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RELATIVE PARENTAL INVESTMENT IN THE RED-WINGED BLACKBIRD

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Abstract.—The parental investment and reproductive success of male Red-winged Blackbirds (*Agelaius phoeniceus*) that fed some of their broods were compared to those of males that did not feed nestlings. Pair-fed nestlings experienced a higher rate of food delivery, showed a significantly faster rate of growth and were less likely to starve than nestlings fed only by females. Thus pair-fed broods produced significantly more fledglings than female-fed broods. Feeding and non-feeding males attracted equal numbers of mates, on average, and their time budgets did not differ significantly, but feeding males tended to be older and more experienced than non-feeding males, and their territories had significantly higher insect emergence than those of non-feeding males. Feeding males produced on average two more young per year than non-feeding males. Feeding males did not feed all of their broods, but generally fed the first brood that hatched on their territories. These pair-fed broods were significantly larger than broods fed only by females paired with feeding males. In addition, pair-fed broods tended to be associated with the oldest females. Thus male parental investment appears to be advantageous, and males appear to be investing in the broods with the highest reproductive value.

INVERSIÓN PARENTAL RELATIVA EN *AGELAIUS PHOENICEUS*

Sinopsis.—Se comparó la inversión parental y el éxito reproductivo de machos de *Agelaius phoeniceus* que alimentaban algunos de sus crías con otros que no lo hacían. Polluelos que fueron alimentados por ambos padres recibieron mayor cantidad de comida, mostraron una tasa de crecimiento mayor y fueron menos propensos a estar hambrientos que polluelos que tan solo fueron alimentados por hembras. Como consecuencia, las camadas alimentadas por ambos padres produjeron más volantones que las camadas atendidas solo por hembras. Machos alimentarios y no-alimentistas atrayeron (en promedio) igual número de hembras y su presupuesto de tiempo invertido no diferió significativamente. Los machos alimentarios tendieron a ser de mayor edad y de más experiencia que los no-alimentistas y sus territorios contuvieron un número significativamente mayor de insectos que los territorios de machos no-alimentistas. Los machos que alimentaron polluelos produjeron un promedio de dos pichones más por año que los machos no-alimentistas. Los machos alimentarios no alimentaron a todas las camadas producidas; por lo general su esfuerzo fue dirigido a la primera camada producida en su territorio. Estas camadas alimentadas por ambos padres, resultaron

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ser significativamente mayor que las camadas alimentadas por hembras apareadas con machos alimentistas. Estas camadas además resultaron estar asociadas a las hembras de mayor edad. La inversión parental por parte de los machos parece ser ventajosa, y estos parecen estar invirtiendo en las camadas con el más alto valor reproductivo.

I studied a population of Red-winged Blackbirds (*Agelaius phoeniceus*) in central Indiana to investigate patterns of male parental investment. Male Red-winged Blackbirds are territorial and polygynous, and many previous studies have reported that they rarely feed nestlings (e.g., Holm 1973, Orians 1961, Robertson 1973). Several recent studies, however, have shown that males in some populations regularly feed nestlings (e.g., Muldal et al. 1986, Whittingham 1989, Yasukawa et al. 1990). In such populations, where some males provide food for some broods, the costs and benefits associated with male feeding of nestlings could be compared.

Studies of reproductive ecology have generally dealt with the maximization of overall reproductive effort, but reproductive effort can be divided into two conflicting components: mating effort, which affects the number of young produced, and parental effort, which affects the quality of offspring. These two components can shift in importance in differing environments (Low 1978), and individuals should allocate effort to parental care or mate attraction to maximize their total reproductive output.

Clearly, optimal cost-benefit ratios are likely to differ between males and females (Trivers 1972). Because of anisogamy, females are usually selected to invest heavily in parental care. For males more often than females, however, both parental behavior and attraction of additional mates can contribute to reproductive success. Males should have a greater range of options in adjusting their investments to maximize their overall fitness.

Selection also operates within each component. Given that the optimal strategy for some males is to divide energy between mate attraction and parental care, selection should favor the allocation of investment among different broods that maximizes the benefits of parental effort. In this investigation I address the following three questions. To what extent do males differ in parental and mating effort? To what extent is reproductive success affected by these differences? How do males distribute their parental effort among broods?

STUDY AREA AND METHODS

I conducted field work during the breeding seasons of 1974–1976 at the marshes of Yellowwood Lake in Yellowwood State Forest, Brown County, Indiana. The lake was bounded by mixed deciduous forest, which was interspersed with small pine plantations and mowed campground. Emergent vegetation remained fairly constant in extent and composition throughout my study, and consisted mainly of cattail (*Typha latifolia*), burreed (*Sparganium eurycarpum*) and bullrush (*Scirpus validus*). The lake was drained completely during the winter of 1976.

Birds were trapped in decoy traps and Potter traps baited with cracked corn, and were banded with USFWS numbered bands and a unique

combination of colored plastic bands. During the study, 92% of the residents were banded. Males were classified by epaulet coloration as either second-year or "adult." Males banded as adults were assigned a minimum age of 2 yr in the year of capture; males banded as second-year birds or nestlings were assigned their true ages. Females, which breed in the year following hatching (in the second year), were assigned a minimum age of 1 yr when first captured as adults. Prior to 1974, banding and aging had been carried out in independent studies by W. H. Barnard and V. Nolan, Jr.

Throughout the nesting season, which began in late April, I searched the marsh regularly to locate nests. Virtually all nests were found during construction or early egg-laying. Each nest was visited once daily at approximately the same time, and its state, contents and associated male and female were recorded. Each day I weighed individual nestlings to the nearest 0.5 g with a Pesola spring balance. On day 6–8 of the nestling period (day 1 was hatching day) I banded nestlings with USFWS numbered bands and, as a precaution against premature fledging, did not handle them thereafter. Nest failure, the total loss of young, was attributed to starvation or predation, which were distinguishable by condition of nest, nestling growth rate and timing of disappearance of young. Successful nests produced at least one fledgling.

During the nestling stage, I observed nests regularly for 1-h periods to record the number of food deliveries, but not number of items per delivery, by each parent. In 1976 I collared young (Willson 1966) in each brood for 1 h on day 7 of the nestling period. Food samples collected in this way were sorted according to taxonomic Order. Percentages by Order of food items were calculated on the basis of number of large body fragments.

In 1976 I measured insect emergence on each territory twice a week throughout the nesting season using standard insect emergence traps. Samples were preserved in alcohol and sorted by Order. Nestling sex was determined by weight after day 5 of the nestling period (Fiala 1981, Holcomb and Twiest 1970, Williams 1940). Data on male time budgets and territory size were provided by K. Yasukawa (1979). Data for each of the 3 yr of the study were treated separately because many individuals in the population were present for more than 1 yr.

RESULTS

Male Parental Effort

Feeding rate.—In 1974–1976, 60% (6/10), 64% (7/11) and 54% (7/13), respectively, of the territorial males I observed fed one or more broods. Males generally did not start feeding until day 4 of the nestling period and their feeding rates were considerably lower than those of females (Fig. 1). Food delivery rates of females assisted by males and rates of females that fed alone were not significantly different at any nestling age in either 1974 or 1975. The combined feeding rate of males and their

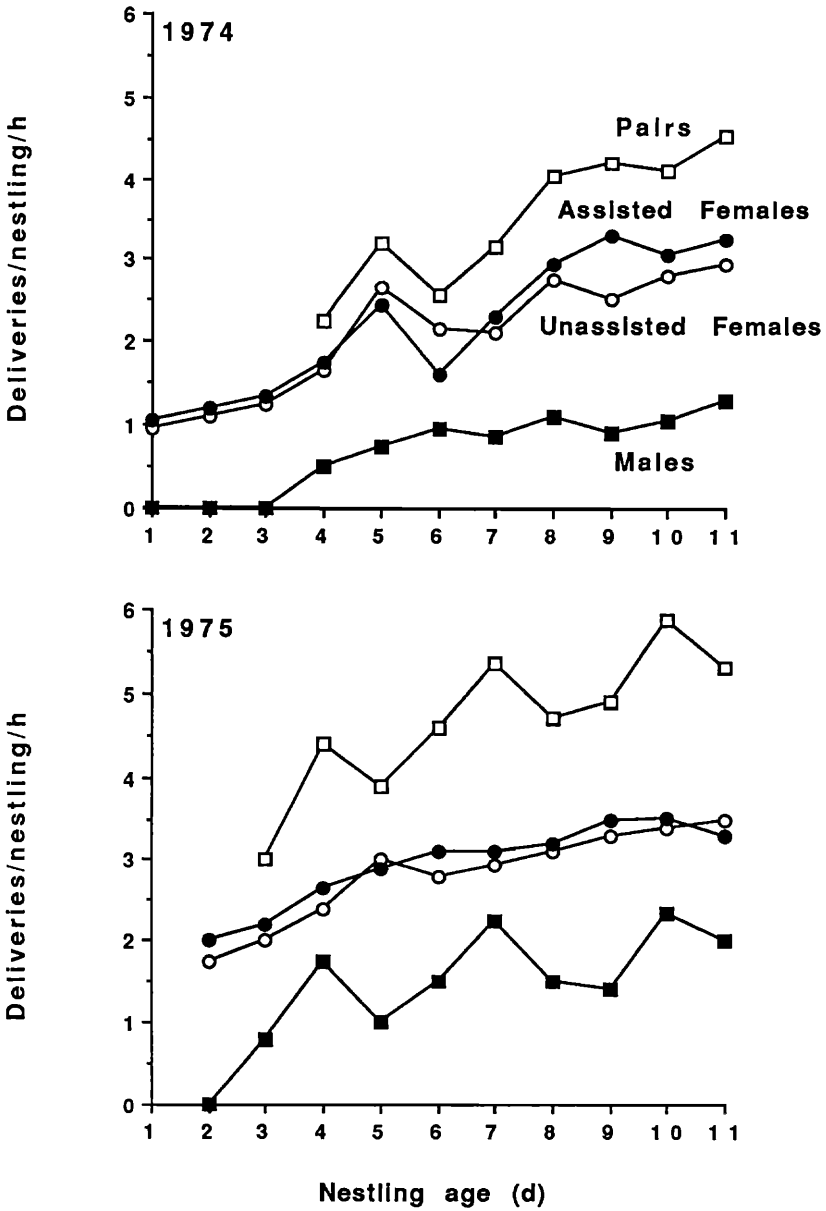


FIGURE 1. Feeding rates (deliveries/nestling/h) of male and female Red-winged Black-birds.

TABLE 1. Percent composition according to Order of food samples brought to Red-winged Blackbird nestlings.

	Territories of feeding males	Territories of non-feeding males
Odonata	55	25
Anisoptera	30	7
Zygotera	25	18
Diptera	23	38
Coleoptera	2	15
Lepidoptera	20	12
Other	—	10

assisted females was significantly higher than the rate of unassisted females every day of the nestling period (Fig. 1).

Food composition.—Food brought to nestlings appeared to differ according to sex of parent (Table 1). Samples brought by both parents contained a larger percentage of odonates and lepidopterans than samples brought only by females. Samples brought by unassisted females nesting on territories of feeding males contained a larger percentage of odonates than samples brought by females nesting on territories of non-feeding males.

Male Mating Effort

Male time budget.—Time budgets of feeding and non-feeding males differed little (Table 2). Proportions of time on territory were similar in all 3 yr. In 1976, feeding males spent significantly more time singing and less time foraging than non-feeding males, but these differences were not significant in 1974 and 1975, and the direction of difference varied among years. The one significant difference therefore appears to be spurious.

Although males from the two groups sang at the same rate, the intensities of the displays accompanying those songs were significantly different. Feeding males had lower intensity Song-Spread displays (see Nero 1956, Yasukawa 1979) than non-feeding males.

Territory size.—Feeding males tended to have larger territories than non-feeding males, both in area of emergent vegetation, where suitable nest sites were located, and in other defended area (Table 3). These differences were statistically significant only in 1975, but the direction of differences was the same in all years. In addition, territories of feeding males contained more edge (interface between emergent vegetation and open water), which has been shown to correlate with insect abundance (Orians 1980).

Harem size.—Harem size is defined here as maximum number of females nesting simultaneously on a male's territory. Although females can and occasionally do copulate with males other than the owners of the territories on which they nest (Bray et al. 1975), the majority of copulations is with the territory holder (Monnett et al. 1984). Thus, harem

TABLE 2. Singing behavior and time budget of feeding and non-feeding male Red-winged Blackbirds. Values shown are medians for feeding and non-feeding males.

	1974	1975	1976
Song rate (number/min)			
Feeding males	2.56	2.82	3.49
Non-feeding males	2.20	3.16	3.58
Song Spread intensity ^a			
Feeding males	0.23	0.42	0.28
Non-feeding males	0.82**	0.71*	0.61*
Proportion of time spent on territory			
Feeding males	0.92	0.86	0.87
Non-feeding males	0.93	0.86	0.80
Proportion of time on territory spent singing and defending			
Feeding males	0.56	0.56	0.67
Non-feeding males	0.57	0.58	0.61*
Proportion of time on territory spent foraging			
Feeding males	0.32	0.35	0.24
Non-feeding males	0.35	0.33	0.33*

^a Song Spread display was divided into four categories based on degree of wing extension: incipient, low, median and high (see Yasukawa 1979).

* $P < 0.05$; ** $P < 0.01$ (Mann-Whitney U -test).

size is an important measure of male success in obtaining mates. In no year did significant differences exist in average harem size between feeding and non-feeding males (Table 4).

Reproductive Success as a Function of Parental Effort

Nestling growth.—Figure 2 compares growth rates of nestlings fed by both male and female with growth rates of nestlings fed only by the female. For the first 3 d after hatching, nestlings grew at approximately the same rate. Starting on day 4, when males began feeding nestlings, weights of the two groups began to diverge sharply, with pair-fed nestlings tending to be heavier than nestlings fed only by the female. By day 5, pair-fed nestlings weighed significantly more than female-fed nestlings. To determine if these differences were caused by male feeding or by territory quality and/or genetic effects, weights of female-fed nestlings on territories where the male fed some broods were compared to weights of female-fed nestlings whose male parent fed no broods (Fig. 3). The weight differences in these two groups were not significant.

Brood reduction.—In many species, initial clutch size exceeds the number of young that successfully leave the nest as a result of asynchronous hatching and thus differential investment in young. This result is generally referred to as brood reduction (Lack 1947, O'Connor 1978). In all three years pair-fed broods lost significantly fewer young per nest than female-fed broods (Table 5). In 1976, significantly fewer pair-fed broods than

TABLE 3. Characteristics of territories of male Red-winged Blackbirds. Values shown are medians for feeding and non-feeding males.

	1974	1975	1976
Emergent vegetation (m ²) ^a			
Feeding males	416	417	322
Non-feeding males	400	205*	240
Other defended area (m ²) ^b			
Feeding males	1190	1307	1020
Non-feeding males	770	788†	564
Edge (m) ^c			
Feeding males	59	60	45
Non-feeding males	54	46†	39

^a Portion of territory where nests were constructed; included cattail, bulrush and burreed.

^b Portion of territory excluding emergent vegetation.

^c Interface between emergent vegetation and open water.

* $P < 0.05$; † $P < 0.10$ (Mann-Whitney U -test).

female-fed broods suffered some starvation (Table 5). When analysis was restricted to female-fed broods from territories of feeding and non-feeding males, I found no significant differences for either measure of brood reduction in any year (Table 6).

Predation.—Predation was the other major cause of nestling mortality in my population. When I limited analysis to broods surviving beyond day 4 of the nestling period, so I could determine whether males would

TABLE 4. Characteristics of male Red-winged Blackbirds. Values shown are medians for feeding and non-feeding males.

	1974	1975	1976
Harem size ^a			
Feeding males	3.3	3.4	3.3
Non-feeding males	3.8	2.8	2.8
Number of fledglings			
Feeding males	7.5	8.0	5.0
Non-feeding males	8.0	6.0*	3.5*
Age (yr) ^b			
Feeding males	4.0	4.0	4.0
Non-feeding males	2.5	2.5	2.0*
Breeding experience (yr) ^c			
Feeding males	1.0	1.0	2.0
Non-feeding males	0.0	0.0	0.0*

^a Maximum number of simultaneously active nests on a territory.

^b Males captured as "adults" were assigned a minimum age of 2 yr.

^c Number of years prior to observation a male defended a territory on the study area.

* $P < 0.05$ (Mann-Whitney U -test).

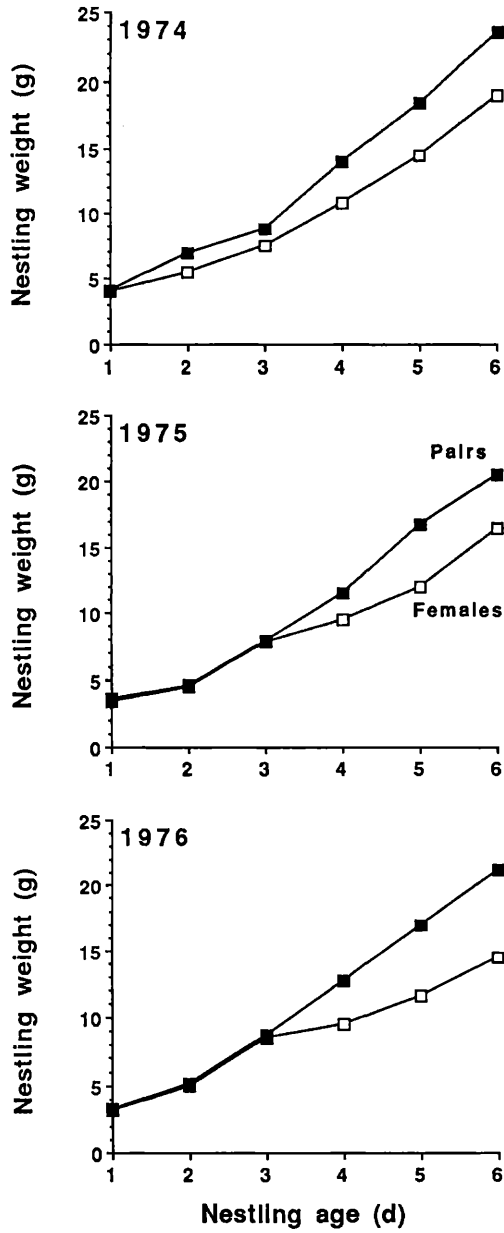


FIGURE 2. Weight gain of nestling Red-winged Blackbirds fed only by females, and by both males and females.

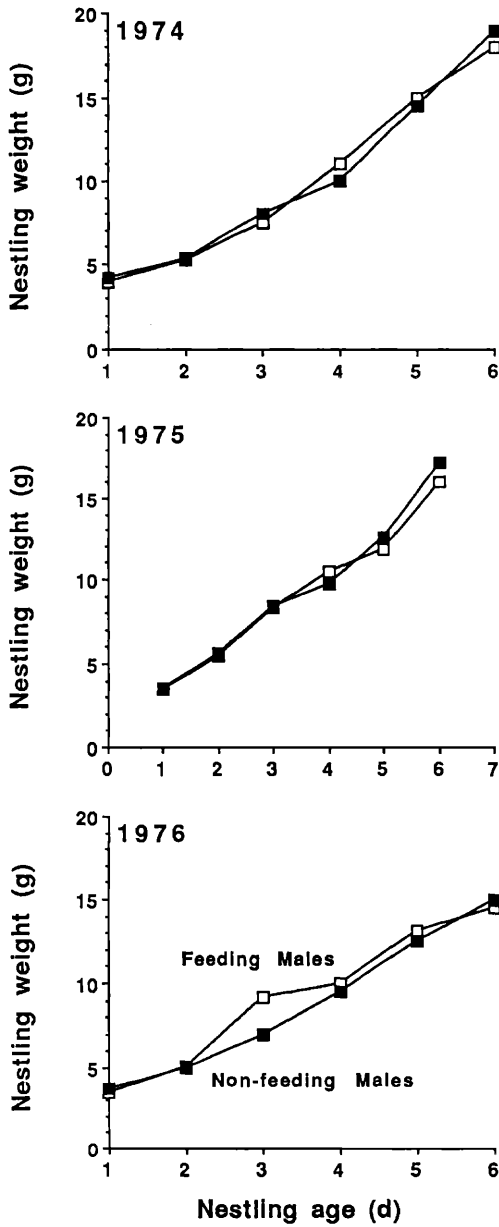


FIGURE 3. Weight gain of nestlings fed only by female Red-winged Blackbirds nesting on territories of feeding and non-feeding males.

TABLE 5. Characteristics of Red-winged Blackbird broods. Values shown are medians for pair-fed and female-fed broods.

	1974	1975	1976
Brood reduction (number/brood)			
Pair-fed broods	0.25	0.22	0.36
Female-fed broods	0.56†	0.69*	2.09**
Nests with some starvation (%)			
Pair-fed broods	25	22	27
Female-fed broods	44	50	88**
Predation (%)			
Pair-fed broods	8	11	9
Female-fed broods	33	12	11
Number of fledglings			
Pair-fed broods	2.5	3.0	3.0
Female-fed broods	2.0*	2.0**	1.0**

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$ (Mann-Whitney U -test).

feed, pair-fed broods consistently suffered less predation than female-fed broods, but the differences were not significant (Table 5). These data, however, were not a measure of total nest predation. When I considered all nests that received eggs, broods on territories of feeding and non-feeding males did not differ significantly in amount of predation (1974: 52% vs. 47%, 1975: 15% vs. 31%, 1976: 31% vs. 27%).

Fledging success.—Fledging success is defined here as number of fledglings produced per nest. When I again analyzed only broods surviving beyond day 4 of the nestling period, pair-fed broods produced significantly more young than female-fed broods in each study year (Table 5). When I compared female-fed broods on territories of non-feeding males with female-fed broods on territories of feeding males, only in 1974 were there significant differences between the two groups. In that year female-fed broods of non-feeding males produced more young than such broods of feeding males (Table 6).

Male Reproductive Success

There was a significant, positive correlation between harem size and male reproductive success over the 3 yr of the study (Fig. 4). In 1974 the difference in number of young produced by feeding and non-feeding males was not significant, but in 1975 and 1976, feeding males produced significantly more young than non-feeding males (Table 4).

Characteristics of Feeding and Non-feeding Males

Age and experience.—Feeding males tended to be older and to have more breeding experience at Yellowwood Lake than non-feeding males (Table 4). Although differences between the two groups in 1974 and

TABLE 6. Characteristics of female-fed Red-winged Blackbird broods. Values shown are medians for broods of feeding and non-feeding males.

Category	1974	1975	1976
Nestlings starved/brood			
Broods of feeding males ^a	0.40	0.43	1.80
Broods of non-feeding males	0.67	1.00	2.35
% of broods with some starvation			
Broods of feeding males	30	36	80
Broods of non-feeding males	53	67	94
Number of fledglings/brood			
Broods of feeding males	1.0	2.0	1.0
Broods of non-feeding males	2.0*	2.0	1.0

^a Broods fed only by females that nested on territories of males that fed nestlings of other broods.

* $P < 0.05$ (Mann-Whitney U -test).

1975 were considerable, they were not statistically significant. In 1976, however, the differences were significant.

Territorial characteristics.—Territories of feeding males had significantly greater insect emergence, especially of larger odonates (Anisoptera), per unit area than those of non-feeding male (Table 7). Coupled with their somewhat larger territories, feeding males had greater total insect emergence than non-feeding males.

Brood Assisted by the Male

Brood order.—Feeding males preferentially assisted their first-hatched broods (the broods of primary females). In only 3 of 20 cases did males first feed non-primary broods. In two of these three, the first nest that received eggs was lost to predation before the eggs hatched, and the males later fed the broods produced when their primary females re-nested. This suggests that males were also influenced by characteristics of females in selecting broods to feed.

Female age.—When I considered only color-banded females, male-assisted females tended to be older than females that nested on territories of feeding males but were not assisted by them. In 1974 and 1975 the differences were significant (3.0 vs. 2.0 and 4.0 vs. 3.0, respectively), but I found no significant age difference between these two groups in 1976 (both 2.0).

Brood size.—Considering only territories of feeding males, pair-fed broods were significantly larger than female-fed broods in 1974 (3.5 vs. 3.0) and 1975 (4.0 vs. 3.0). In 1976, however, there was no significant difference between the two groups (both 3.0).

Nestling sex ratio.—Brood sex ratios did not deviate significantly from 1:1 despite a bias toward males in pair-fed broods (0.59 of 27 and 0.65 of 23 nestlings were male in 1975 and 1976, respectively) and toward

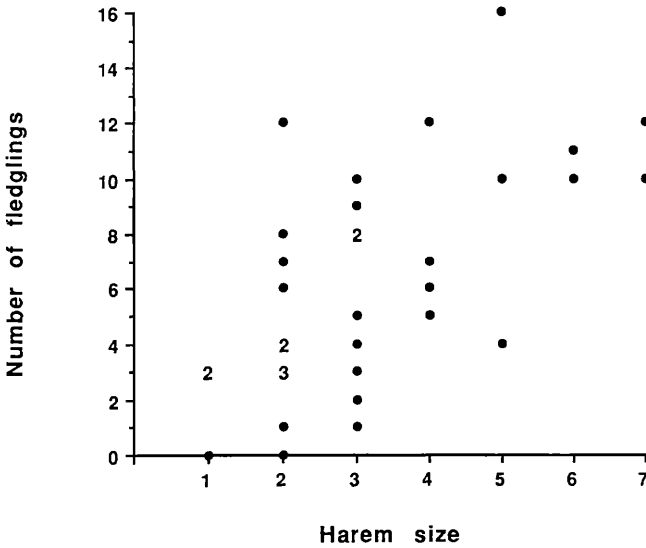


FIGURE 4. Relationship between male Red-winged Blackbird reproductive success (number of fledglings) and harem size (maximum number of simultaneously active nests). Spearman rank correlation $r_s = 0.624$, $P < 0.05$.

females in female-fed broods (0.42 of 28 and 0.43 of 21 nestlings were male in 1975 and 1976, respectively) on territories of feeding males.

DISCUSSION

Differences Among Males in Mating and Parental Effort

Substantial differences existed in investment strategies of male Red-winged Blackbirds in my population, with some investing considerably more parental effort than others. Investment in parental care did not appear to cause a decrease in mating effort or mating success, however. Both feeding and non-feeding males apportioned considerable amounts of time to territory defense, and feeding males acquired territories that were, if anything, larger than those of non-feeding males. The two groups also attracted similar numbers of females. Thus the only difference in reproductive effort between the two groups of males appeared to be parental effort.

Reproductive Effort and Reproductive Success

Pair-fed broods received significantly more food than female-fed broods because females fed at the same (presumably maximal) rate regardless of whether males fed. The result was a faster nestling growth rate, and the weight advantage enjoyed by pair-fed nestlings resulted in a significant reduction in nestling starvation when compared with female-fed broods.

TABLE 7. Insect emergence (mean/m²/d) on territories of feeding and non-feeding male Red-winged Blackbirds.

	Feeding males	Non-feeding males
Odonata	0.8	0.4*
Anisoptera	0.1	0.01*
Zygotera	0.7	0.4*
Diptera	3.1	2.5
Ephemeroptera	2.3	1.5*

* $P < 0.05$ (Mann-Whitney U -test).

Coupled with similar rates of predation on the two groups, pair-fed broods experienced higher fledgling success than female-fed broods.

Comparison of data from 1975 and 1976 is especially striking. Brood reduction in pair-fed broods was only slightly higher in 1975. Insect productivity was probably lowest in 1976, as drainage of the lake and marsh during the winter almost certainly reduced populations of insects that overwinter as late instars. Thereafter, erratic spring weather probably kept insect availability low during critical nestling stages. In addition, because of cool, rainy weather in 1976, females brooded for much longer periods than in 1975. All these circumstances would increase the importance of male feeding.

Frequency of food deliveries, however, is not the only parameter of feeding effort. Type of food could also be important. Although Orians (1973) demonstrated a positive correlation between amount of food brought to nestlings and nestling growth and success, the correlation is probably not perfect. Tempo of feeding trips can alter food quality (Martin 1974), and males and females may differ in types of food brought (Nice 1943, Willson 1966).

As I have already shown, rate of female feeding was not altered by male feeding in my population. Males did, however, bring larger food items than females. Males would be expected to take larger prey, as they are approximately 50% heavier than females. In addition, because they fed young at a slower rate than females, males might be more selective in prey capture. Thus, young fed by both parents would presumably receive more average value per item delivered than young fed only by females. In addition, utilization of different food resources could prevent overlap in male and female foraging, and thus increase the food reservoir available to offspring.

Mating effort obviously also influences male reproductive success. The reproductive advantage of polygyny has been amply demonstrated in birds (e.g., Carey and Nolan 1975, Holm 1973, Searcy 1979) and was shown also for my population. In addition, male feeding effort increased the fledging rate of pair-fed broods, particularly in the year of low resources, so that feeding males realized a greater total reproductive success than non-feeding males. In 1975 and 1976, feeding males produced an average of two more young per season, a 25–30% yearly increase in reproductive

output. In those years the benefits of increased parental effort were quite high. In 1974, increased parental effort did not result in increased reproductive output. Heavy spring rains and flooding caused higher mortality of nestlings on territories of feeding males than of non-feeding males. Environmental variability from year to year might cause the selective advantage of increased parental (or mating) effort to vary, but on average, parental effort would still affect reproductive output.

Determinants of Amount of Reproductive Effort Expended

It appears that some males increased their total reproductive effort by increasing parental effort. What then are the factors that cause a male to increase his reproductive effort?

High reproductive effort will be favored any time the cost of the effort is low (Hirshfield and Tinkle 1975). As males become more experienced, cost will decrease, so reproductive effort should increase with age (Gadgil and Bossert 1970, Williams 1966). The feeding males in my population tended to be older than non-feeding males, and in every instance (3 cases) of "switching" between years the direction was from non-feeding to feeding. Surviving males that fed young in one year never failed to do so the next. Not all older males fed young, however, and not all young males failed to do so.

Cost could also be low on productive territories. A male on a productive territory could potentially feed both himself and his young at a reasonable cost, while a male on an unproductive territory could afford to feed only himself. Feeding males in my population tended to have territories that were larger, contained more edge and had significantly higher insect emergence, especially of the larger odonates.

How closely male age and territory productivity are correlated is not clear. Once established, male Red-winged Blackbirds tend to be faithful to a core territory, although they may expand its overall size (Nero 1956). Thus, age is correlated with territory size, but not necessarily with quality. Younger males might find unoccupied territories of good quality and thus become feeding males. When a feeding male of the previous year failed to return and his territory was taken over (i.e., not subdivided into smaller territories by more than one new male or substantially encroached upon by old neighbors) by a new male (3 cases), those new males fed some of their broods. Cost of parental effort and thus male investment strategy appears to have been influenced by a complex of age, experience and territory quality.

Why did feeding males increase parental effort rather than mating effort? If feeding males are usually older and possess better territories, they should also be more efficient in acquiring territories and females (Coulson and White 1958, Dixon 1963, Nero 1956, Yasukawa 1979). Monahan (1977) found a positive correlation between harem size and male age in an old-field population of Red-winged Blackbirds, but he suggested that male age affects harem size primarily through quality of territory (see also Searcy 1979, Yasukawa 1981).

My results show that feeding males displayed at lower intensity than non-feeding males, but feeding and non-feeding males did not differ significantly in time apportionment. Absence of a difference in reproductive success between unassisted females mated to feeding males and females whose mates fed no broods suggests that the measure of territory quality used in this study (insect emergence) influenced only male behavior; its only effect on female success was indirect, through male assistance. Yasukawa (1981), studying this same population of Red-winged Blackbirds, found that the territory feature important to females choosing mates was the non-emergent or terrestrial area, on which females foraged extensively. His finding is supported by my result that the major difference in insect emergence among territories was quantity of larger odonates, a source of food not widely used by females.

In addition to male experience and territory quality, a predictable increase in juvenile mortality might select for greater investment to reduce that mortality even if this results in increased effort (Hirshfield and Tinkle 1975). Even though harem size remained fairly constant over the 3 yr of study, overall male reproductive success declined. Yet, productivity of pair-fed nests stayed the same. Thus, a given amount of parental effort had a predictable effect on reproductive success, but mating effort did not.

Optimization of Parental Effort

Selection also operates within components of reproductive effort. Thus, if males provide parental care but cannot feed all their broods, selection will favor investment in broods that yield the highest return. Male Red-winged Blackbirds in my population assisted the first broods that hatched, a pattern exhibited in other populations (Yasukawa et al. 1990, Yasukawa and Searcy 1982, but see also Muldal et al. 1986) as well as by other male blackbirds (Martin 1974, Patterson et al. 1980, Williams 1952, Willson 1966). The first brood to hatch is the oldest, and thus has the highest reproductive value of all broods. In addition, early broods are more likely to succeed because nesting conditions are most favorable early in the breeding season. At Yellowwood, there is a seasonal decline in reproductive success (Barnard 1979). Thus, the benefit-to-cost ratio of feeding first broods is better than that of later broods.

In addition, most males assisted their oldest females. Older females have demonstrated superior survival, and their greater experience should make them better mothers. Young female Red-winged Blackbirds lay smaller clutches, feed nestlings at lower rates and produce fewer fledglings than older females (Barnard 1979, Crawford 1977, Yasukawa et al. 1990). Food given by males to progeny of older females would be expected to result in more offspring, or more fit offspring, and would thus be a better investment for males (see Gori 1988).

Except in 1976, males more frequently assisted larger broods. Such broods benefit from male help and have high reproductive potential, so they are a good investment for the male (Fiala 1981, Martin 1974).

Considering that mean female age and age range were smaller in 1976, absence of a difference in size of assisted and unassisted broods for that year is not surprising. Barnard (1979) found a significant positive correlation between clutch size and age in female Red-winged Blackbirds (see also Crawford 1977). Nesting order, age of female and clutch size are all highly related (see Crawford 1977, Yasukawa et al. 1990). These three factors act in concert to increase the probability of male assistance for the first brood that hatches.

Paternal investment is highly variable, but for males that make the investment, it is also highly effective. As selection favors effective allocations of effort (Fisher 1930), males should adjust the balance between mating effort and parental effort to changing conditions. In addition, although Trivers (1972) predicted paternal/maternal patterns that reflect initial investment, others (Boucher 1977, Dawkins and Carlisle 1976, Maynard Smith 1977) have suggested that future investment, not prior expenditure, determines the probability of success. This appears to be the case in my population. As males age and acquire better territories, they increase their parental investment. For these males, insuring the success of their most valuable (first) brood might be more predictably productive than acquiring late-nestling females.

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FROM THE NEW EDITOR

As this is my first issue of the Journal of Field Ornithology, I want to address our readers about several important issues. First and foremost, I thank my predecessor, Edward H. (Jed) Burt, Jr., for his outstanding service. Not only did Jed maintain the high standards of the journal, he also improved and streamlined its operation, and constantly worked to improve its image and scope. I inherited a journal in excellent condition, merely awaiting a new pair of hands to guide its production. Jed and his Assistant Editor, C. Colleen Bilsing, did everything possible to smooth the transition of editorship; any rough spots I encountered were my own fault. Second, I thank Raúl A. Pérez-Rivera for continuing as Spanish Editor. His professionalism and willingness to assist the journal are greatly appreciated. I also thank the staff at Allen Press, who have been very patient with and supportive of an inexperienced and frazzled new editor. And last, I sincerely thank the Association of Field Ornithologists for its confidence in me. Although many of my colleagues openly wondered whether they should congratulate me or offer their condolences, I believe that the AFO has given me a challenge and an opportunity. I hope my performance will justify their choice of a new editor.

The Journal of Field Ornithology is undergoing a few changes. As you will note, the page limit has been relaxed, although preference will still be given to short articles whenever appropriate. In addition, the journal is increasing its coverage of two vital aspects of field ornithology: life history and conservation, as shown by several papers in this issue.

Finally, please note that the first paper in my first issue of the journal is somewhat different from the typical JFO article. Cindy Patterson's study of parental behavior in Red-winged Blackbirds was the first of its kind, and has had a tremendous impact on avian behavioral ecology. Unfortunately, Cindy died before she was able to publish her study. When I learned of her untimely death, I made a promise that, if I ever became an editor, I would publish her paper. Cindy, it is a few years later, but here is your paper. I know you would be pleased to see it in print, and I trust you would forgive my heavy-handed editing.