ADJUSTMENT OF PARENTAL INVESTMENT WITH MATE QUALITY BY MALE YELLOW-HEADED BLACKBIRDS (*XANTHOCEPHALUS XANTHOCEPHALUS*)

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ABSTRACT.—By removing young from the nests of competent females, I tested whether male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) could assess the parental competence of mates and adjust their parental investment accordingly. The purpose of this experimental reduction was to equalize the number of young in nests of parentally competent and incompetent females in order to control for the effect of offspring number on parental investment by males. Males had a greater probability of feeding at nests of competent-reduced females and they fed at a higher rate than they did at nests of incompetent females. The latter broods were fed only when nests belonging to competent females were unavailable. Males adjust their parental investment with mate quality independent of the number of young in nests. To explain this preference, I constructed functions to relate the amount of paternal investment (i.e. male feeding rate) to the number of young fledged from nests and the fledging mass of young. The latter are two components of male reproductive success and, therefore, estimates of the "return" on a male's parental investment. Male feeding had no effect on the number of young fledged from starvation-reduced or experimental nests. However, the fledging mass of young increased more when males helped competent females than when incompetent females were helped. Thus male preference for helping competent females may result because the return per unit of their investment is greater at these nests. *Received 6 October 1987, accepted 12 May 1988.*

IN species with bi-parental care, the number and quality of offspring an individual produces depends on its own competence as a parent and on the abilities of its mate. Parental ability is not constant among individuals but may vary with age, rank, breeding experience, mate familiarity, physical condition, and genetic quality (Coulson 1966, Lack 1968, Burley and Moran 1979, Burley 1981). Because of the importance of parental care in producing offspring, individuals should be under strong selective pressure to evaluate the parental abilities of mates and potential mates, and to adjust their investment in young accordingly.

Numerous authors have recognized the theoretical importance of selecting mates with superior parental abilities (Trivers 1972, Williams 1975, Burley 1977, Maynard Smith 1978). However, little attention has been devoted to the corollary question of how individual investment should vary with mate quality after mate choice occurs. Polygynous individuals have a choice of where to direct aid, and they should prefer to help mates that give them the greatest return on their investment. Return per unit of investment is defined as the incremental increase in the number or quality of young pro-duced as a result of a unit of parental investment; it is the slope of a function that relates the amount of parental care to the number and quality of offspring produced (Trivers 1972, Patterson et al. 1980). The greater the slope, the greater the return on investment. Therefore, males should prefer to invest in young of either parentally competent or incompetent mates depending on which yield the greater return on investment.

I present evidence that male Yellow-headed Blackbirds are capable of distinguishing the parental abilities of their mates. Males adjust their parental investment with mate quality in a way that does not compensate for the quality of their mate but rather augments it. This adjustment appears to provide males with higher returns per unit of their investment.

STUDY AREA AND METHODS

Study area and organism.—The research was conducted in 1981, 1982, and 1984 in the Hutchinson Lake drainage area, Columbia National Wildlife Refuge, Grant Co., Washington. The study area was previously described by Horn (1968) and Orians (1980).

Yellow-headed Blackbirds are polygynous, marsh-nesting birds of the subfamily Icterinae. Detailed ac-

counts of their breeding biology are given in Willson (1966) and Orians (1980). Harem sizes in the study marshes were 3.1 ± 1.5 (mean ± standard deviation) females/male ($n = 57$) in 1981, 3.9 ± 1.9 females/male ($n = 42$) in 1982, and 2.4 ± 1.4 females/male ($n = 30$) in 1984. Females arrive asynchronously on territories to breed so that young are available for males to raise for a substantial period of time during the breeding season. Males vary in the amount of parental care directed to young, especially in the rate at which they feed nestlings, and I restricted analysis to this component of parental care. In this population, feeding by males normally begins 5 days after the first egg in the nest hatches (i.e. day 6; day 1 corresponds to the hatching date of the first egg) but may commence a day or 2 later. Because males do not begin feeding young before day 6 and because females provide all the food up until this time, the number of young in nests on day 6 should be positively correlated with the parental competence of females. That is, given an equal hatching success, females that are more competent at foraging and raising young should have more young alive on day 6 than females that are less competent at performing these tasks.

Yellowheads feed themselves and their young primarily on emergent damselflies and dragonflies during the breeding season (Willson 1966, Orians 1966). In the study area, females with young foraged almost exclusively off the territory, while males obtained food both on and off the territory.

Observations and experiment.—I color-banded all males and over 60% of the females in the study marshes. Territory boundaries were mapped throughout the season by observing male perch sites and territorial disputes between adjacent males. Every 2 to 3 days I censused colonies, marked all new nests, and recorded the progress of those marked previously. Seven days after the first egg in a clutch hatched (day 8), I watched the nest for 1 or 2 h and recorded the feeding rate of both the male and female. All nests on territories used in the analyses were observed at least once between 0900–1200 and 1400–1600 Pacific Standard Time. On the morning of day 11, I weighed, sexed by mass, and banded nestlings with aluminum Fish and Wildlife Service bands. Some young were capable of leaving the nest at this time, although fledging normally occurs later in the day or on the following morning (day 12). Male offspring fledge at a significantly greater mass than females. This difference first appears several days after hatching. Male and female weight distributions are completely non-overlapping at fledging (Willson 1966, Richter 1983, Gori unpubl. data).

Females varied considerably in parental ability. Normally, they hatch 3–4 young and at least 3 young were still alive on day 6. I considered these females to be parentally competent. In some cases, however, 3–4 young hatched but only 2 were alive on day 6. I defined these females as parentally incompetent, as-suming that starvation resulting from parental incompetence was the primary cause of clutch reduction in these cases. Nest predation was uncommon in the marshes and, when it occurred, all young were usually removed from nests (Orians 1980, Patterson et al. 1980). In addition, the disappearance of marked individuals from complete nests was preceded first by cessation of mass gain, then by mass loss beginning a day prior to disappearance. Other young in the nest gained mass during this period. I assumed that these conditions were a likely prelude to starvation. Unfortunately, dead young were removed from nests by females, which made it difficult to test this assumption. In the rare cases where they were left, these individuals had no food in their stomachs.

To decouple the correlation between mate quality and the number of young in nests, I randomly selected 24 territories in 1981, 13 territories in 1982, and 17 territories in 1984 for experimental brood reductions. I performed the reductions either on the first nest (primary) or on the first 2 nests (primary and secondary) initiated on the territory, and I removed the last egg(s) or the last young to hatch. The number of young was reduced to 2 in each of 70 nests. These reductions were performed from day 1 to day 4 with a mean day of 2.7 ± 1.5 ($n = 70$). Starvation-reduced nests contained 2 young by day 4.4 ± 0.9 ($n = 59$). Because only primary and secondary nests were experimentally reduced, most females in this group were competent parents (see Fig. 2 and text for further explanation) but, following the reductions, they had the same number of young as incompetent females with starvation-reduced nests. Therefore, comparing the behavior of males at experimental and starvation-reduced nests will indicate their response to competent and incompetent mates and control for the number of young in nests. In addition, because experimental reductions were performed sooner after young hatched than reductions in starvation-reduced nests occurred, male preference for experimental broods would not result because young were lighter and therefore needier.

I used two measures of male investment: first, whether or not nestlings were fed during observation periods; and, second, the male's feeding rate (No. of trips/h). Male feeding rates correlated significantly with another measure of male investment: the time spent foraging for young (Gori 1984).

RESULTS

The analyses involved 2 groups of females. Starvation-reduced females were females that hatched 3–4 young but had only 2 young alive on day 6. Experimentally reduced females hatched 3–4 young and I removed young from the nest prior to day 6 so that 2 young remained

TABLE 1. Fledging success and female feeding rates to starvation-reduced and experimentally reduced nests that received no male parental care. For comparisons of female performance, *t*-tests were used.[a]

	Starvation-reduced nests ($n = 37$)	Experimentally reduced nests ($n = 37$)
No. of young alive, days 5 and 8	2.0 ± 0.0	2.0 ± 0.0
Female feeding rate, day 8 (trips/h)	6.6 ± 3.7	9.2 ± 3.4**
No. of young fledged/nest	1.62 ± 0.49	1.97 ± 0.16**
Male fledging mass (g) 2-young nests[b]	53.8 ± 5.9	58.2 ± 5.3*
	($n = 19$)	($n = 38$)
Female fledging mass (g) 2-young nests[b]	36.6. ± 5.1	39.8 ± 2.8*
	($n = 27$)	($n = 34$)

[a] Significance levels (2-tailed): * = $P < 0.01$, ** = $P < 0.001$.

[b] Sample sizes reflect the number of males and females from nests that fledged 2 young but received no male care; 23 starvation-reduced and 36 experimental nests.

on day 6. Starvation of young after day 6 occurred in both groups.

Parental competency.—I compared experimental and starvation-reduced females with respect to the number of young fledged/nest, the fledging mass of male and female offspring, and the female's rate of food delivery to the nest (Table 1). I attempted to test whether females defined as parentally incompetent on the basis of the number of young in nests on day 6 were also less competent than experimentally reduced females at feeding and raising these young after day 6. I restricted the analysis to nests that received no male care to control for possible differences in male investment between groups. In addition, I used only nests that fledged 2 young to compare fledging mass. All nests contained 2 young at the time of nest observation.

Experimental females were more competent parents than starvation-reduced females (Table 1). Experimental females delivered food to young at a significantly greater rate than starvation-reduced females. In addition, experimental females fledged significantly more young/nest and both male and female young were heavier at fledging than young raised by starvation-reduced females.

The lower fledging success and smaller young in starvation-reduced nests was not due to more young than in experimental nests until day 6. Unreduced nests with 3 or 4 young on day 6 (hereafter referred to as unreduced nests) fledged 2.5 ± 0.6 young/nest without male care ($n = 29$), significantly more than both experimental and starvation-reduced nests (*t*-tests, $t > 5.15$, 64 df, $P < 0.001$). In addition, unreduced nests that fledged 2 young contained 3 or more young until day 8.7 ± 0.9, a significantly longer period of time than starvation-reduced nests (*t*

= 16.3, 50 df, $P < 0.001$), yet larger male young were fledged from unreduced nests than from starvation-reduced nests (male fledglings from unreduced nests: 57.2 ± 5.3 g; $t = 1.81$, 48 df, $P < 0.05$, one-tailed).

Seasonal trends in parental competency.—I determined the occurrence of starvation-reduced nests as a function of the date of nest initiation and the order of nest initiation on territories (nest rank). For the analysis of initiation dates, I divided the breeding season into 3-day intervals starting on 1 May to ensure an adequate sample of nests. Nest initiation was defined as the date the first egg appeared. This date was a reliable estimate of female settlement or arrival since females typically settled on territories 3–5 days prior to the appearance of the first egg (Gori 1984). In all 3 yr, nesting commenced during the first 3-day interval (i.e. 1–3 May).

The proportion of starvation-reduced nests increased until 22 May and then decreased (Fig. 1). Similarly, the proportion of starvation-reduced nests was greater among late-arriving females (Fig. 2). Tertiary and later-nesting females were significantly more likely to have starvation-reduced nests than primary and secondary females ($\chi^2 = 7.3$, 1 df, $P < 0.008$). I believe that a greater proportion of late-nesting females were poor or inexperienced parents. The reduced occurrence of starvation-reduced nests in the last week of nest initiation (Fig. 1) is consistent with this explanation because early-breeding females whose first nests failed due to predation renested at this time. The trends were not explained by the seasonal availability of food as insect emergence increased throughout the season and was several orders of magnitude greater later in the season (Orians 1980, J. Wittenberger and D. Gori unpubl. data). The
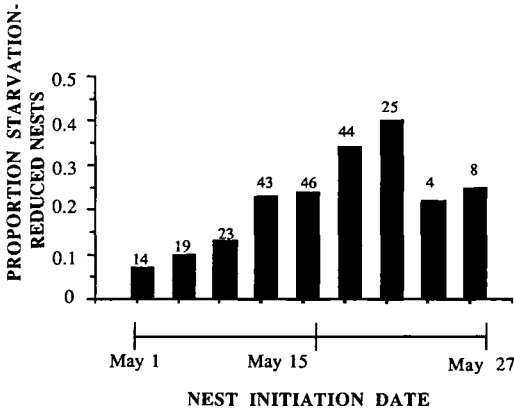
Fig. 1. Proportion of nests that were starvation-reduced as a function of the nest initiation date. Bars represent 3-d intervals in breeding season. The number above each bar is the total number of nests including starvation-reduced nests initiated during that interval.
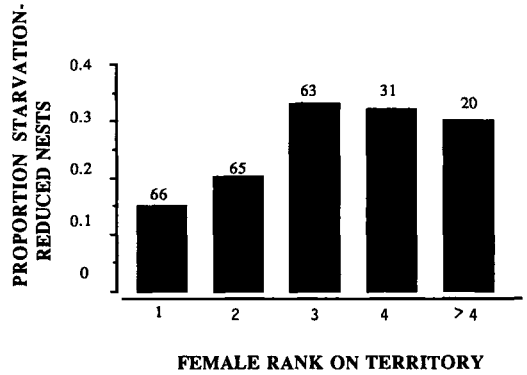

FEMALE RANK ON TERRITORY

Fig. 2. Proportion of starvation-reduced nests as a function of female nesting order on territories. The total number includes starvation-reduced nests in each rank category.

trends were also not explained by the seasonal occurrence of cold or rainy weather, which are infrequent and restricted to the early season.

Males prefer to help competent females.—Males fed at 30 out of 42 (71%) experimental nests but only 2 out of 10 (20%) starvation-reduced nests (Fisher exact test, $P = 0.004$). I used only primary nests in the analysis to control for differences in nest rank between groups. Primary experimental nests were initiated on the Julian date of 126.5 ± 5.0 (1 May corresponds to a Julian date of 121.0), while primary starvation-reduced nests were initiated on 129.2 ± 5.4. The difference was not significant (t-test, $t = 1.48$, 50 df, $P > 0.10$). Initiation date had no apparent effect on the probability that a primary nest received male care in this population. When the period of nest initiation was divided into 3 intervals of equal length, there was no significant difference between intervals in the probability that unreduced primary broods were fed by males ($G = 0.08$, 2 df, $P > 0.7$).

Considering all experimental and starvation-reduced nests together, males fed young in 33 out of 70 (47%) experimental nests and 22 out of 59 (37%) starvation-reduced nests. This difference was not significant ($\chi^2 = 1.27$, 1 df, $P > 0.1$). However, the result is misleading because on territories where both primary and secondary nests were reduced, parental males fed only a single brood, usually the primary. Males continued to feed at the primary nest when sec-

ondary nests were observed (25 of 28 cases). Inclusion of secondary nests greatly reduced the proportion of experimental broods fed. To control for this, I considered only experimental and starvation-reduced nests on territories where males were not simultaneously feeding older young. In this case, males fed young in 33 out of 49 (67%) experimental nests but in only 12 out of 33 (36%) starvation-reduced nests ($\chi^2 = 7.4$, 1 df, $P < 0.025$). The difference is difficult to interpret because experimental nests belonged mostly to primary females, in contrast to starvation-reduced nests (Fig. 2), and males had a greater probability of feeding primary broods (Gori 1984). Stronger evidence that males preferred to feed young of competent females comes from the comparison among primary nests.

Males fed young of competent females at a higher rate than young of incompetent females. For reduced broods that received male care and had 2 young at the time of nest observation, males made 4.8 ± 3.3 trips/h to experimentally reduced ($n = 33$) and 2.1 ± 1.0 trips/h to starvation-reduced nests ($n = 22$). The difference was significant when I controlled for the effect of nest rank and initiation date in a stepwise multiple regression. Treatment, entered as a "dummy" variable, explained 20% of the variation in male feeding rates ($F_{1,53} = 12.8$, $P < 0.001$). Initiation date and rank had no significant effect on male feeding rates at reduced nests (initiation date: partial $r = 0.20$, $P > 0.2$; nest rank: partial $r = .04$, $P > 0.5$). Furthermore, males fed young in starvation-reduced nests at

TABLE 2. Effect of availability of nests of competent females on helping by males.[1]

	Helped	Not helped
Starvation-reduced nests (nests of competent females available)	5	25
Starvation-reduced nests (nests of competent females unavailable)	17	12

[1] $\chi^2 = 11.1$, 1 df, $P < 0.001$.

the same rate regardless of whether they were still feeding older young (fledglings) on the territory (2.3 ± 1.0 trips/h for males not feeding older young [$n = 12$] vs. 1.9 ± 0.9 trips/h for males still feeding older young [$n = 10$], $t = 0.95$, 20 df, $P > 0.2$). Thus, the reduced feeding rate of males at starvation-reduced nests was not because they fed other young. Most males had stopped feeding older young before initiating care at starvation-reduced nests, although some were still feeding fledglings at extremely low rates.

Decreased investment at starvation-reduced nests may result if incompetent females were more likely to be mated to parentally incompetent males. To test this, I compared feeding rates to unreduced broods (i.e. 3–4 young) for males that fed at starvation-reduced nests and for those that fed at experimental nests. Males that helped at experimental nests fed unreduced broods at 5.6 ± 3.1 trips/h. Males that helped starvation-reduced nests fed unreduced broods at 6.8 ± 5.8 trips/h. This difference was not significant (t-test, $t = 0.64$, 45 df, $P > 0.5$). There was no difference in the number of young fledged from the unreduced nests (2.8 ± 0.6 young/nest for "experimental" males vs. 2.9 ± 0.6 young/nest for "starvation-reduced" males; $t = 0.6$, 45 df, $P > 0.5$) and no difference in the mass of young at fledging (ANOVA: males, $F_{1,51} = 0.07$, $P > 0.7$, females, $F_{1,63} = 0.001$, $P > 0.9$). Males that helped at starvation-reduced nests were as competent at feeding and raising 3–4 young as males that helped at experimental nests.

Males had a greater probability of feeding starvation-reduced broods when experimental or unreduced nests were unavailable on the territory (Table 2). A nest was considered to be "available" for male care if it contained young that were 5 days or older. When unreduced nests became available for care at a later time, in 11 of 12 cases, males stopped feeding at starvation-reduced nests and commenced feeding at unreduced ones.

Male investment functions.—I constructed in-

vestment functions for experimental and starvation-reduced nests to examine the basis of male preference for helping parentally competent females. I tested the hypothesis that males preferred to help competent females raise young because the return per unit of their investment was greater at these nests. I used 2 measures for the return on investment, the number of young fledged/nest and fledgling mass. I plotted each of these against male feeding rate. Broods that received no male aid were assigned values of zero for male investment. The hypothesis predicts that the slope of the investment function for experimental nests will be greater than the slope for starvation-reduced nests. The outcome is statistically independent of the fact that males fed a greater proportion of experimental broods and fed them at a greater rate than starvation-reduced broods. These results determine only what values the independent variable, male feeding rate, takes for the 2 groups. However, the fact that male feeding rates were greater for experimental nests does not mean that the slope of the investment function will also be greater because the slope measures the rate of change of the dependent variable (fledging success or fledging mass) per *unit* change of the independent variable (male feeding rate). The slope for experimental nests may be greater, smaller, or equal to the slope for starvation-reduced nests depending on how an incremental increase in feeding rate affects fledging success and fledging mass in experimental vs. starvation-reduced nests.

For the analysis of fledging mass, I used only nests that produced 2 young (for sample sizes, see Figs. 3, 4). Fledging mass was normalized according to sex and year to control for differences in male and female young, and variation in marsh productivity between years. I calculated sex-specific mass averages for each treatment and year using only broods that received no male care. Young from experimental broods that received no male care were, on average, 4 g heavier at fledging than young from starvation-reduced nests (Table 1). Then, for all broods,
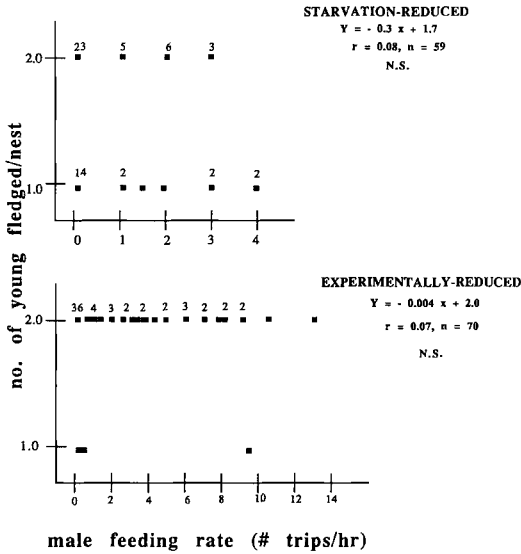
Fig. 3. Relationship between male parental investment (hourly feeding rate) and fledging success for starvation-reduced and experimentally reduced nests. All nests contained 2 young at time of observation.
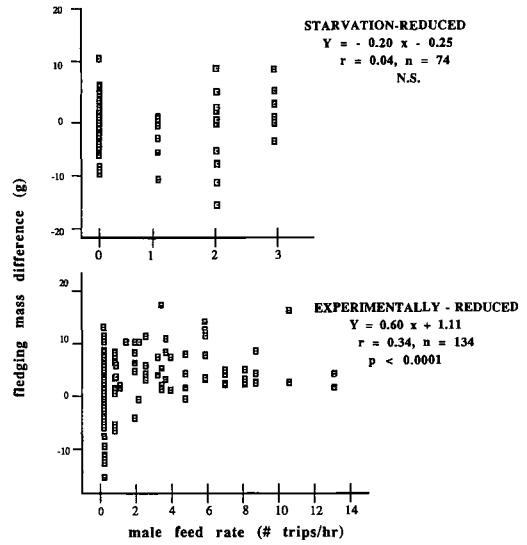

Fig. 4. Relationship between male parental investment and fledging mass of young from starvation-reduced and experimentally reduced nests. Fledging mass difference is the difference between an individual's fledging mass and the mean mass appropriate for its sex, treatment, and year. Mean masses were calculated using nests that fledged 2 young but received no male care: 23 starvation-reduced and 36 experimental nests (see text).

including those receiving male care, I determined the difference between an individual's fledging mass and the calculated mean appropriate for its sex, year and treatment. I then plotted these values against male feeding rates. If male feeding increased the fledging mass of young, these values should be positive and increase with increasing male investment.

There was no significant relationship between male feeding rate and the number of young fledged/nest for either experimental or starvation-reduced nests (Fig. 3). Furthermore, there was no difference between the regression slopes for experimental and starvation-reduced nests ($t = 0.78$, 125 df, $P > 0.4$). Fledging mass difference, however, was positively correlated with male feeding rate for experimentally reduced nests, but there was no significant correlation for starvation-reduced nests (Fig. 4). The regression slope for experimental nests was significantly greater than that for starvation-reduced nests using a one-tailed test ($t = 1.71$, 204 df, $P < 0.05$). In addition, the proportion of positive mass differences was significantly greater for experimental broods that received male care than for starvation-reduced broods that received care (Table 3). I used only experimental broods that received 3 or fewer male

feeding trips/h in this analysis (3 trips/h was the maximum feeding rate at starvation-reduced nests that produced 2 young) to control for differences in feeding rates between the groups. Male feeding rates were equal for the two groups (1.7 ± 0.8 trips/h at experimental nests vs. 1.9 ± 0.8 trips/h at starvation-reduced nests, $t = 0.6$, 24 df, $P > 0.5$). I believe that males prefer to raise the young of competent mates because they have a greater effect on the fledging mass of these young.

DISCUSSION

Male yellowheads appear to distinguish parentally competent and incompetent mates independently of the number of young in the nests. Males had a greater probability of feeding young in experimental nests and they also fed these broods at a greater rate than broods in starvation-reduced nests. In theory, preference for raising the young of competent females should arise if males obtained greater returns in fitness per unit of their investment (Trivers 1972, Patterson et al. 1980). I tested this hy-

TABLE 3. Effect of male care on fledging mass of young in experimental and starvation-reduced nests.[a]

	Fledging mass of young	
	$>\bar{M}$[b]	$<\bar{M}$
Experimental nests	19	5
Starvation-reduced nests	13	15

[a] $\chi^2 = 5.9$, 1 df, $P < 0.025$.
[b] Mean mass of young from unassisted nests.

pothesis by constructing investment functions for experimental and starvation-reduced nests. I estimated the returns on the investment using two commonly used components of reproductive success in birds: the number of young fledged/nest and the fledging mass of young. Consistent with the hypothesis, males increased the fledging mass of young in experimental nests more per unit of their investment than they did at starvation-reduced nests. This occurred independent of the fact that males fed young in starvation-reduced nests at a lower rate than young in experimental nests. When the analysis was restricted to broods that males fed at a rate of 3 trips/h or less, males were more likely to increase the fledging mass of young by helping competent females than by helping incompetent ones. In yellowheads, heavier young were more likely to survive through the post-fledging period of parental dependency and were also more likely to breed in subsequent years than lighter young (unpubl. data). A similar condition occurs in Great Tits (*Parus major*; Perrins 1965).

The results raise the question of why male feeding had a reduced effect on the fledging mass of young in incompetent females' nests. There are 3 possible explanations. First, incompetent females may be mated to parentally incompetent males. This possibility was rejected because males that helped at starvation-reduced and experimental nests both fed unreduced broods at the same rate. In addition, there was no difference in the number of young fledged from these unreduced nests or in the fledging mass of young.

Second, male feeding may have a reduced effect at starvation-reduced nests if incompetent females produced incompetent young. There is no direct evidence to support this hypothesis, although it provides an explanation for the lower feeding rate of males at starvation-reduced nests. If young were genetically infe-

rior and had a low probability of survivorship, large parental investments by males would result in negligible returns. Males then could benefit more by devoting time and energy to territory defense or feeding themselves than to feeding young. However, after the former activities are fulfilled, feeding young at low rates would have minimal costs but may have some small but significant advantage. A number of theoretical studies have proposed that females may select mates based on the vigor of their displays or the elaboration of body ornaments because they are reliable indicators of male genetic quality (Andersson 1982, Nur and Hasson 1984, Kodric-Brown and Brown 1984). It is also possible that males may adjust their parental investment with female parental competence if the latter reflects the overall genetic quality of offspring produced.

Third, male feeding may have a reduced effect on the fledging mass of young in starvation-reduced nests if the development of young in these nests was delayed relative to experimental nests. Because of the delay, young in starvation-reduced nests may have devoted more energy to feather production and thermoregulation, leaving less energy available for weight gain (Richter 1983). This explanation does not account for the lower feeding rates of males at starvation-reduced nests.

The relationship between male feeding and fledging mass for experimental broods that received male care is not a linear one (Fig. 4). Fledging mass increased rapidly with male feeding rate until a rate of 4 trips/h (slope = 1.9, $r = 0.36$, 33 df, $P < 0.04$) and then leveled off (slope = -0.02, $r = 0.01$, 27 df, $P > 0.9$). This implies that there may be a threshold mass above which survivorship does not increase and that males adjust their feeding rates so that young of competent females reach this threshold. There is currently no evidence to support this interpretation.

Despite the correlation between mate quality and the number of young in nests on day 6, the ability to assess the parental abilities of mates would be advantageous for males if parental competence also varied within broods of a given size. This variation is likely to exist for the following reasons. First, individuals in the population probably show continuous variation for parental competence while the number of young in nests is discrete. Second, extremes in weather and food availability may affect the survivor-

ship of young in nests independently of the ability of females to feed them. Third, the food demands of young continue to increase after day 6 and peak before fledging (Hussell 1972, Ricklefs 1974, Richter 1983). As a result of these factors, females with the same number of young in nests on day 6 will vary with respect to their competence at raising them. Males benefit by distinguishing both the number of young in nests and the ability of females to raise them.

There is some evidence that male yellow-heads can distinguish the number of young in nests. Broods of 3-4 young have a greater probability of receiving male care than broods with 2 young. This preference presumably arises because males can fledge greater numbers of young/unit of investment when feeding nests with 3-4 young (Patterson et al. 1980, Gori 1984). In Red-winged Blackbirds, males also appear to assess the number of nestlings. Females assisted by males had significantly larger broods on day 5 than unassisted females. There was no significant difference in female feeding rates (parental competence) prior to the onset of male feeding (Muldal et al. 1986).

The cues used by male yellowheads to assess parental competence are unknown, although individuals may monitor the food delivery rate of the female or how well-fed the young look. Males often enter nests without food, initiate begging by young, and then leave several seconds later either to resume activity on the territory or to forage for young. Males may use the intensity of food-begging calls to assess parental competence because hungry young beg louder and longer than surfeit ones (Henderson 1975, Bengtsson and Ryden 1983). Begging calls by nestlings were often louder and more persistant at starvation-reduced nests than at experimental nests.

The determinants of parental competence in yellowheads are currently unknown. Parental competence may reflect a female's overall genetic quality or may be a function of age and breeding experience. The proportion of starvation-reduced nests increased with female nesting order on territories and initiation date. These results are consistent with previous studies that show greater nesting success for early breeders (Paynter 1949; Richdale 1957, 1963; Kluijver 1951; Coulson and White 1956, 1958; Davis 1957; Snow 1958; Perrins 1965, 1966, 1970; Potts 1966; Nelson 1966; Coulson 1966; Lack 1966, 1968; Goddard and Board 1967; Haartman

1967; O'Donald 1972; Martin 1974; Davis 1976; Crawford 1977). Early breeders tend to be older, more experienced, and in better physical condition than late breeders and thus may be more competent as parents. In yellowheads, older females have brighter plumage than yearlings (Crawford 1977) and in eastern Washington, the chest and throat feathers of early-nesting female yellowheads appeared brighter than those of later-nesting females (pers. observ.). Thus, some starvation-reduced nests may belong to yearling females. Further studies are needed to determine the causes of parental incompetence in females which may be a function of a female's genetic quality or of breeding experience.

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