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NESTLING PROVISIONING BY THE EXTREMELY DICHROMATIC NORTHERN CARDINAL

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ABSTRACT.—We measured feeding rates of nestlings during 143 h of observation on 23 pairs of the extremely dichromatic and socially monogamous Northern Cardinal (*Cardinalis cardinalis*). Males fed at higher rates than did females, both when measured as rate per brood and as rate per nestling. Only males maintained their feeding rate per nestling with an increase in brood size and increased their feeding effort as nestlings aged. Feeding efforts by mates were correlated, even when controlling for the effects of brood size. These results provide support both for hypotheses predicting substantial male parental effort in socially monogamous birds and for the assortative mating hypothesis, predicting that birds of similar quality mate with one another. We reject the deflection hypothesis predicting low paternal provisioning effort in strongly dichromatic species and conclude that any cost to male cardinal ornamentation is not simply related to male activity at the nest. *Received 26 Jan. 1996, accepted 10 Sept. 1996.*

Socially monogamous, biparental passerines expend considerable parental effort in provisioning altricial nestlings and fledglings (Skutch 1976, Breitwisch 1989, Zaias and Breitwisch 1989, Clutton-Brock 1991). Although this effort potentially is costly to parents, our knowledge of the relative efforts expended by the sexes during parental care is incomplete. Verner and Willson (1969) concluded that in all socially monogamous North American passerines sampled, males feed both nestlings and fledglings. Their samples of dimorphic species included 42 species (nestling data) and 10 species (fledging data) in which "dimorphic" pertained either to size or plumage sexual dimorphism. However, whether the relative paternal effort in provisioning differs with increasing dichromatism in socially monogamous species is unknown. We simply do not have data from enough species along the spectrum of dichromatism to make this comparison.

Northern Cardinals (*Cardinalis cardinalis*) are strongly dichromatic (Rohwer et al. 1980). Males are scarlet red and females are brown. Both sexes have orange-red bills, and there is variation in plumage and bill color among individuals of both sexes. It is very probable that such distinctive and/or conspicuous coloration is the product of sexual selection (Butcher and Rohwer 1989). Both males and females are involved in raising offspring, especially in provisioning nestlings and fledglings (Laskey 1944, Bent 1968, RB and TSF, pers. obs.).

Cardinals are socially monogamous, and although Ritchison et al.

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(1994) have recently found that extrapair fertilizations occur in a northern Kentucky population, the 14% incidence is relatively low for a socially monogamous passerine. They suggested that this low incidence may be a function of significant male parental effort. Although they knew from their own observations that male feeding effort may be substantial, they presented no data on this effort.

We studied parental feeding of nestling Northern Cardinals to determine the effort by males and females in feeding nestlings and to thereby provide information pertinent to the question of relative parental investment by the sexes. Because parental investment contains a variety of components (Trivers 1972, Breitwisch 1989), the relative rate of provisioning by the sexes cannot, in general, be predicted by parental investment hypotheses (Clutton-Brock 1991). Nonetheless, as the primary behavioral component of parental investment, provisioning effort is of interest in itself.

In addition, two hypotheses do indeed predict relative levels of provisioning. The "deflection" hypothesis (Cott 1964, Baker and Parker 1979) assumes that in dichromatic species the activity of brightly plumaged males near the nest is costly in terms of increasing nest conspicuousness to visually orienting predators and, therefore, predicts that female provisioning exceeds male provisioning. The "skewed sex ratio" hypothesis (Breitwisch 1989) assumes that commonly occurring male-biased sex ratios in birds arise from causes other than parental investment. It predicts that in species with male-biased adult sex ratios, male provisioning exceeds female provisioning because females as a limiting resource demand high parental investment by their mates under the threat of "divorce." For most species, provisioning is the component of care that males can most readily increase.

Finally, the assortative mating hypothesis predicts that birds will mate with individuals of similar quality (Burley 1981, 1983, Breitwisch 1988). For the focus of this study, it predicts that feeding efforts by mates will be correlated, once controlling for the effects of brood size.

STUDY AREA AND METHODS

We conducted this study at the Aullwood Audubon Center and Farm located ca 15 km northwest of Dayton, Ohio (39°52′N and 84°16′W) from April to August 1991 and 1992. The Aullwood property is an 80 ha sanctuary with a variety of habitats from secondary forest and open woodlands to meadows and prairies (see Filliater-Lee [1992] for further details on vegetation). This mixture of habitats is ideal for Northern Cardinals, and they are abundant on the property, frequently on contiguous territories.

We measured nestling feeding rates of males and females in 23 pairs by recording the number of feeding trips by each parent during 1-h sampling periods (N = 143 h). In 20 of 23 cases, we knew the brood size and could standardize feeding rates as feedings per nestling per hour. In three cases where brood size was unknown, we assumed the modal brood size for the population of two nestlings. This assumption is unbiased insofar as dispersion around this value is essentially symmetrical in this population (see Results). We report feeding rates both as overall rates and as rates per nestling. The former reflects the total effort made by each parent, while the latter allows comparison of parental efforts from the standpoint of an individual nestling.

We made all observations from distances of at least 5 m, usually partially hidden by vegetation to avoid disturbing parent birds. We recorded feeding data during at least 4 h of observations on each pair ($\bar{x}$ = 6.2 ± 1.5 h, N = 23), with sampling periods scattered throughout daylight hours (07:00–19:00 EST) and on several days distributed over the 10-d nestling period. The sampling protocol represented a compromise between attempting to sample as many pairs as possible and achieving a reasonable sample of observations for each pair. Filliater-Lee (1992) demonstrated that neither male nor female feeding effort is related to time of day. Sampling distribution with respect to mean age of nestlings was similar for broods of different sizes (Kruskal-Wallis one-way ANOVA, $H = 2.91$, df = 3, $P > 0.05$). No data were collected during rainy periods because rainfall may affect female feeding rate by extending brooding time (Johnson and Best 1982).

Cardinals carry food to nestlings deep in their bills, and food items only occasionally projected beyond the margins of the bill (e.g., caterpillars). Therefore, it was not possible to estimate by observation the relative load sizes delivered to nestlings. Although we attempted to sample foods through the use of pipe cleaner collars, we found that the bolus of mashed food items slid past the point of constriction on the nestling's throat. Mobley (1993) has shown that male cardinals provision nestlings with larger food loads than do females, and we conservatively assume that male loads are at least as large as female loads. It has similarly been shown for other passerines that males tend to bring similar-sized or larger food loads to nestlings than do females (Wittenberger 1982, Breitwisch et al. 1986, Carlson and Moreno 1986, Grundel 1987).

The sample sizes in analyses are the numbers of pairs of cardinals. Analyses employed non-parametric tests (one exception; see below) due to moderately-sized samples and unknown underlying distributions of variables (Siegel and Castellan 1988). We used the Wilcoxon matched-pairs signed-ranks test (smaller W value reported) in comparing male and female feeding rates within pairs. We used tests of independence to ask if differences in distributions of variables occurred between years; all were corrected due to small sample sizes using Williams' correction (Sokal and Rohlf 1995). We tested for monotonic relationships with Spearman rank correlations (r_s value reported), and all correlation coefficients were corrected for ties. To determine if mates display similar feeding rates, we employed a Kendall partial rank correlation ($T_{xy.z}$ value reported). First, we calculated three Kendall rank correlation coefficients (corrected for ties): (1) male feeding rate/nestling correlated with brood size, (2) female feeding rate/nestling correlated with brood size, and (3) male and female feeding rates correlated with one another (T value reported). Then, we used these to compute the partial rank correlation coefficient for feeding rates by mates that controls for the effect of brood size on individual feeding rates (Siegel and Castellan 1988). We employed the parametric F-test for the comparison of variability in feeding rates among males and females. Tests related to questions of male-female differences were two-tailed. Tests of questions relating provisioning to brood size and age were one-tailed because the predicted relationship to these variables is unidirectional. We report results as significant if associated with an *alpha* value of $P < 0.05$.

We pooled data from the two years of the study for analysis after testing for differences in the distributions of variables between years. Tests of independence revealed no differences between years in either feeding rates or brood sizes (all Ps > 0.05). For unbanded pairs,

TABLE 1

FEEDING RATES BY MALE AND FEMALE NORTHERN CARDINALS AND MALE PROPORTION OF TOTAL FEEDING EFFORT AS A FUNCTION OF BROOD SIZE

	Feedings/nestling/h		Feedings/h		
Brood	Male ($\bar{x}$ ± SE)	Female ($\bar{x}$ ± SE)	Male ($\bar{x}$ ± SE)	Female ($\bar{x}$ ± SE)	Male proportion
1 (6)[a]	1.51 ± 0.18	1.04 ± 0.12	1.51 ± 0.18	1.04 ± 0.12	0.59
2 (10)	1.08 ± 0.16	0.89 ± 0.15	2.16 ± 1.04	1.78 ± 0.31	0.55
3–4 (7)	0.94 ± 0.21	0.71 ± 0.21	3.06 ± 0.78	2.24 ± 0.25	0.58
Total (23)	1.14 ± 0.11	0.87 ± 0.08	2.30 ± 0.31	1.76 ± 0.18	0.57

[a] Number of pairs in parentheses.

we think it unlikely that a pair was sampled twice because we sampled from different territories in the two years, and it is known that pairs maintain the same territory in successive years (RB, unpubl. data).

RESULTS

Cardinals provided few feedings per hour to their broods, typically a total per pair of 2–3 feedings for broods of one nestling up to 5–6 feedings for broods of three or four nestlings (Table 1). Through binoculars, we could see that items varied from single large caterpillars to loads of many small items mashed into pulp.

Males fed nestlings at higher rates than did their mates. For total feeding rates, males surpassed their mates, averaging 2.30 ± 0.31 (SE) feedings/h, while females provided 1.76 ± 0.18 feedings/h ($W = 63.5$, N = 23 [with one pair tied], $P < 0.05$). Mean feeding rate per nestling by males was 1.14 ± 0.11 and by females was 0.87 ± 0.08 feedings/nestling/h ($W = 57.5$, N = 23 [with one pair tied], $P < 0.05$) (Table 1). The proportion of the total feeding effort provided by males was related neither to brood size ($r_s = -0.06$, N = 23 pairs, $P > 0.05$) nor to the magnitude of the total effort by the pair ($r_s = 0.18$, N = 23 pairs, $P > 0.05$) The male's proportion of total effort was as low as 0.33 and as high as 0.76 (see Fig. 1). The variance among males in mean overall feeding rate was greater than the variance among females ($F_{22,22} = 2.75$, $P < 0.05$). On a per-nestling basis, the variance in male feeding rate tended to be greater than the variance among females, but not significantly so ($F_{22,22} = 2.16$, $P = 0.08$).

Brood sizes ranged from one to four (six broods of 1 nestling, 10 broods of 2, six broods of 3, and one brood of 4). Both males and females increased their total feeding rate with brood size (for males, $r_s = 0.36$, one-tailed $P < 0.05$, N = 23; for females, $r_s = 0.52$, one-tailed $P < 0.01$,

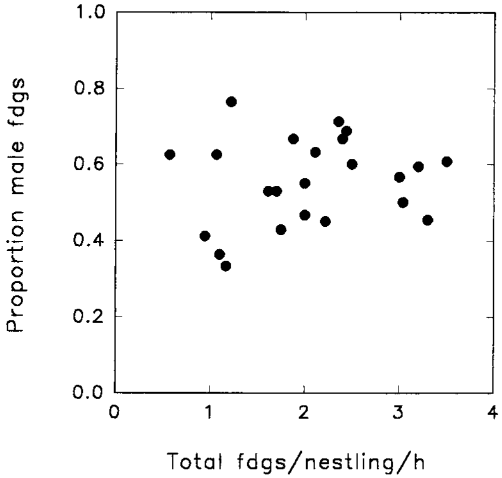

FIG. 1. Proportion of nestling feedings contributed by male Northern Cardinals as a function of total feeding effort. Data represent 23 pairs of cardinals.

N = 23). On a per nestling basis, although both sexes reduced feeding rates to larger broods, the reduction was significant only for females (for males, $r_s = -0.34$, one-tailed $P > 0.05$, N = 23; for females, $r_s = -0.47$, one-tailed $P < 0.05$, N = 23). From the standpoint of an individual nestling, the overall result was a decrease in feeding rate as brood size increased ($r_s = -0.46$, N = 23, $P < 0.05$) (Table 1).

Both males and females increased feeding effort as nestlings aged, but only males significantly did so (for males, $r_s = 0.93$, one-tailed $P < 0.01$, N = 8 days [days 0 and 1 pooled and days 8 and 9 pooled, due to small sample sizes]; for females, $r_s = 0.57$, one-tailed $P > 0.05$, N = 8 days; Fig. 2). Although not significant, the gap between feeding rates by males and females was greatest in the mid-nestling period, when altricial nestlings grow most rapidly. Females did increase their feeding rate in the four days prior to fledging.

Feeding rates by mates were correlated ($T = 0.42$, N = 23 pairs, $P < 0.01$); broods in which nestlings were fed at relatively high rates per nestling were characterized by both mates expending such high effort (Fig. 3). This was probably due in part to a brood size effect (see above). However, once we controlled for brood size, there remained a significant correlation between per-nestling feeding rates of mates ($T_{xy.z} = 0.35$, $P < 0.05$).

DISCUSSION

Male cardinals surpassed their mates in effort in feeding nestlings, better maintained their feeding rates to individual nestlings even in large

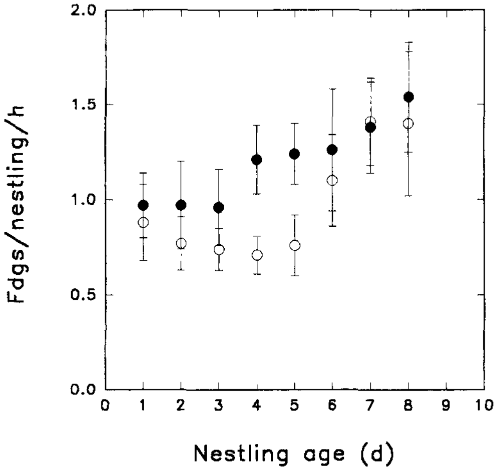

FIG. 2. Male and female Northern Cardinal nestling feeding rates as a function of nestling age. Shown are means and standard errors for each parental sex. Mean sample size (number of pairs) for each day was 13.6 ± 3.5 (range: 8–18). Males = closed circles, and females = open circles.

broods than did their mates, and tracked the growth of nestlings by consistently increasing their feeding rate as nestlings aged. These results are consistent with a prediction of the skewed sex-ratio hypothesis: males should expend the greater parental effort when they are forced to do so

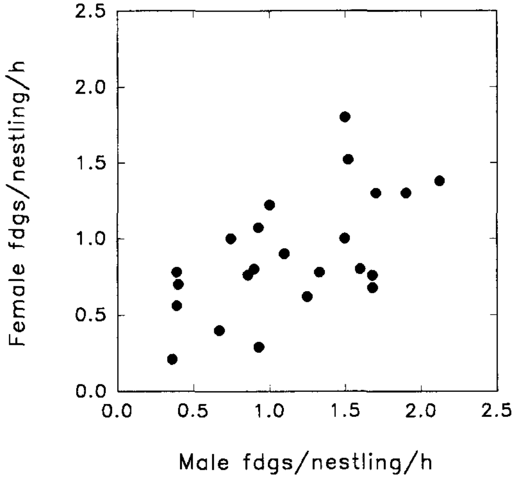

FIG. 3. Male and female Northern Cardinal mean feeding rates to nestlings standardized on a per nestling basis. Data represent 23 pairs of cardinals.

by "demands" of scarce females (Breitwisch 1989). A necessary condition for the hypothesis is that males display significant variability in their parental effort, which is the case here. Further, the difference among males is not simply related to brood size; rather, it is patternless individual variability. Unfortunately, we cannot directly address the skewed sex ratio hypothesis because we do not know the adult sex ratio of this population.

Do female cardinals threaten their mates with divorce if male provisioning rates are low? This is not yet known, although we have documented divorces. Data across three years have revealed that, of 10 pairs in which both birds were banded and detected in the following year, two pairs (20%) divorced and eight remained together. In addition, of 21 banded pairs monitored during a breeding season, two (10%) divorced and 19 remained together for all nesting attempts. Based on the findings reported here, we predict that it will be shown that this population of cardinals displays a male-biased adult sex ratio, as is common in socially monogamous passerines (Lack 1954, Breitwisch 1989). If the adult sex ratio is not male-biased, the skewed sex ratio hypothesis would be refuted (Breitwisch 1989).

The positive correlation in feeding efforts between mates is predicted by the assortative mating hypothesis (Burley 1981, 1983, 1986, Breitwisch 1988). We conclude either that birds of similar quality mate assortatively or that females mated to high quality males can benefit from the resources defended by these males and, thereby, match the efforts of their mates. The latter possibility perhaps simply reduces to the former, if high quality females mate with males able to defend high quality territories. These possibilities warrant further investigation.

These data also allow rejection of the deflection hypothesis (Cott 1964, Baker and Parker 1979). The prediction of the deflection hypothesis that extremely dichromatic male cardinals should either refrain from nest visits or, at least, curtail their activity at the nest is refuted. The 57% overall proportion of male feedings places cardinals toward the upper end of the range of male contributions tabulated by Searcy and Yasukawa (1995, p. 260) for a small sample of passerine species, both mono- and dichromatic. It thus seems unlikely that brilliantly-plumaged male cardinals are significantly endangering nest contents in the course of provisioning nestlings. Perhaps this is because the overall nest predation incidence is high and may be largely independent of any defensive efforts by cardinals (Filliater et al. 1994, Nealen and Breitwisch, in press).

Finally, two other hypotheses are yet to be addressed. The honest advertisement of good parenting hypothesis (Hoelzer 1989, Kirkpatrick 1985) predicts that the exaggeration of the male ornament (here, scarlet plumage) will itself predict the level of paternal care. Thus, the relative contribution to provisioning by a male should be positively correlated with the degree of ornamentation. Second, the "mixed-strategy" hypothesis (Trivers 1972, Westneat et al. 1990) predicts that males display a reproductive strategy involving both parental investment and mating effort expended on attempts to secure extra-pair copulations; as the latter increases, the former is predicted to decrease. Ritchison et al. (1994) suggested several reasons for the relatively low incidence of extra-pair fertilizations in cardinals: proportionately low fitness gains for males from extra-pair copulations relative to paternal effort, female ability to assess male quality prior to mating in this non-migratory species, and diligent male mate-guarding. We currently have no evidence for a mixed strategy in which males expend significant effort in seeking extra-pair copulations.

In summary, these results demonstrate that even in an extremely dichromatic bird species, males may expend significant parental effort, and birds of similar quality may mate with one another. Whether the degree of male ornamentation is related to paternal effort, and thus predictable by females, is yet to be determined.

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LITERATURE CITED

BAKER, R. R. AND G. A. PARKER. 1979. The evolution of bird coloration. Philos. Trans. R. Soc. Lond. B 287:63–130.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part 1. U.S. Natl. Mus., Smithsonian Inst. Bull. 237.

BREITWISCH, R. 1988. Sex differences in defence of eggs and nestlings by Northern Mockingbirds (*Mimus polyglottos*). Anim. Behav. 36:62–72.

———. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. Current Ornithol. 6:1–50.

———, P. G. MERRITT, AND G. H. WHITESIDES. 1986. Parental investment by the Northern Mockingbird: male and female roles in feeding nestlings. Auk 103:152–159.

BURLEY, N. 1981. Mate choice by multiple criteria in a monogamous species. Am. Nat. 117:515–528.

———. 1983. The meaning of assortative mating. Ethol. Sociobiol. 4:191–203.

———. 1986. Sexual selection for aesthetic traits in species with biparental care. Am. Nat. 127:415–445.

BUTCHER, G. S. AND S. ROHWER. 1989. The evolution of conspicuous and distinctive coloration for communication in birds. Current Ornithol. 6:51–108.

CARLSON, A. AND J. MORENO. 1986. Foraging behavior and parental care in the Fieldfare. Ardea 74:79–90.

CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, New Jersey.

COTT, H. B. 1964. Colouration, adaptive. Pp. 139–142 *in* A new dictionary of birds (A. L. Thomson, ed.). Newton, London, England.

FILLIATER-LEE, T. S. 1992. Parental roles in feeding nestlings, and nest sites and nest success in Northern Cardinals (*Cardinalis cardinalis*). M.S. thesis, Univ. of Dayton, Dayton, Ohio.

———, R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

GRUNDEL, R. 1987. Determinants of nestling feeding rates and parental investment in the Mountain Chickadee. Condor 89:319–328.

HOELZER, G. A. 1989. The good parent process of sexual selection. Anim. Behav. 38:1067–1078.

JOHNSON, E. J. AND L. B. BEST. 1982. Factors affecting feeding and brooding of Gray Catbird nestlings. Auk 99:148–156.

KIRKPATRICK, M. 1985. Evolution of female choice and male parental investment in polygynous species: the demise of the "sexy son." Am. Nat. 125:788–810.

LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, Oxford, England.

LASKEY, A. R. 1944. A study of the cardinal in Tennessee. Wilson Bull. 56:27–44.

MOBLEY, J. E. 1993. A general model for iteroparity: development of the model and investigation of phylogenetic patterns with specific reference to the Northern Cardinal. Ph.D. diss., Univ. of Arkansas, Fayetteville, Arkansas.

NEALEN, P. M. AND R. BREITWISCH. 1997. Northern Cardinal sexes defend nests equally. Wilson Bull. 109 (in press).

RITCHISON, G., P. H. KLATT, AND D. F. WESTNEAT. 1994. Mate guarding and extra-pair paternity in Northern Cardinals. Condor 96:1055–1063.

ROHWER, S., S. D. FRETWELL, AND D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. Am. Nat. 115:400–437.

SEARCY, W. A. AND K. YASUKAWA. 1995. Polygyny and sexual selection in red-winged blackbirds. Princeton Univ. Press, Princeton, New Jersey.

SIEGEL, S. AND N. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences, second ed. McGraw-Hill, New York, New York.

SKUTCH, A. F. 1976. Parent birds and their young. Univ. of Texas Press, Austin, Texas.

SOKAL, R. R. AND F. J. ROHLF. 1995. Biometry, 3rd ed. W.H. Freeman, New York, New York.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, ed). Aldine, Chicago, Illinois.

VERNER, J. AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. Ornithol. Monogr. 9. Am. Ornithol. Union., Washington, D.C.

WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON. 1990. The ecology and evolution of extra-pair copulations in birds. Current Ornithol. 7:331–369.

WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84:22–39.

ZAIAS, J. AND R. BREITWISCH. 1989. Intra-pair cooperation, fledgling care, and renesting by Northern Mockingbirds (*Mimus polyglottos*). Ethology 80:94–110.