

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

DAVID F. GORI¹

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; $z = 0.53$, $n_1 = 10$, $n_2 = 14$, $P >$

¹ The Nature Conservancy, Arizona Field Office, 300 East University Boulevard, Suite 230, Tucson, Arizona 85705 USA.

0.4), indicating that the presence, timing, or size of secondary broods cannot account for male preference for competent females.

I combined males that received SCRs and DCRs in the original analysis (i.e. Gori 1988) precisely because the probability that males assisted the reduced 1° brood was independent of the number of young in the secondary brood. Nine of 14 males (64%) that received SCRs (secondary brood with 3-4 young) fed the reduced 1° brood compared with 21 of 28 males (75%) that received DCRs (secondary brood with 2 young; $\chi^2 = 0.5$, $df = 1$, $P > 0.5$). This result differs from Patterson et al. (1980), who found that when only the 1° nest was reduced, males fed the secondary brood but not the 1° brood. In my experiment, males that received SCRs fed both 1° and secondary broods.

Differences in the results of these two studies may be due to differences in marsh productivity because the studies were conducted on different lakes and in different years. Marshes in the Columbia National Wildlife Refuge vary considerably in the productivity of blackbird food resources (Orians 1980, Gori 1984). This may have affected the ability of females to raise young unassisted and, therefore, the fitness gains to males that provide parental care (Gori 1984, 1988). If the productivity of my study marshes was lower, males would have obtained greater fitness gains by feeding broods with 2 young than males in Patterson et al.'s study. Alternatively, primary and secondary broods may have been closer temporally in Patterson et al.'s study so that males could feed only one brood. Unfortunately, the information needed to test these hypotheses is not given in Patterson et al. (1980).

The second issue that Cash and Johnson raise is whether my measure of parental investment (a male's feeding rate to young on day 8) was an accurate estimate of total parental investment. They set 3 criteria for this to be true. First, a male's feeding rate must be constant throughout the day (I observed males for 1-2 h during the midday). Second, a male's feeding rate on day 8 must be representative of the total investment period. Third, the feeding rate must be an accurate measure of male parental investment.

The first criterion is not strictly correct: male feeding rates need not be constant throughout the day. Rather, they must be constant only over the period when nests are observed, but there must be a positive covariance between a male's feeding rate during this period and at other times of the day. I do not have sufficient data to address this point directly; however, the first criterion is irrelevant if the other criteria are shown to be true.

I can address the other two criteria using observations that I made on Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) from 1981 to 1984. First, a male's feeding rate on day 8 is representative of his feeding rate at other times during the nestling and fledgling period. Male feeding rate on day 8 was positively correlated with feeding rate on day 10 ($r^2 =$

0.48, $n = 54$, $P < 0.001$) and with his feeding rate to fledglings ($r^2 = 0.16$, $n = 74$, $P < 0.001$).

Second, male feeding rate on day 8 is an accurate measure of male parental investment because it was correlated with the number of young fledged from nests and the fledging mass of young. Both estimate male fitness. Controlling for brood size on day 8 in an analysis of variance, broods that were assisted by males fledged significantly more young than unassisted broods ($F = 11.6$, $df = 1$, 410 , $P < 0.001$). In addition, there was a significant, positive correlation between the male feeding rate and the number of young fledged from nests for broods that contained 3 young on day 8 ($r_s = 0.39$, $n = 86$, $P < 0.001$), and for broods with 4 young on day 8 ($r_s = 0.38$, $n = 40$, $P < 0.05$). The correlation for broods with 2 young was also positive but was nonsignificant ($r_s = 0.06$, $n = 92$, $P > 0.5$). I used only male-assisted nests for the regression analysis. None of the nests used in either analysis suffered predation so that differences in fledging success reflect differences in the number of young that starved. Thus, higher feeding rates by males at nests with 3-4 young on day 8 produced more young fledged.

I also examined the effect of male feeding rate on the fledging mass of young and found that the rate of male feeding on day 8 correlated positively with fledging mass. For the analysis, I normalized mass according to sex, marsh, and year (as described in Gori [1988]) to control for differences associated with these factors (Willson 1966, Orians 1980, Gori 1984). I calculated sex-specific mass averages for broods that received no paternal care for each year and marsh. Separate averages were calculated for nests fledging 2, 3, and 4 young. Then for each nest, including those fed by males, I determined the difference between an individual's fledging mass and the calculated mean appropriate for its sex, year, and brood size. I plotted these deviations against male feeding rates. If male feeding increased the fledging mass of young, these deviations should be positive and increase with increasing male investment, e.g. feeding rate. There was a significant, positive correlation between male feeding rates on day 8 and fledging mass difference for nests fledging 3 and 4 young ($r_s = 0.37$, $n = 384$, $P < 0.001$) and for nests fledging 2 young ($r_s = 0.33$, $n = 208$, $P < 0.001$). The correlations remained significant when unassisted nests were excluded from the analysis (3-4 young fledged: $r_s = 0.38$, $n = 183$, $P < 0.001$; 2 young fledged: $r_s = 0.38$, $n = 92$, $P < 0.001$). On the average, young from assisted nests that fledged 3-4 young were 4.2 ± 4.8 g heavier at fledging than young from unassisted nests (Mann-Whitney U -test, $z = 3.5$, $P < 0.001$), while young from 2-young broods were 3.0 ± 5.7 g heavier ($z = 3.7$, $P < 0.001$). Thus, higher rates of feeding by males also resulted in heavier young fledged from nests.

The fledging mass of young Yellow-headed Blackbirds strongly affected survivorship after fledging.

Forty-nine out of 64 banded young (77%) found dead in marshes after fledging were below the mean fledging mass of young that year ($\chi^2 = 15.5$, $df = 1$, $P < 0.001$). I assumed that these young starved because there was no sign of physical damage by predators and their stomachs contained little or no food. Thus, young fledged at a greater mass have a higher probability of survivorship than lighter birds.

Finally, Cash and Johnson suggest from the results in Patterson et al. (1980) that nesting success in Yellow-headed Blackbirds may be influenced to a greater extent by nest guarding than by male feeding. In evaluating this hypothesis, it is important to note that Patterson et al.'s results were suggestive but not statistically significant. Thus, there is no quantitative evidence that male feeding or nest guarding reduces the probability of nest predation in Yellow-heads. In contrast, the relationship between male feeding rate, fledging success, and fledging mass are statistically significant. I conclude that male feeding in Yellow-heads is an important component of their parental investment in young.

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Half a Million Eiders off Cape Cod: Compounded Errors or Changed Populations?

ANTHONY J. ERSKINE¹

The Christmas Bird Counts (CBCs) at Monomoy, Massachusetts, in 1946–1951 reported Common Eider (*Somateria mollissima*) numbers increasing from 100,000 to 500,000 birds (Bailey 1955). Those figures have been widely quoted (e.g. Bellrose 1976; although Palmer 1976 was sceptical), but they appear implausible in relation to recent data from other sources. A fresh look at the Monomoy estimates, with other eider population and distributional data (not available in 1946–1951), is warranted.

Only the southern (*dresseri*) race of Common Eiders winters in Massachusetts; the northern race (*borealis*) comprises a small percentage of the wintering birds south of Newfoundland (Bailey 1955, Mendall 1968). Some *dresseri* birds that breed in southern Labrador winter off Newfoundland and along the north shore of the Gulf of St. Lawrence (Gulf north shore). Eiders that winter farther south come largely from those breeding in the Maritimes, New England, and in the St. Lawrence estuary (Reed and Erskine 1986). Few now breed on the island of Newfoundland or on the Gulf north shore. The known breeding populations

of the three southern regions—with their offspring and nonbreeding adults and subadults minus the annual hunting kill in these areas—could give rise only to ca. 200,000 wintering birds (Reed and Erskine 1986). Recent Midwinter Waterfowl Inventory (MWI) counts (USDI 1984) revealed similar numbers, mainly in Massachusetts and Maine, but these counts varied greatly between years and areas.

The counts in the Monomoy area in 1946–1951 might not be anomalous. The distribution patterns of eiders then and now might differ. The overall populations might have changed. The extrapolation from breeding pairs to winter populations might be at fault. Failing other explanations, however, I suggest that the 1946–1951 CBC observers overestimated the eider flocks.

The specimen records of *borealis* eiders in Massachusetts (Bailey 1955) gave no suggestion that northern birds ever came that far south in numbers. Likewise, I have no indication that severe ice conditions occurred on more northern wintering areas in 1946–1951 to force *borealis* eiders—or, still less probably, *sedentaria* eiders from Hudson Bay—to winter farther south. The breeding populations of *dresseri* eiders in Newfoundland, on the Gulf north shore, and in Labrador south of latitude 53°N were only remnants of primeval numbers by 1950 and have since decreased

¹ Canadian Wildlife Service, Atlantic Region, P.O. Box 1590, Sackville, New Brunswick E0A 3C0, Canada.