

# PATTERNS OF PARENTAL PROVISIONING BY EASTERN PHOEBES<sup>1</sup>

KELVIN F. CONRAD<sup>2</sup> AND RALEIGH J. ROBERTSON

Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada

**Abstract.** We compared patterns of male and female provisioning to nestlings in first and second broods of Eastern Phoebes (*Sayornis phoebe*). Female Eastern Phoebes made more trips to the nest throughout the nestling cycle. Male and female feeding rates increased with nestling age in parallel until day 11 and decline slightly to day 14 (nestlings leave the nest at approx. day 17). The median total number of feeding trips per nestling did not differ between broods for either sex. We manipulated brood sizes, within the limits of naturally occurring brood sizes, and found that the per-nestling feeding rates of both sexes were unaffected. The increasing food requirements of older or larger broods caused male and female Eastern Phoebes to increase their per-nestling feeding rates in a similar pattern. Because of similarities between the sexes in size and foraging behavior, additional costs of feeding imposed by older or enlarged broods are expected to affect members of the sexes equally.

**Key words:** *Eastern Phoebe; feeding nestlings; Sayornis phoebe; parental care; intersexual differences; parental investment.*

## INTRODUCTION

ESS (Evolutionary Stable Strategy) and optimality models of parental investment by monogamous species with biparental care predict that, within reasonable limits, the male and female of a pair should provide equal care to their offspring (Maynard-Smith 1977, Houston and Davies 1985, Winkler 1987). In many monogamous passerines, males and females make approximately the same number of food deliveries to nestlings (Kendeigh 1952, Lack 1968, Emlen and Oring 1977, Smith et al. 1988), as predicted by the models. However, there are additional factors that may influence the relative amount of care each parent provides. Intersexual differences in provisioning may be of two general types: (1) differences in absolute amounts of food delivered (number of trips, biomass, quality) and, (2) differences in the intensity of response to changes in demands for food by nestlings (i.e., the slopes of male and female provisioning rates versus nestling demand differ).

## DIFFERENCES IN ABSOLUTE AMOUNT

Trivers (1972) suggested that female birds should invest more in raising offspring than their mates because their investment up to the point that eggs are laid is greater than that of males. Also, se-

lection may favor reduced investment by males because they cannot be as certain of their paternity as females are certain of their maternity (Davies 1985, Houston and Davies 1985, Møller 1988). If there is opportunity to obtain additional fertilizations, males may devote time to obtaining them, rather than feeding their nestlings (Westneat 1988). One parent may provide disproportionately more care when the other parent is temporarily handicapped (Wright and Cuthill 1989, Slagsvold and Lifjeld 1990).

## DIFFERENCES IN THE INTENSITY OF RESPONSE

Males are expected to increase their relative contribution to feeding nestlings when difficult feeding situations, such as the period of most rapid nestling growth, arise (Wittenberger 1982, Bédard and Meunier 1983, Breitwisch et al. 1986, Grundel 1987). When females are responsible for brooding, males may take a relatively larger share of feeding early in the nesting cycle so females can spend more time brooding (Johnson and Best 1982, Grundel 1987). As a result, female feeding rates may increase more rapidly than male feeding rates as nestlings age (Johnson and Best 1982). In double-brooded species, males might take a greater share of feeding in first broods so that females have energy available to prepare for a subsequent brood or reneat more quickly (Smith 1978, Smith et al. 1988). Johnson and Best (1982) have shown that in Gray Catbirds (*Dumetella carolinensis*), extrinsic factors such as tempera-

<sup>1</sup> Received 1 July 1992. Accepted 26 October 1992.

<sup>2</sup> Present address: Biology Department, Acadia University, Wolfville, Nova Scotia B0P 1X0, Canada.

ture affect male and female feeding rates differently. In general, older and larger broods require more food and one sex, usually males, provides a larger proportion of provisioning to older or larger broods (e.g., Grundel 1987).

The relative response of each sex to increasing demands for food by nestlings is an important consideration in manipulative studies of reproductive tradeoffs or the evolution of clutch size. Slagsvold and Lifjeld (1990), for example, found that male Tits (*Parus* spp.) did not increase their parental investment when their mates had been "handicapped" and concluded that the determination of clutch size in Tits should be based on the female's own ability to provide for young and not on the quality of her mate. Intersexual inequalities in the intensity of response to changes in nestling food demands may amplify the effect of a manipulation in one sex and ameliorate the effect in the other.

We observed pairs of Eastern Phoebes (*Sayornis phoebe*) feeding their nestlings at various stages of the nesting cycle to determine if the relative role of either parent in delivering food changed over time. We also manipulated the size of broods to see how feeding rate changed with brood size. This study is part of a more general study of parental investment in Eastern Phoebes and we were particularly interested to see if the sexes responded differently to changes in their brood size and age.

## METHODS

### STUDY SITES

This study was conducted from April to August of 1989 and 1990, near the Queen's University Biological Station, Chaffeys Locks, Ontario (44°34'N, 76°19'W). Phoebe nests were found on anthropogenic structures and natural cliff sites. Eastern Phoebes were mist-netted and individually marked with colored plastic and metal numbered leg bands. We added small patches of white non-toxic paint to the tails of females and the wings of males because phoebes cannot be sexed at a distance from field markings. The data presented are from nests where at least one parent (usually the female) was banded.

### CLUTCH MANIPULATIONS

All first clutches were initially three to six eggs, with the majority either four (24%) or five eggs (63%,  $n = 78$ ). Nests were assigned to groups of three, matched for the day the final egg was laid.

Within two days after the last egg was laid, two eggs were moved from one randomly chosen nest to another. The third nest was not manipulated and served as the control. Only first clutches were manipulated. This produced first clutches of three to seven eggs, which is within the range of normal clutch sizes in our area (Peck and James 1987), and subsequently resulted in broods of two to seven nestlings.

### FEEDING WATCHES

In 1989 we performed feeding watches when nestlings were three and nine days old (nestling days 3 and 9, day 0 = day first egg hatched). Days three and nine were chosen as corresponding to a period of roughly linear growth of nestlings (Murphy 1981) and roughly linear increase in feeding rates (Kendeigh 1952, and see below), which we hoped would limit within-day variability. Nestling mortality was also relatively low between days three and nine and these nestling ages provided us with measurements before and after nestlings attained homeothermy. In 1990, we increased our watches to days 3, 6, 9, and 11 and performed watches at a subset of nests on days 2 and 14 to examine changes in provisioning patterns of parents over the nesting cycle (nestlings leave the nest on approximately day 17, unpubl. data). A feeding watch consisted of 30 min of observation with binoculars or telescope from concealment or from greater than 30 m away. We recorded all feeding trips to the nest according to the sex of the parent. Prey became large enough after day 3 for us to verify delivery of food to the nest. We counted the nestlings at the end of a watch and divided the number of trips to the nest by the number of nestlings to produce a per-nestling feeding rate that was standardized across different brood sizes.

### STATISTICAL ANALYSIS

Per-nestling feeding rates were non-normal so comparisons between attempts and sexes were made using non-parametric Wilcoxon matched-pairs signed ranks tests or Kruskal-Wallis (K-W) tests. Accordingly, we present medians and interquartile ranges as our descriptive statistics, rather than means and variance measures, which are only appropriate to normally distributed data. To analyze changes in male and female feeding rates and compare total feeding rates between the sexes over the whole nesting cycle, the per-nestling feeding rates were  $\log_e(x+1)$  trans-

TABLE 1. Comparison of per-nestling feeding rates (trips/nestling/30 min; medians followed by interquartile ranges, *n*) by males and females. Increased and decreased nests were increased or decreased by two eggs, respectively. Control nests and second attempt nests were not manipulated.

	Controls	Increased	Decreased	H <sup>a</sup>	P
<b>Males</b>					
Attempt 1					
Day 3 <sup>b</sup>	0.00 (0.00–0.40), 9	0.43 (0.00–0.67), 17	0.33 (0.00–0.67), 13	2.03	0.36
Day 9	0.67 (0.25–1.50), 6	0.80 (0.43–1.00), 13	0.50 (0.17–1.17), 12	0.21	0.90
Attempt 2					
Day 3	0.32 (0.00–0.75), 6	0.37 (0.00–1.00), 10	0.40 (0.22–0.63), 8	0.18	0.91
Day 9	0.25 (0.20–0.50), 5	0.58 (0.00–1.00), 6	0.55 (0.35–0.76), 8	0.45	0.80
<b>Females</b>					
Attempt 1					
Day 3	0.33 (0.33–0.75), 9	0.50 (0.17–0.67), 17	0.67 (0.42–0.83), 12	0.95	0.62
Day 9	0.75 (0.33–1.75), 6	1.00 (0.80–1.14), 13	0.83 (0.33–1.00), 12	1.35	0.51
Attempt 2					
Day 3	0.37 (0.25–0.50), 6	0.60 (0.25–1.00), 10	0.45 (0.40–0.68), 8	1.29	0.52
Day 9	1.25 (1.00–1.40), 5	1.15 (0.50–1.75), 6	1.00 (0.65–1.45), 8	0.29	0.86

<sup>a</sup> Results of Kruskal-Wallis test among treatments. Probability is compared to a chi-square distribution with 2 degrees of freedom in all cases.  
<sup>b</sup> Age of nestlings fed. Hatching day = day 0.

formed and an analysis of covariance (ANCOVA), with nestling age as the covariate, was applied. All statistical tests were performed with a critical value of *P* = 0.05.

**RESULTS**

Our manipulations of clutch size created significantly different brood sizes among treatments in first nesting attempts (K-W H = 25.4, *df* = 2, *P* < 0.001), but did not affect second nesting attempts (K-W H = 3.56, *df* = 2, *P* = 0.17, see also Conrad and Robertson 1992). Despite differences in first attempt brood sizes, the per-nestling feeding rates of males and females did not differ among increased, decreased and control nests for either attempt (Table 1). We subsequently combined the manipulation groups to examine patterns of feeding rates at individual nests.

Individual males and females did not change their per-nestling feeding rates between nesting

attempts on either nestling day 3 or nestling day 9 (Table 2). However, female per-nestling feeding rates were greater than those of males on days 3 and 9 for both attempts, resulting in greater female per-nestling feeding rates when both attempts were combined (Table 3).

Male and female per-nestling feeding rates increased from days 2 to 11 and declined slightly on day 14 (Fig. 1). The feeding rates of the sexes increased in parallel as the nestlings aged (Fig. 1).

We used ANCOVA to test for differences in overall male and female per-nestling feeding rates between attempts (Table 4) while removing the effects of nestling age. Correlations between first and second attempt feeding rates of individual males and females were not significant (Kendall's *Tau*, all *P*'s > 0.20), first and second broods occurred at different times of the season, when food resources and weather conditions differed greatly and first and second broods were not nec-

TABLE 2. Pairwise comparisons of per-nestling feeding rates (trips/nestling/30 min; medians followed by interquartile ranges) within sexes between attempts.

Group	Day <sup>a</sup>	Attempt 1	Attempt 2	<i>n</i>	Z <sup>b</sup>	<i>P</i>
Males	3	0.40 (0.00–0.90)	0.33 (0.10–0.71)	19	0.46	0.65
Males	9	0.45 (0.17–0.90)	0.50 (0.10–0.75)	20	0.42	0.67
Females	3	0.60 (0.50–0.76)	0.50 (0.33–0.75)	19	0.72	0.47
Females	9	1.00 (0.41–1.46)	1.00 (0.50–1.63)	20	0.38	0.70

<sup>a</sup> Age of nestlings fed. Hatching day = day 0.  
<sup>b</sup> Results of a Wilcoxon matched-pairs signed ranks test between groups. Probability is calculated by comparing Z with a normal distribution.

TABLE 3. Pairwise comparisons of per-nestling feeding rates (trips/nestling/30 min; medians followed by interquartile ranges) between sexes within attempts.

Group	Day <sup>a</sup>	Males	Females	n	Z <sup>b</sup>	P
Attempt 1	3	0.40 (0.00–0.67)	0.59 (0.33–0.71)	44	2.70	0.007
Attempt 1	9	0.83 (0.37–1.07)	1.00 (0.46–1.46)	47	2.19	0.03
Attempt 2	3	0.37 (0.00–0.67)	0.45 (0.33–0.75)	26	2.28	0.02
Attempt 2	9	0.60 (0.37–1.00)	1.25 (0.80–1.63)	27	3.24	0.001
Both attempts	3	0.40 (0.00–0.67)	0.50 (0.33–0.71)	70	3.66	<0.001
Both attempts	9	0.75 (0.33–1.00)	1.00 (0.50–1.50)	74	3.78	<0.001

<sup>a</sup> Age of nestlings fed. Hatching day = day 0.

<sup>b</sup> Results of Wilcoxon matched-pairs signed ranks test between groups. Probability is calculated by comparing Z with a normal distribution.

essarily the same size. Therefore, for this analysis, we assumed that first and second attempts of individual pairs were statistically independent events. When we found no differences in per-nestling feeding rate within sexes, we combined attempts to compare overall per-nestling feeding rates between males and females (Table 4). The fact that the slopes of the feeding trips versus nestling ages are homogenous between the sexes (Table 4, slopes) confirms that the feeding rates of both sexes increase in parallel. From nestling days 2 to 14, on average, females provide more frequent deliveries to the nest than males (Fig. 1, Table 4).

## DISCUSSION

Overall, parental provisioning rates of Eastern Phoebes increased as nestlings aged, although fewer trips than might be expected from a linear pattern were made on day 14. Kendeigh (1952) found that trips to the nest by parental Eastern Phoebes reached a maximum on nestling day 12 and decreased slightly thereafter, as we observed. We have shown elsewhere (Conrad and Robertson 1992) that provisioning rates increase with brood size, however, per-nestling feeding rate of both sexes was unaffected by brood size manipulations.

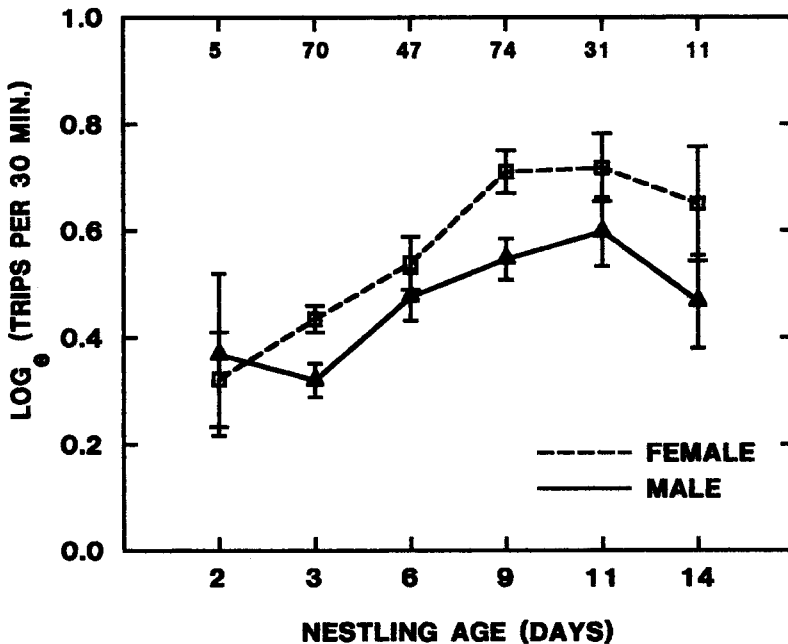


FIGURE 1. Mean number of per-nestling feeding trips, transformed as  $\log_e(x + 1)$ , per 30 min by male and female parents of first and second broods 2, 3, 6, 9, 11 and 14 days old. The number of broods for each comparison appears above the plotted points. Error bars are  $\pm$ SE.

TABLE 4. Results of analyses of covariance (ANCOVA) comparing overall per-nestling feeding rates ( $\log_e [x + 1]$ ) transformed for males and females in first and second attempts and between sexes.

Group	Source	Sum-of-squares	df	Mean-square	F	P
Males	Slopes*	0.06	1	0.06	0.62	0.43
	Error	22.7	234	0.10		
	Attempt	0.01	1	0.01	0.08	0.78
	Covariate (age)	1.92	1	1.92	19.7	<0.001
	Error	22.8	235	0.97		
Females	Slopes*	0.13	1	0.13	1.36	0.24
	Error	22.8	234	0.10		
	Attempt	0.15	1	0.15	1.56	0.21
	Covariate (age)	3.22	1	3.22	33.0	<0.001
	Error	22.9	235			
All	Slopes*	0.07	1	0.07	0.76	0.38
	Error	45.9	472	0.10		
	Sex	1.73	1	1.73	17.8	<0.001
	Covariate (age)	5.01	1	5.01	55.6	<0.001
	Error	46.0	473	0.10		

\* Test of the assumption of homogeneity of slopes of male and female per-nestling feeding rates versus age.

Female Eastern Phoebes made more trips per nestling than males but male and female phoebes increased their provisioning in parallel as broods grew older. Males and females responded similarly to changes in brood age and the relative contribution of both sexes remained constant. The average number of trips per nestling also did not differ between nesting attempts.

Several studies of passerines have shown that male and female feeding rates are similar, with the female providing slightly more deliveries (Breitwisch et al. 1986, Northern Mockingbirds, *Mimus polyglottos*; Leffelaar and Robertson 1986, Tree Swallows, *Tachycineta bicolor*; Alatalo et al. 1988, Pied Flycatchers, *Ficedula hypoleuca*; Smith et al. 1988, double-brooded Great Tits, *Parus major*). Royama (1966, Great Tits) and Morehouse and Brewer (1968, Eastern Kingbirds, *Tyrannus tyrannus*) found that males provided more food only in the early nestling stages, while the female brooded. Johnson and Best (1982) found similar results for Gray Catbirds and attributed the difference to the time females spent brooding and shading the nestlings. Female Eastern Phoebes provided equal or greater per-nestling provisioning rates throughout the nestling period, even while they brooded.

Maynard-Smith (1977, see also Breitwisch et al. 1986, Smith et al. 1988, Westneat 1988) proposed that males should provide relatively less care to nestlings when their opportunity for ad-

ditional fertilizations was high. Because of replacement nests and second clutches, phoebes initiated nests from mid-April to late June in our study area and males should have had opportunity to obtain additional fertilizations through most of the nesting cycle. Therefore, male phoebes should feed nestlings less than females, but should feed second brood nestlings more because there is lower potential for additional fertilizations late in the season. However, the male share of feedings was consistent between attempts, suggesting that potential for additional fertilizations did not influence male provisioning rates, or at least that other factors are involved.

Eastern Phoebes feed on a wide variety of insects (Bent 1942; pers. observ.), rarely leave the vicinity of the nest when foraging for food for nestlings and appear to carry prey one at a time. Because both parents forage in the same limited area, they both probably deliver similar prey to their young and experience similar foraging costs (unlike Great Tits, Smith et al. 1988).

The absolute number of trips made by females was greater than the number made by males. If parental provisioning can be assumed to reflect relative parental effort in raising offspring, then female phoebes appear to be investing more effort in raising their broods. However, the intensity of response to increased nestling demand for food was similar between the sexes, whether that increased demand resulted from increased brood

size or age. Thus, both sexes are expected to be affected approximately equally by the increased costs imposed by brood or clutch size manipulations and, unlike the Tits studied by Slagsvold and Lifjeld (1990), the quality of male phoebes is expected to influence the size of the clutch laid by their mates.

## ACKNOWLEDGMENTS

This research was funded by the Natural Sciences and Engineering Research Council of Canada through a scholarship to KFC and an operating grant to RJR, and by a Sigma Xi Grant-In-Aid to KFC. J. Lifjeld, T. Herman, D. Winkler, R. Breitwisch and an anonymous reviewer provided useful comments. Saul Schneider and Lorraine Standing provided assistance in the field. We thank cottagers and landowners along the shores of Lake Opinicon, Ontario, for their help and cooperation with this project.

## LITERATURE CITED

- ALATALO, R. V., K. GOTTLANDER, AND A. LUNDBERG. 1988. Conflict or cooperation between parents in feeding nestlings in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scan.* 19:31-34.
- BÉDARD, J., AND M. MEUNIER. 1983. Parental care in the Savannah Sparrow. *Can. J. Zool.* 61:2836-2843.
- BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows and their allies. U.S. Natl. Mus. Bull. 179.
- BREITWISCH, R., 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.
- CONRAD, K. F., AND R. J. ROBERTSON. 1992. Intra-seasonal effects of clutch manipulation on parental provisioning and residual reproductive value of Eastern Phoebes (*Sayornis phoebe*). *Oecologia* 89: 356-364.
- DAVIES, N. B. 1985. Cooperation and conflict among Dunnocks, *Prunella modularis*, in a variable mating system. *Anim. Behav.* 33:628-648.
- EMLÉN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- GRUNDEL, R. 1987. Determinants of nestling feeding rates and parental investment in the Mountain Chickadee. *Condor* 89:319-328.
- HOUSTON, A. J., AND N. B. DAVIES. 1985. The evolution of cooperation and life history in the Dunnock, *Prunella modularis*. In R. M. Sibley and R. H. Smith [eds.], *Behavioural ecology*. Blackwell Scientific, Oxford, England.
- JOHNSON, E. J., AND L. B. BEST. 1982. Factors affecting feeding and brooding of Gray Catbird nestlings. *Auk* 99:148-156.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. III. *Biol. Monograph.* 22:1-356.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LEFFELAAR, D., AND R. J. ROBERTSON. 1986. Equality of feeding roles and the maintenance of monogamy in Tree Swallows. *Behav. Ecol. Sociobiol.* 18: 199-206.
- MAYNARD-SMITH, J. 1977. Parental investment—a prospective analysis. *Anim. Behav.* 25:1-9.
- MÖLLER, A. P. 1988. Paternity and paternal care in the Swallow, *Hirundo rustica*. *Anim. Behav.* 36: 996-1005.
- MOREHOUSE, E. L., AND R. BREWER. 1968. Feeding of nestling and fledgling Eastern Kingbirds. *Auk* 85:44-45.
- MURPHY, M. T. 1981. Growth and aging of nestling Eastern Kingbirds and Eastern Phoebes. *J. Field Ornithol.* 52:309-316.
- PECK, G. K., AND R. D. JAMES. 1987. *Breeding birds of Ontario. Nidology and distribution, Vol. 2. Passerines*. Royal Ontario Museum Life Sciences Miscellaneous Publications, Toronto.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of Great Tits *Parus major*. *Ibis* 108:313-347.
- SLAGSVOLD, T., AND J. T. LIFJELD. 1990. Influence of male and female quality on clutch size in tits (*Parus* spp.). *Ecology* 71:1258-1266.
- SMITH, H. G., KÄLLANDER, H. FONTELL, K., AND LJUNGSTRÖM, M. 1988. Feeding frequency and parental division of labour in the double-brooded Great Tit *Parus major*. Effects of manipulating brood size. *Behav. Ecol. Sociobiol.* 22:447-453.
- SMITH, J.M.N. 1978. Division of labour by Song Sparrows feeding fledged young. *Can. J. Zool.* 56: 187-191.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. In B. Campbell [ed.], *Sexual selection and the descent of man*. Aldine Press, Chicago.
- WESTNEAT, D. F. 1988. Male parental care and extra-pair copulations in the Indigo Bunting. *Auk* 105: 149-160.
- WINKLER, D. W. 1987. A general model for parental care. *Am. Nat.* 130:526-543.
- WITTENBERGER, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. *Condor* 84:22-39.
- WRIGHT, J., AND I. CUTHILL. 1989. Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* 25:171-181.