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## Food abundance and parental care in yellow warblers (*Dendroica petechia*)

Received: 17 May 1994/Accepted after revision: 19 February 1995

**Abstract** Emlen and Oring (1977) suggested that monogamy in birds is maintained because of the need for strict biparental care. A corollary of their suggestion is that paternal care should decrease under conditions of high food abundance. An alternative is that paternal care would increase if males take advantage of the higher food abundance by trying to reduce the length of the nestling feeding period. We tested these two ideas using yellow warblers (*Dendroica petechia*) by providing some pairs with supplemental food, thereby reducing the importance of biparental care. However, the extra food did not decrease paternal effort, nor did it increase it (Fig. 2). Early in the nestling period experimental females brooded more but visited their nestlings less than did control females, but later, when brooding times decreased, experimental females fed their nestlings more than did control females (Fig. 3). There were no significant differences in nestling survival (Fig. 5), but nestlings in the control treatment were larger and heavier up to 6 days old (Fig. 6). The main effect of supplemental food was on maternal, not paternal behaviour. Models of biparental care assume interdependence between the parental effort of both parents. In this species, however, males and females provide for their brood independently from each other.

**Key words** *Dendroica petechia* · Food Supplementation Parental care · Maternal Care · Nestling growth and survival

### Introduction

Lack (1968) noted that one likely advantage of monogamy is that two parents can feed young, and hence raise more offspring than if one parent does all the work. Emlen and Oring (1977) suggested that monogamy in birds is maintained because two parents are required to rear young successfully, and, even if the opportunity for polygyny exists, the requirements of parenthood prevent males from exploiting this polygyny potential. Emlen and Oring were attempting to explain interspecific differences in mating systems, but their idea also generates predictions about patterns of parental care, which can be and have been tested intraspecifically. Two corollaries about parental care in monogamous species arise from Emlen and Oring's suggestion. First, paternal care is expected to increase offspring survival and/or growth. Second, in conditions of high food abundance when strict biparental care is not required, males should reduce their paternal care to attempt to exploit any opportunities for polygyny.

In many studies that have tested the first prediction male help has been reduced by removing the males. Sometimes no effect has been observed (e.g. Gowaty 1983; Greenlaw and Post 1985; Martin and Cooke 1987; Sasvári 1990; Dunn and Hannon 1992; Hipes and Hepp 1993). Other studies have found significant effects only if the male is removed when nestlings are very young (Sasvári 1986), only in some years (Bart and Tornes 1989; Duckworth 1992), or only in some localities (Dunn and Robertson 1992). The expected decreases in nestling survival (e.g. Sasvári 1986; Lyon et al. 1987; Wolf et al. 1988; Johnson et al. 1992; Meek and Robertson 1994) or growth (e.g. Weatherhead 1979; Smith et al. 1982; Björklund and Westman 1986; Whillans and Falls 1990) have also been found. A limitation of these studies is that although the presence of a male may increase the reproductive output, it cannot be concluded that paternal care is the main

contributing factor. Studies in which paternal care is reduced without actually removing the males (e.g. Wright and Cuthill 1989) show that even partial reductions of paternal care significantly reduce nestling growth.

A second corollary of the suggestion of Emlen and Oring (1977) is that males should reduce their paternal care when the need for such care is lower, such as in conditions of high food abundance. In western gulls (*Larus occidentalis*), a species in which both sexes incubate, Pierotti (1981) found that in populations for which food was more abundant, females spent more time incubating, and males, freed from this task, devoted more time to interspecific aggression and the pursuit of extra-pair copulations. In bobolinks (*Dolichonyx oryzivorus*) feeding of nestlings by males is greater in years of low food abundance than in years of high food abundance (Wittenberger 1982). Dunn and Robertson (1992) compared two tree swallow (*Tachycineta bicolor*) populations and found that parental contribution of males relative to that of females was greater in the population with a lower food abundance; however, there were no differences in the frequency of polygyny. All these studies rely on comparisons across populations or years, which, understandably, limits the sample sizes.

An alternate approach to comparing populations would be to experimentally manipulate food abundance only at some nests. In this study, pairs of yellow warbler (*Dendroica petechia*) broods, matched by hatching day, were allocated to one of two treatments: supplemental food or control. Supplemental food could affect male behaviour in two ways: males may decrease their paternal effort, perhaps to devote time to the pursuit of additional mates or EPCs, or they may increase their paternal care in an attempt to decrease the length of the nestling period and perhaps attempt to breed again.

## Methods

The field work was conducted from May to July 1993 at Point à Fourneau (45.22°N, 73.51°W), on Île Perrot, Québec, Canada. Mist nets were used to capture the birds. Each bird was banded with a numbered aluminium United States Fish and Wildlife Service (USFWS) band and a unique combination of three coloured plastic bands. The tarsus, wing chord, rectrix, 9th primary feather length and weight of each bird were recorded at the time of banding. Dates of nest completion, first eggs, hatching and fledging were also recorded, as well as cases of predation or destruction of nests, and re-nesting attempts. Cowbird parasitism was widespread; all cowbird eggs were removed.

Five days into the incubation period (incubation lasts about 10 days) a tray of 5 cm diameter was placed within 30 cm of each nest. Every morning until hatching five mealworms (*Tenebrio molitor*) were placed in each tray. This presumably allowed the parents to learn to recognize the tray as a potential food source. Pairs of nests matched by their hatch date were, on the day after hatch, randomly assigned to the two treatments: one in the experimental group and the other in the control group. In the experimental group supplemental food was increased to 30 mealworms per day, and in the

control group food was no longer added. A total of 38 nests was used, 19 in each treatment.

The nutritional content of mealworms is similar to that of items normally consumed by yellow warblers. The protein content of chironomids and larvae consumed by yellow warblers is 59.8% and 62.6% respectively (Biermann and Sealy 1982). Mealworms were 63.5% protein and 20.9% fat. The daily supply of 30 worms weighed about 3 g and provided 77.7 J of energy.

When nests were assigned to a treatment, nestlings were mixed among broods. We considered all nestlings from a particular pair of nests plus all others from the population at approximately the same stage of development. From this pool, four nestlings, excluding those particularly small or large, were assigned to each nest. Clutch and brood sizes are smaller later in the season, so in some cases only three nestlings per nest were available for a given pair of nests. Each nest ended up with four or three relatively uniform-sized young, some of which had been originally at that nest. This procedure removed any potential correlations between the quality of the parents and their young.

Forty-minute nest watches were carried out every 2 days at each nest, beginning 2 days after hatch. During the first 10 min behavioural data were not collected, but the presence and identity of the parents was confirmed. Nest watches of experimental nests were conducted immediately after the food was added. During these watches the number of times parents visited the nest, visited the nest to feed their nestlings, and the time spent brooding were recorded. Nest visits include nestling feeding visits. The two variables were noted because parents sometimes visit their nests with food but fail to deliver it, visit without any food, or visit to remove faecal sacs. Nestlings were weighed after the first and second nest watches. After the third watch we recorded the weights, wing chord, ninth primary feather and tarsus lengths. Nestlings were not disturbed after the fourth and fifth watches because of the risk of forced fledging, which normally occurs around day 10. To eliminate other potential sources of variance, nest watches were not conducted during inclement weather, and, if possible, they were conducted before noon.

Differences in feeding and visiting rates, brood size, mean nestling mass and total nestling biomass between the two treatments were tested using type III sums of squares mixed-effects unbalanced repeated-measures ANCOVAs. Treatment was the grouping variable and nestling age the covariate; treatment  $\times$  age interaction and nestling age effects were removed from the model if not significant (i.e.  $P > 0.10$ ). All effects were tested using the nest-within-treatment mean sums of squares as the error term (Winer 1971; LaTour and Miniard 1983; Potvin et al. 1990). When testing for differences in paternal care only 30 nests were used because data obtained after nests were no longer being built or first eggs being laid were excluded from the analysis.

Because fledging may occur before day 10, fifth-watch data were obtained from only five nests: three control and two experimental. The aforementioned analyses were also carried out excluding these data, as well as with feeding and visiting rates calculated based only on the time not spent brooding, and on a per-nestling basis. Only cases when these latter analyses yield statistically different results will be shown hereafter. Similarly, nestling feeding rates were significantly and highly correlated with nest visiting rates for both males ( $r_s = 0.8896$ ,  $n = 139$ ,  $P < 0.0001$ ) and females ( $r_s = 0.7867$ ,  $n = 139$ ,  $P < 0.0001$ ). So, for ease of presentation, only nest visiting rates will be shown. Differences in nestling size at day 6 were analysed using type III sums of squares fixed effects unbalanced ANOVAs.

## Results

During most of the study period new nests were constantly being built, and first eggs were continuously

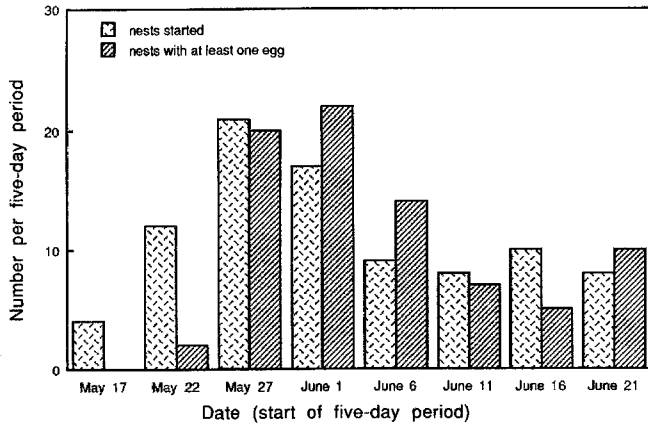


Fig. 1 Frequency of new nest building and first egg laying during the breeding season

being laid (Fig. 1). This shows that the potential to obtain additional territories, extra-pair copulations or fertilizations existed for all males, except those who nested very late. Data obtained after nests were no longer being built or first eggs being laid were excluded from comparisons of paternal care.

There was a significant increase in male visiting rates with nestling age, but supplemental food had no significant effects on male visiting rates (Fig. 2). Similar conclusions are drawn if the analyses are carried out with day 10 data deleted, or if nestling feeding of nest visiting rates are calculated in a per-nestling basis.

Female parental care involves two mutually exclusive activities: providing food, and brooding. When nestlings were 2 days old control females visited more than experimental females, but the reverse was true thereafter, which resulted in significant treatment × nestling age interaction effects (Fig. 3a). The opposite

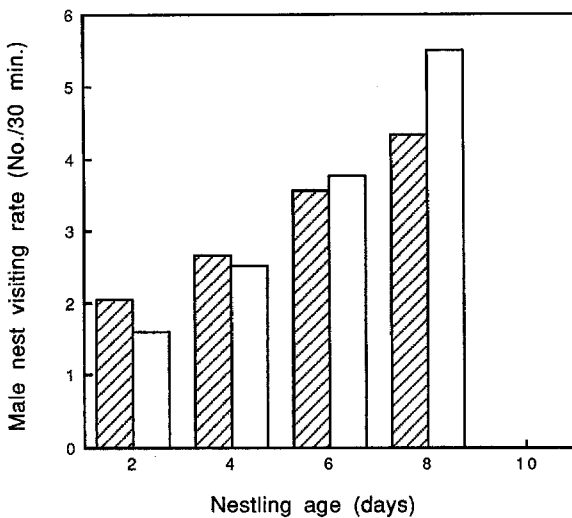


Fig. 2 Effect of supplemental food on paternal effort as estimated by nest visiting rates. Data obtained after 25th June are excluded, as well as day 10 data, when data were obtained from only two males. Nestling age  $P = 0.006$ ; treatment N.S. (Shaded bars control, open bars experimental birds)

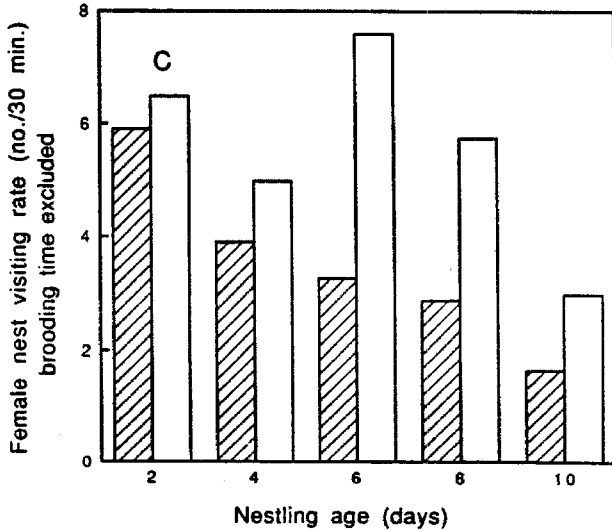
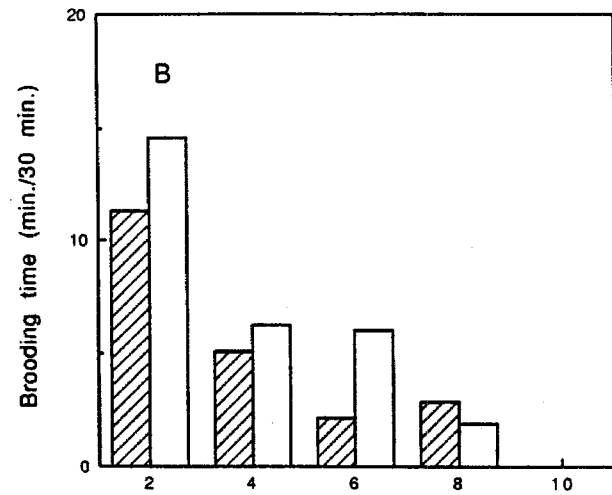
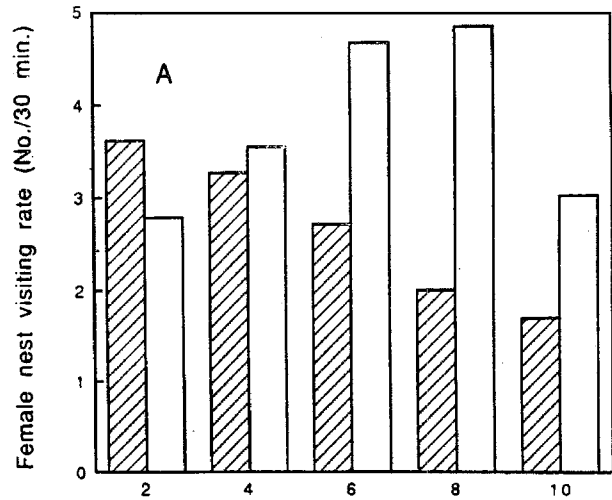


Fig. 3A–C Effect of supplemental food on maternal care. A Visiting rate: Treatment × nestling age interaction  $P = 0.024$ . B Time spent brooding: Treatment N.S., nestling age  $P = 0.006$ . C Visiting rate excluding time spent brooding: treatment  $P = 0.035$ , Nestling age  $P = 0.079$ . (Shaded bars control, open bars experimental birds)

pattern occurred in female brooding times: females in the supplemental food treatment spent more time brooding, especially when their young were 6 days old or younger, but these differences were not significant (Fig. 3b). This lack of significance is likely because of the reversal of the trend when nestlings were 8 days old, when only four females brooded. If maternal care is analysed excluding the time spent brooding, experimental females visited significantly more than did control females (Fig. 3c).

The patterns of total nest-visiting rates were similar to those of female nest-visiting rates. Initially, control nestlings received more attention than experimental nestlings, but later the reverse was true (Fig. 4).

Supplemental food did not have a significant effect on nestling survival. Brood sizes were standardized

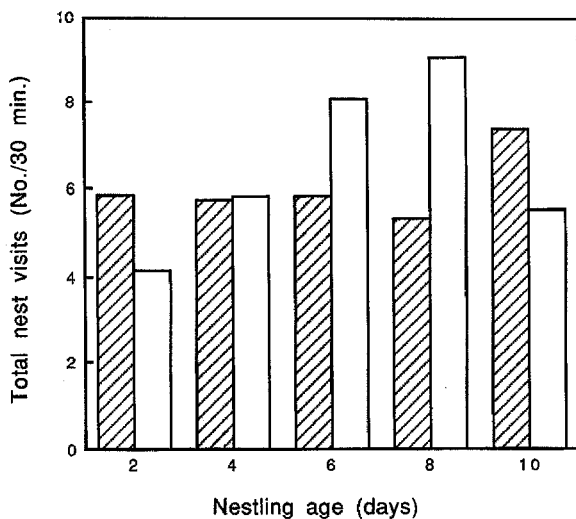


Fig. 4 Effect of supplemental food on total parental care, as estimated by nest visiting rates. Treatment  $\times$  nestling age interaction  $P = 0.0625$ . (Shaded bars control, open bars experimental birds)

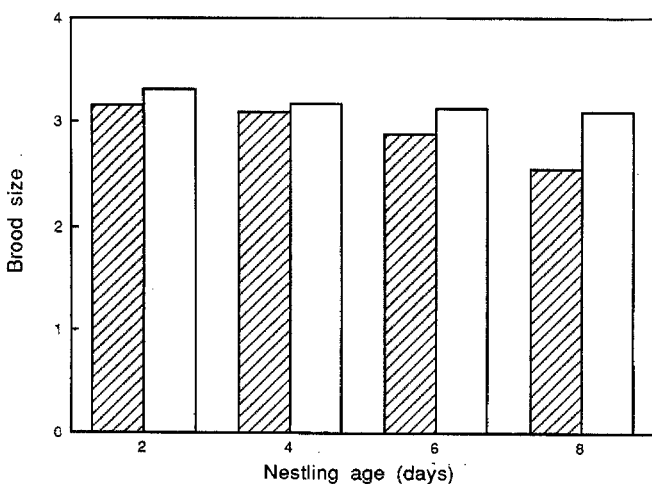


Fig. 5 Effect of supplemental food on nestling survival. Treatment N.S., nestling age N.S. (Shaded bars control, open bars experimental birds)

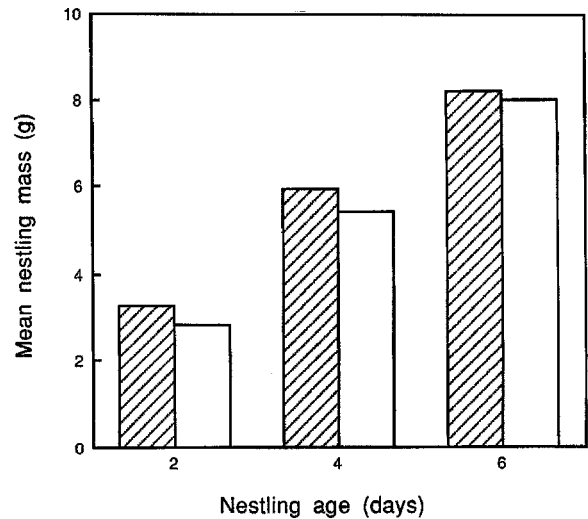


Fig. 6 Effect of supplemental food on nestling growth. Treatment  $P = 0.001$ , nestling age  $P = 0.001$ . (Shaded bars control, open bars experimental birds)

Table 1 Relationship between supplemental food and mean nestling size at 6 days of age. Shown are the means, SEs and 2-tailed  $P$ -values resulting from univariate ANOVAs;  $n = 28$ , 15 control and 13 experimental nests

	Control	Experimental	$P$
Wing chord (mm)	28.2 (0.81)	25.8 (0.92)	0.056
9th primary (mm)	12.2 (0.66)	10.2 (0.64)	0.038
Tarsus (mm)	18.4 (0.26)	17.5 (0.26)	0.024

at the start of the experiment (means = 3.39, SEs = 0.1118, for both control and experimental nests); however, brood sizes of experimental nests were higher than those of control nests (Fig. 5), although not significantly so. Nestling growth reflected parental care effort and nestlings from experimental nests were significantly lighter up to day 6 (Fig. 6) and, at day 6, smaller (Table 1) than nestlings from control nests.

Only one pair renested after having successfully raised a brood. This pair had been in the supplemental food treatment. No instances of social polygyny were observed.

## Discussion

Previously, the effect of food abundance on parental care has been studied only correlationally by comparing two or more populations, or one population across several years. In this study the relationship was examined experimentally by manipulating food abundance and quantifying parental care. Additional food did not decrease the amount of parental care provided by males. The alternative, which is that males would

instead cooperate with their mates and increase their paternal care, did not occur either.

The lack of an effect calls into question whether males should have been expected to react at all to the manipulations of food abundance. However, parents at experimental nests used food from the trays regularly, both to feed themselves and their offspring, so parents were obviously aware of the food trays. Second, changes in parental feeding rates according to brood size (e.g. Carey 1990; Wright and Cuthill 1990), nestling age (e.g. Grundel 1987; Carey 1990) or nestling condition (e.g. Henderson 1975; Wittingham and Robertson 1993) occur in several species. Also, it has often been shown that if one member of a pair is removed, the remaining parent can increase its food delivery rate (e.g. Smith et al. 1982; Gowaty 1983; Björklund and Westman 1986; Lyon et al 1987; Whillans and Falls 1990; Wolf et al. 1991; Duckworth 1992). Therefore, it is likely that males noticed the change in conditions, but simply failed to react. Although the food provided did not significantly affect patterns of male care, it did influence other aspects of parental care.

Supplemental food had a significant impact on female behaviour. Female parental care involves a trade-off between brooding and providing food. Up to the time nestlings were 6 days old, females supplied with additional food spent more time brooding than control females, but the reverse occurred at a nestling age of 8 days. Brooding is most important for younger nestlings who have not yet developed the ability to thermoregulate, so females in the experimental treatment, not having to spend as much time foraging, brooded more when their young needed it most. In contrast, early in the nestling period experimental females visited their nests less than did control females, but later, as brooding times decrease, experimental females visited their nests more than did control females.

Control nestlings were larger up to 6 days old, but there were no significant differences in survival. The data seem to indicate that brooding mainly affects nestling survival whereas absolute feeding rates affect nestling growth. This may explain why early in the nestling period females under conditions of higher food abundance preferred to increase their brooding time at the cost of decreasing their nest visiting rates. Experimental nestlings were smaller at day 6 (Table 1). However, it is possible that by the time fledging occurred, experimental nestlings were larger than control nestlings, mirroring the differences in total parental care in the later stages of the nestling period. Unfortunately, it was impossible to measure older nestlings without causing early fledging.

These comparisons do not reflect time spent foraging by females, but rather number of nest visits. When nest visiting rates are considered exclusive of the time spent brooding (Fig. 3), it becomes apparent that, at all times during the nestling period, experimental

females visited their nests relatively more often than control females. So, despite having less time to obtain food, experimental females provided more for their offspring, and this is probably because the costs of obtaining food were much lower.

We have previously found that male help is important and variable, but females do not compensate for decreases in male help (Lozano and Lemon in press). Taken together, our findings indicate that the parental contribution of males is less flexible than that of females, and that males and females provide for their brood independently from each other. Female effort does not depend on the amount of paternal care males provide, and only increases if the costs of obtaining food are lowered. On the other hand, males do not react to these same changes in food abundance. This system is at odds with models explaining how biparental care is maintained (Chase 1980; Houston and Davies 1985), which view biparental care as cooperation or reciprocal altruism, whereby the amount of parental effort an individual provides depends on the amount of parental effort provided by its mate. Perhaps biparental care can be maintained simply if both parents face fitness costs due to reductions in parental care.

**Acknowledgements** We thank G. Goggin-Michaud for helping with the field work, and J. Mountjoy, S. Perreault and K. Motley for helping to find nests. The financial support provided by NSERC, FCAR Funds, and the John K. Cooper Foundation is much appreciated. P. Dunn, M. Elgar, J. Mountjoy and S. Perreault reviewed previous versions of the manuscript.

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Communicated by M. A. Elgar