence. By removing nestlings or eggs from nests of presumed competent females before day 6, Gori created broods of 2 tended by competent females (experimentally reduced broods) for comparison with the starvation-reduced broods of incompetent females. Competent females fledged more and heavier young than incompetent females. Males were more likely to feed broods of competent females and feed them at a higher rate than broods of incompetent females. Although the level of male assistance was not related to the number of young fledged per nest for either experimentally reduced or starvation-reduced broods, male assistance was correlated with an increase in fledging weight in experimentally reduced broods (explaining 12% of variation) but not in starvation-reduced broods. Gori mentions but does not present data to show that those young that fledge at a heavier weight are more likely to survive and breed. Gori concluded that the apparent male preference for assisting competent females may result from a higher expected return on their investment at these nests.

Unfortunately, most experimentally reduced nests in Gori's study were those of primary (1°) females,

whereas starvation-reduced broods typically belonged to secondary (2°), tertiary, or later-paired females. Previous studies of Yellow-headed Blackbirds in the same region (eastern Washington; Willson 1966) and in the same study area (Columbia National Wildlife Refuge; Patterson et al. 1980) demonstrated that males are more likely to assist females at 1° nests. Gori himself found that whether a starvation-reduced female was assisted depended on the presence or absence of other "available" females. To control for this problem, Gori considered male investment only at 1° nests. He found that males assisted 30 of 42 (76%) competent 1° females but only 2 of 10 (20%) incompetent 1° females. Gori failed, however, to control for the presence or absence of 2° broods and, if present, their size and degree of overlap with 1° broods. This is critical because Patterson et al. (1980) showed that males directly assisted 2° broods when 1° broods were reduced in size. Gori indicated that on some territories both 1° and 2° broods were reduced experimentally, but on others 2° were not manipulated. Secondary broods on the latter territories may have contained 3–4 young. Given the small sample of incompetent 1° females, small differences in the distribution of 2° broods between the two categories of 1° females may have significantly influenced the results. We appreciate the difficulty in controlling for the presence and status of 2° broods, but this seems essential here.

We are also concerned with Gori's measure of paternal investment. Gori measured paternal investment by monitoring male feeding rate for 1 or 2 h between 0900–1200 and 1400–1600 on day 8 of the nestling period. For this to be an accurate estimate of total male investment, several assumptions must be met: first, that the rate at which young are fed remains constant throughout the day; second, that male feeding rates on day 8 are representative of the entire investment period; third, that feeding rate is an accurate measure of male investment in the brood.

Willson (1966) found that some male Yellow-headed Blackbirds showed diurnal changes in provisioning rates, whereas Fautin (1941) and Lightbody and Weatherhead (1987) suggested that this species is inactive in the early afternoon. Because Gori measured feeding rates for only 1 or 2 h of only 1 day, we feel that documentation of diurnal constancy in male feeding rates should have been provided. Also, Willson (1966) found that the percentage of feedings by the male increased as nestlings aged. If males increase investment at different rates or if there is variation in male feeding rates at different points in the nest-

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ling period, investment measurements taken on day 8 may not reflect overall differences in investment.

Finally, Patterson et al. (1980) found that Yellow-headed Blackbird nesting success at the same site may be influenced to a greater extent by nest guarding than by male feeding rate. This implies that male feeding rate alone may not be the best measure of overall investment strategies.

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Response to Cash and Johnson

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Cash and Johnson raise two criticisms concerning my experimental controls and measure of male parental investment (see Gori 1988). Operationally, I defined parentally competent females as those capable of rearing 3 or 4 young to day 6 in the nestling period. I considered females that hatched 3 to 4 young but had only 2 alive on day 6 as parentally incompetent. To control for the number of young in nests, I experimentally reduced the number of young in primary (1°) and secondary nests. Most of these nests belonged to competent females. Competent-reduced females that were unassisted by males fledged more and heavier young than incompetent females. This justified my operational definition of competence.

To test whether males preferred to assist parentally competent or incompetent females, I compared the incidence of male feeding at experimentally reduced and starvation-reduced nests (see Gori 1988). I restricted the original analysis to 1° broods (i.e. the first brood to hatch on the territory) because they had a greater probability of being fed by males than broods that hatch later (Willson 1966, Patterson et al. 1980). I found that males were more likely to assist competent 1° females than incompetent females even though brood sizes were equal. Cash and Johnson suggest this result may be due to differences in the presence, timing, and number of young in secondary nests on experimental and starvation-reduced territories and not the parental quality of females per se. Their explanation is, however, unlikely to account for the result for two reasons. First, all territories in-

cluded in the original analysis had secondary nests. Second, the timing of these secondary nests relative to the primary nest was similar for experimental and starvation-reduced groups. Secondary broods hatched 5.6 ± 3.1 days after the 1° nest on territories with starvation-reduced 1° nests and 6.2 ± 3.5 days after the 1° nest on territories with experimentally reduced 1° nests (Mann-Whitney *U*-test, $z = -0.15$, $n_1 = 10$, $n_2 = 42$, $P > 0.6$). Thus, there was no difference in the presence or timing of secondary nests on territories with experimental and starvation-reduced 1° nests.

The number of young in secondary broods differed between the two groups. Secondary broods had 3-4 young on territories with starvation-reduced 1° nests. On territories with experimentally reduced 1° nests, secondary broods had 2-4 young. This was so because on some experimental territories, I also experimentally reduced secondary nests (i.e. double clutch reduction, DCR). It was possible, however, to control for the number of young in secondary nests by comparing experimental territories in which only the 1° brood was reduced (i.e. single clutch reduction, SCR) with territories that had starvation-reduced 1° broods. In this case, males assisted 9 of 14 (64%) experimental 1° broods but only 2 of 10 (20%) starvation-reduced 1° broods (Fisher exact test, $P = 0.04$). Secondary broods were similar in size in the two groups (secondary broods: 3.5 ± 0.7 young on territories with experimental 1° nests vs. 3.3 ± 1.0 young on territories with starvation-reduced 1° nests; Mann-Whitney *U*-test, $z = 0.5$, $n_1 = 14$, $n_2 = 10$, $P > 0.5$). In addition, secondary broods hatched a similar number of days after the 1° nest in the two groups (5.6 ± 3.1 days after starvation-reduced 1° nests vs. 6.6 ± 3.1 days after experimentally reduced 1° nests; $z = 0.53$, $n_1 = 10$, $n_2 = 14$, $P >$

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