Parental-care responses by yellow warblers (*Dendroica petechia*) to simultaneous manipulations of food abundance and brood size

G.A. Lozano and R.E. Lemon

Abstract: Theoretical models view biparental care as a state of equilibrium that can be maintained only when the amount of parental care provided by one parent depends on the amount provided by its mate. According to these models, biparental care results when a decrease in the contribution of one parent is partially, but not completely, compensated for by an increase in the contribution of the other parent. Furthermore, this equilibrium state can only be stable if any other external factor affects male and female effort equally. We used yellow warblers (*Dendroica petechia*) to examine whether changes in brood size and food abundance affect the parental contributions of the sexes equally. Supplemental food did not affect parental care by either sex, but brood size did. Both males and females provided more to larger broods, and in large broods only, their provisioning rates increased with nestling age. Parental effort per nestling was similar in the two sexes, being higher for smaller broods and increasing with nestling age. Based on brood biomass, parental effort was greater for smaller broods, and decreased with nestling age in females only. Therefore, in agreement with current models of the maintenance of biparental care, the effects of brood size and nestling age on parental care did not differ significantly between the sexes. Nonetheless, data from other species and theory indicate that the costs and benefits of providing parental care differ between the sexes, so it is unlikely that biparental care can be maintained solely by a partial compensation response.

Résumé : Les modèles théoriques définissent les soins biparentaux comme un état d'équilibre qui ne peut être maintenu que lorsque l'importance des soins assurés par un parent dépend de l'importance de ceux assurés par son conjoint. D'après ces modèles, les soins apportés aux petits sont biparentaux lorsque la diminution de la contribution d'un parent est partiellement, mais pas entièrement, compensée par une augmentation de la contribution de l'autre. De plus, cet état d'équilibre n'est stable que si tout facteur externe affecte également l'effort du mâle et celui de la femelle. Nous avons tenté de déterminer si la taille de la couvée et l'abondance de la nourriture affectent également la contribution des deux parents chez la Paruline jaune (*Dendroica petechia*). L'addition de nourriture n'affecte pas les soins apportés par l'un ou l'autre parents, mais la taille de la couvée a de l'influence. Les mâles et les femelles apportent une contribution accrue aux couvées plus grosses et il n'y a que chez les grosses couvées que la fréquence des apports parentaux de nourriture augmente en fonction de l'âge des oisillons. L'effort parental par oisillon est égal chez les deux parents, est plus élevé dans le cas des petites couvées et augmente avec l'âge de l'oisillon. L'effort parental calculé par biomasse de couvée est plus élevé dans le cas des petites couvées et diminue avec l'âge des oisillons seulement chez les femelles. Ces résultats sont en accord avec les modèles courants sur le maintien des soins biparentaux, à savoir que les effets de la taille des couvées et de l'âge des oisillons sur les soins parentaux ne diffèrent pas chez les mâles et les femelles. Néanmoins, les données sur d'autres espèces et d'autres théories indiquent que les coûts et bénéfices reliés aux soins parentaux diffèrent chez les mâles et les femelles et il est donc peu probable que les soins biparentaux ne puissent être que le résultat d'une réaction de compensation partielle.
[Traduit par la Rédaction]

Introduction

Biparental care can be viewed as a compromise between two individuals with both common and conflicting interests. Chase (1980) and Houston and Davies (1985) used this

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approach to develop similar models to explain how biparental care is maintained. Both models are based on the assumption that an individual's parental effort depends on the amount of parental effort contributed by its mate. Depending on how individuals respond to each other's parental effort, several equilibrium states are possible, ranging from the absence of parental care to complete biparental care. Biparental care results when a decrease in the contribution of one parent is partially, but not completely, compensated for by an increase in the contribution of the other parent. According to these models the compensatory response must be partial; complete compensation would lead to uniparental care.

This prediction has been tested recently in several biparental, socally monogamous species by experimentally decreas-

ing parental care in one parent and observing the response of its mate. Testosterone implants have been used to reduce male care in dark-eyed juncos (*Junco hyemalis*) (Ketterson et al. 1992) and barn swallows (*Hirundo rustica*) (Saino and Møller 1995). In both studies females compensated fully for reductions in male help. Wright and Cuthill (1989) found incomplete compensation when tail weights were used to manipulate the parental care of starlings (*Sturnus vulgaris*). Markman et al. (1995) used the tail-weight method in orange-tufted sunbirds (*Nectarinia osea*) and found incomplete compensation in only some aspects of parental care. In yellow warblers (*Dendroica petechia*), experimental reductions of male care significantly reduced nestling growth, but females did not match or compensate for the decreases in male help (Lozano and Lemon 1996). More examples are needed before generalizations can be made, but clearly, partial compensation does not always occur, and may not be a required feature of biparental care.

The aforementioned models do not negate the possibility of other factors affecting parental care. However, the assumption of interdependence, coupled with the prediction of partial compensation, means that any external factor must affect the parental contribution by the two sexes equally. The two parents cannot simultaneously use each other's contributions to regulate their parental effort and also respond independently to some other, external factor. Biparental care can only be maintained as long as any other factor increases or decreases the parental effort of both parents, in effect merely shifting the equilibrium point. In this experiment we used yellow warblers to test this corollary of current models of biparental care (Chase 1980; Houston and Davies 1985). We tested whether the two sexes responded similarly as we simultaneously decreased the costs of providing parental care by increasing food abundance, and manipulated presumed benefits by altering brood sizes.

We used brooding time and nestling-feeding and nest-visiting rates as estimates of parental care. Previous work with yellow warblers (Lozano and Lemon 1995) indicated that food abundance affects maternal care but not paternal care. On the other hand, we expected brood size to be an important determinant of parental effort for both sexes (Trivers 1972; Winkler 1987). However, changes in parental effort may not necessarily reflect changes in brood size (Lack 1947; Nur 1984), so we also considered parental care per nestling. Finally, parents often face a trade-off between the quality and quantity of the offspring they produce, so parental care may be regulated not solely by the number of nestlings but also by the size of these nestlings. Therefore, we also analyzed the effects of brood size and food abundance in terms of parental effort per total brood biomass.

Materials and methods

The fieldwork was carried out at Pointe à Fourneau (45°22′N, 73°51′W) on Île Perrot, Quebec, Canada, from May to July in 1994 and 1995. Upon their arrival at the breeding grounds, birds were captured in mist nets. Each bird was banded with a numbered aluminum USFWS band and a unique combination of three colored plastic bands. Several morphological measures were taken from each bird at the time of banding, including body mass, wing-chord length, and tarsus, rectrix, and ninth primary feather lengths.

Starting in the third week of May, the study area was searched

daily for nests. All nests were visited daily to determine the chronology of egg laying. Five days after incubation began, a clear tray (5 cm in diameter) was placed within 20 cm of each nest. At each nest, 10 mealworms were placed in the tray every morning until the day of hatch. This was done to give parents the opportunity to identify the tray as a potential food source and to confirm that the food in these trays was being consumed.

As nests became available they were grouped into quartets. All nestlings at a nest usually hatch within a 30-h period. The day after hatching started at a nest, the nest was randomly assigned to one of four treatments: supplemental food/large brood, supplemental brood/small brood, control/large brood, and control/small brood. These treatments entailed cancelling the supplemental food or increasing it to 50 mealworms per day, and exchanging chicks among nests to obtain a brood size of six or two. For each such exchange, all available nestlings from the population were used, which means that nestlings allocated to a nest may have hatched at several other nests, but they were all 1 day old and of approximately the same size. The median clutch size of nests used in this experiment was five eggs.

Nest watches were carried out daily at each nest when nestlings were from 2 to 6 days of age. Before each nest watch began, the nest was approached to count the nestlings, and if appropriate, to deliver food. The nest was then observed for 10 min from a concealed location about 10 m from the nest. This time was used to verify the identity of the parents, to ensure that they were continuing to feed their nestlings despite our presence, and, for nests in the supplemental food treatment, to confirm that the mealworms were being consumed. The test does not depend on whether the food is given to the nestlings or consumed by the parents; the intent was to provide an environment of higher food abundance and observe what the parents did under these conditions. In most cases, consumption of mealworms began as soon as they were placed in the dish. Data collection started following the 10-min pretrial period and continued for 30 min, during which time the number of nestling-feeding and nest-visiting trips and the time spent brooding by the female were recorded. Nest visits include nestling-feeding visits. The two variables were noted because parents sometimes visit the nest with food in their beaks but fail to deliver it, visit without any food, or visit only to remove faecal sacs.

Nestling masses were recorded after all nest watches. When nestlings were 6 days old their wing chords, ninth primary feathers, and tarsi were also measured. Nestlings were not disturbed thereafter because of the risk of forcing fledging. To eliminate other potential sources of variance, nest watches were conducted only under favorable weather conditions, and, if possible, only during the morning.

Data from 8 quartets were obtained in 1994 and 6 in 1995, for a total of 56 nests, 14 per treatment. However, because of inclement weather, time constraints, and nest losses, it was not possible to obtain data from nestlings of all five ages from every nest, therefore sample sizes range from 8 to 13 nests per treatment for each nestling age.

Variance due to differences between the two years was removed by carrying out a one-way ANOVA with year as the independent variable; the residuals of these ANOVAs were used in later tests. This procedure was carried out for brooding times, nestling-feeding rates, and nest-visiting rates, and not for the derived per-nestling and per-brood biomass variables. The derived variables were calculated after correction for year differences. All variables were subsequently transformed as required to remove any existing heteroscedasticity.

Parental effort was analyzed using type III sum of squares univariate unbalanced three-way repeated-measures ANOVAs (Ferguson and Tanake 1989; Maxwell and Delaney 1989; von Ende 1993; Winer et al. 1991). This analysis has the advantage of using all available data while avoiding pseudoreplication. Parental effort was first analyzed separately for each sex with brood size and food presence as the main factors, nestling age as the repeated-measures factor, and all interactions. Parental care was also analyzed for all birds together,

Table 1. Correlations between male and female parental care, separately for each treatment.

Group	n	r	p
Nestling-feeding rate			
No supplemental food			
Two nestlings	44	0.2346	0.1253
Six nestlings	55	0.3762	0.0046
Supplemental food			
Two nestlings	51	–0.1357	0.3423
Six nestlings	49	0.3051	0.033
Total			
Two nestlings	95	0.0395	0.704
Six nestlings	104	0.3394	0.004
Nest-visiting rate			
No supplemental food			
Two nestlings	44	0.3386	0.0246
Six nestlings	55	0.3664	0.0059
Supplemental food			
Two nestlings	51	0.0784	0.5845
Six nestlings	49	0.2699	0.0607
Total			
Two nestlings	95	0.205	0.0464
Six nestlings	104	0.3106	0.0013

with sex and brood size as the main effects and nestling age as the repeated-measures factor. In these comparisons, interaction effects involving the factor "sex" were examined to determine whether statistically significant factors from previous analyses affected the parental effort of the sexes differently. Also, males' nest-visiting rates were compared with those of females and also with females' nest-visiting rates exclusive of brooding time.

Differences in nestling size were compared using a multivariate ANOVA with brood size and food presence as the predictor variables and tarsus, ninth primary, and wing-chord lengths as the dependent variables. All tests were two-tailed, and effects were accepted as statistically significant at $p < 0.05$.

Animals were handled in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Results

A one-way ANOVA was first carried out to account for variance between the two years. There were no significant differences between the years in males' nestling-feeding and nest-visiting rates, nor in females' nestling-feeding rates. The only significant differences between the two years were for females' nest-visiting rates ($F_{[1,197]} = 6.86$, $p = 0.0095$) and brooding times ($F_{[1,193]} = 7.51$, $p = 0.0067$). The mean number of female visits per half hour was higher in 1994 than in 1995 (4.61 vs. 3.30), but conversely, brooding times were higher in 1995 than in 1994 (744 vs. 526 s).

Nestling-feeding and nest-visiting rates were highly and significantly correlated for males ($r_s = 0.919$, $n = 199$, $p = 0.0001$) and females ($r_s = 0.8929$, $n = 199$, $p = 0.0001$). Therefore, for ease of presentation, only nest-visiting data will be mentioned hereafter, except when nestling-feeding data show distinct patterns and yield statistically different conclusions.

Male parental effort was weakly but significantly corre-

lated with female effort, in terms of both nestling-feeding ($r = 0.366$, $n = 199$, $p = 0.0001$) and nest-visiting rates ($r = 0.357$, $n = 199$, $p = 0.0001$). The strength of these correlations differed among treatments. Generally, the correlations were stronger in nests with six nestlings than in nests with two nestlings (Table 1), but this difference was statistically significant only for nestling-feeding rates ($Z = 6.55$, $p < 0.0001$).

Several results were consistent throughout all analyses. Food abundance did not have a significant effect on any aspect of parental care. Two-way interactions involving food abundance and all three-way interactions were not significant.

Parental care
The crucial prediction of the models was that the two parents would react differently to the manipulations. This prediction was tested by examining the interaction effects of sex with nestling age and brood size. However, this factor was not significant, therefore the effects of brood size and nestling age on parental care did not differ between the sexes.

Males attending larger broods visited their nests significantly more than males with reduced broods ($F_{[1,53]} = 20.05$, $p < 0.0001$). There was a significant increase in nest visits with nestling age among broods with six chicks ($F_{[4,68]} = 11.36$, $p < 0.0001$) but not among broods with two chicks ($F_{[4,58]} = 1.63$, $p = 0.1781$). Although the response of males with large broods was large enough to lead to a significant overall increase in nest visits with nestling age ($F_{[4,126]} = 8.99$, $p < 0.0001$), the brood size × nestling age interaction effect was not significant ($F_{[4,126]} = 2.17$, $p = 0.0766$), so the nestling age effect did not differ significantly between broods of two and six nestlings (Fig. 1a). The results were the same in terms of nestling-feeding rates, except that the brood size × nestling age interaction term was indeed significant ($F_{[4,126]} = 3.00$, $p = 0.0210$).

Female care consists of two activities that cannot be carried out simultaneously: brooding and feeding the nestlings. As with those of males, females' nest-visiting rates were significantly higher for larger broods ($F_{[1,53]} = 12.95$, $p = 0.0007$) and at older nestling ages ($F_{[1,126]} = 3.32$, $p = 0.0127$), but the differences were not as pronounced. When analyzed separately for each brood size, maternal care increased significantly with nestling age among enlarged broods ($F_{[4,68]} = 3.45$, $p < 0.0126$) but not among broods with two chicks ($F_{[4,58]} = 0.88$, $p = 0.4788$) (Fig. 1b). Brooding time decreased with nestling age ($F_{[4,122]} = 8.52$, $p = 0.0001$), so females' nest-visiting rates excluding the time spent brooding were not affected by nestling age ($F_{[4,114]} = 0.53$, $p = 0.7133$). Nestling-feeding rates excluding brooding time were higher for enlarged broods ($F_{[1,53]} = 6.58$, $p = 0.0132$), but there were no differences in nest-visiting rates ($F_{[1,53]} = 0.86$, $p = 0.3576$) (Fig. 1c).

Parental care per nestling
We also analyzed the effects of our manipulations on parental effort on a per-nestling basis. As before, the interaction effects involving sex were not significant. Therefore, when analyzed on a per-nestling basis, the effects of nestling age and brood size did not differ between the sexes.

Among males there was a highly significant increase in nest-visiting rates with nestling age ($F_{[4,126]} = 7.57$, $p = 0.0001$). However, in contrast to the previous analysis, male

Fig. 1. Male and female parental care responses to brood-size and food-abundance manipulations.
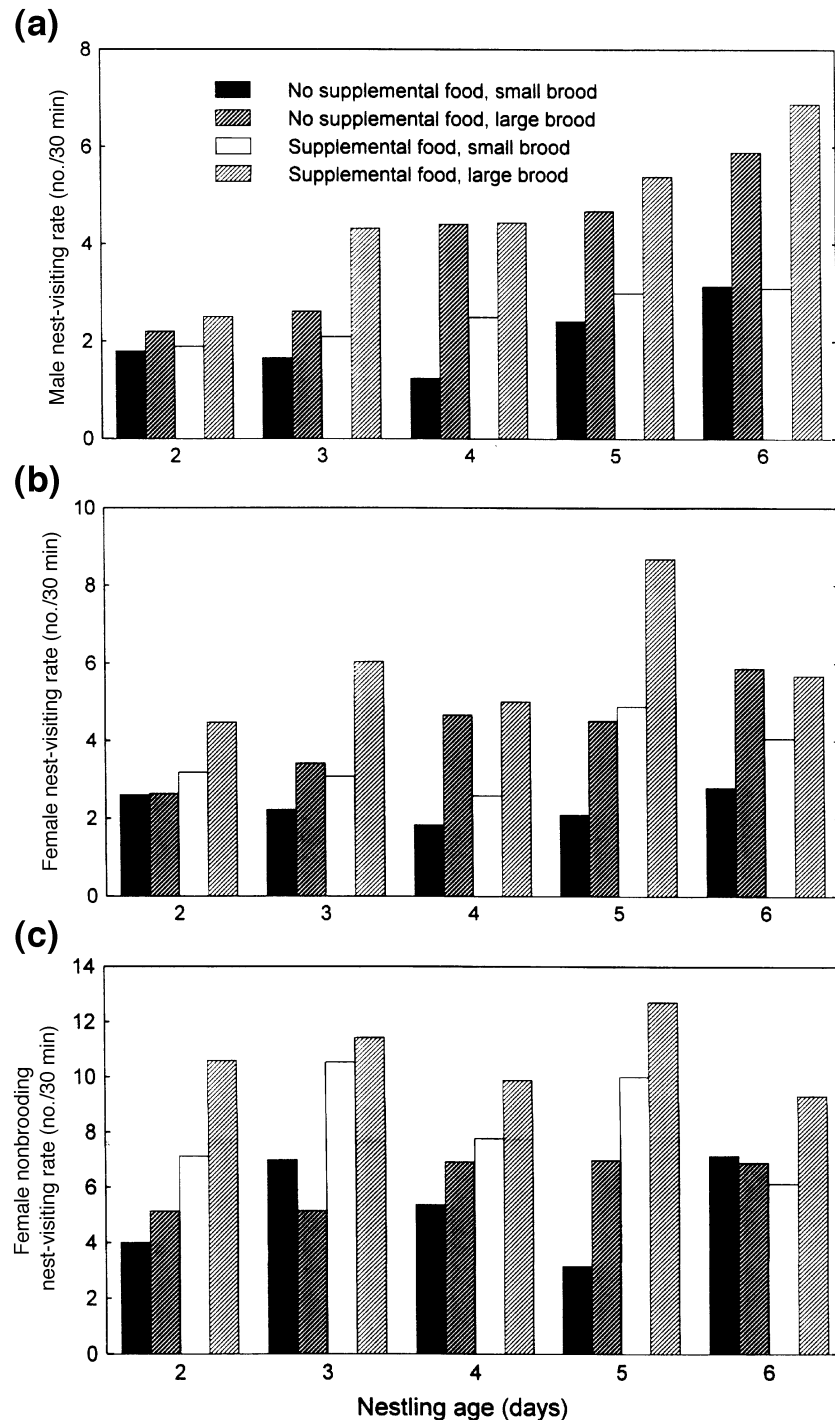
effort per nestling was greater in reduced broods than in enlarged broods ($F_{[1,53]} = 4.06$, $p = 0.0490$) (Fig. 2a).

Females responded similarly. Females' visits per nestling increased with nestling age ($F_{[1,126]} = 3.83$, $p = 0.0057$), although not as markedly as in males, and the number was higher for smaller broods ($F_{[1,53]} = 7.00$, $p = 0.0107$) (Fig. 2b). The time spent brooding per nestling was greater in reduced broods than in enlarged broods ($F_{[1,53]} = 8.80$, $p = 0.0045$), and there was also a significant decrease as nestlings grew older ($F_{[4,122]} = 5.90$, $p = 0.0002$). Consequently,

females' nest-visiting rates per nestling, exclusive of brooding time, were higher for reduced broods ($F_{[1,53]} = 8.57$, $p = 0.0050$) but did not change with nestling age ($F_{[4,114]} = 0.81$, $p = 0.5221$) (Fig. 2c).

Parental care per unit of brood biomass

Again, the interaction effects of nestling age and brood size with sex were not significant, which indicates that the effects did not differ between the sexes.

Even after accounting for differences in total brood bio-

**Fig. 2.** Male and female parental effort per nestling versus food abundance and brood size.
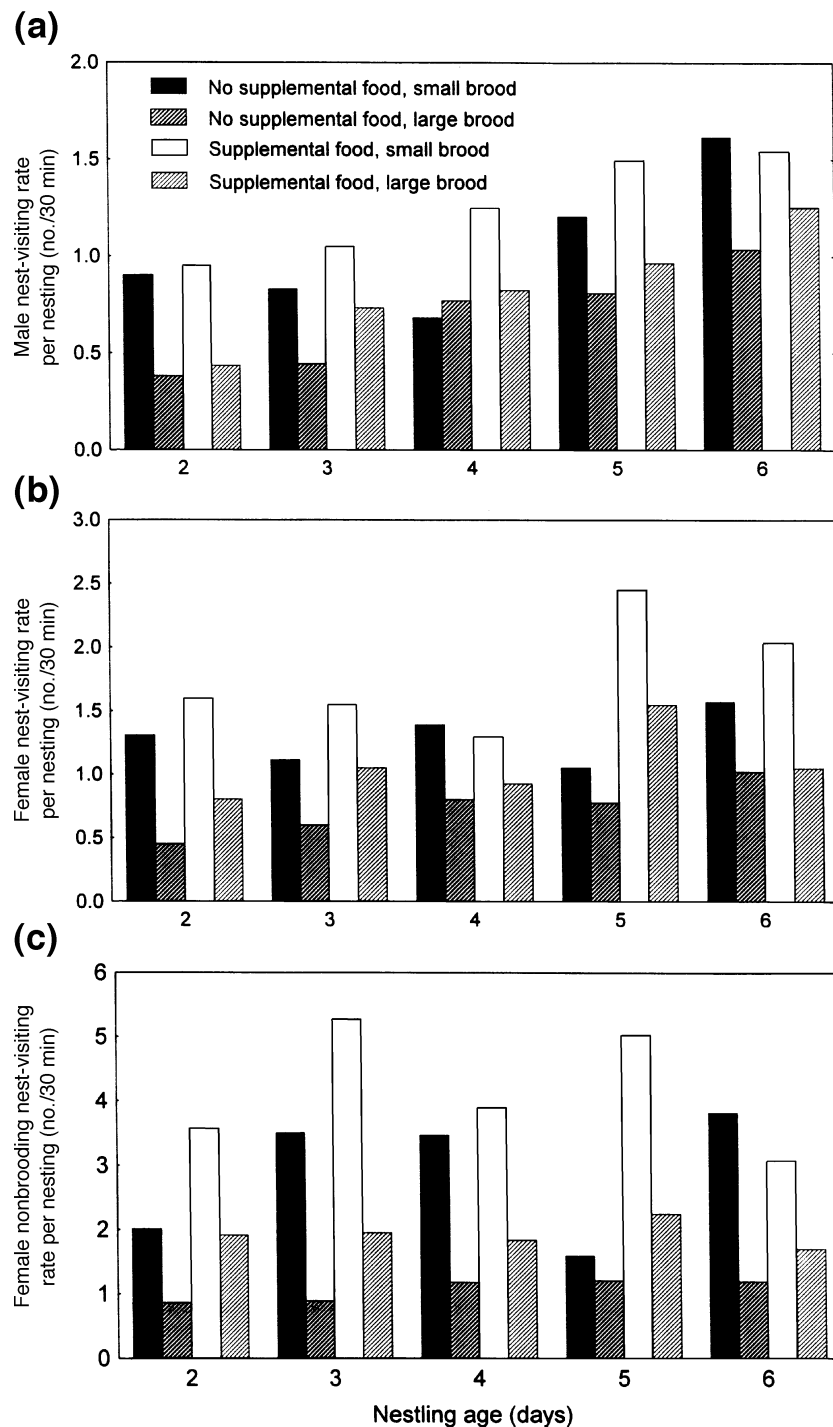
mass, both male and female care was significantly greater for reduced broods than for enlarged broods (males: $F_{[1,53]} = 8.41$, $p = 0.0057$; females: $F_{[1,53]} = 7.81$, $p = 0.0072$). This difference was more pronounced at 2 days of age, sufficiently so in females to yield a significant age effect ($F_{[4,124]} = 3.37$, $p = 0.0117$) (Figs. 3a and 3b)

The time spent brooding per unit of biomass was also significantly greater for reduced broods than for enlarged broods ($F_{[1,53]} = 16.32$, $p = 0.0002$) and decreased with age

($F_{[4,120]} = 23.48$, $p = 0.0001$). Females' visiting rate per unit of brood biomass, exclusive of time spent brooding, was also higher for reduced broods ($F_{[1,53]} = 9.61$, $p = 0.0031$), and decreased with nestling age ($F_{[4,112]} = 5.74$, $p = 0.0003$) (Fig. 3c). These results were generally similar to those of the previous "per-nestling" analysis.

Nestling survival and growth

Nestling survival was assessed separately for enlarged and

Fig. 3. Male and female parental effort per total brood biomass versus food abundance and brood size.
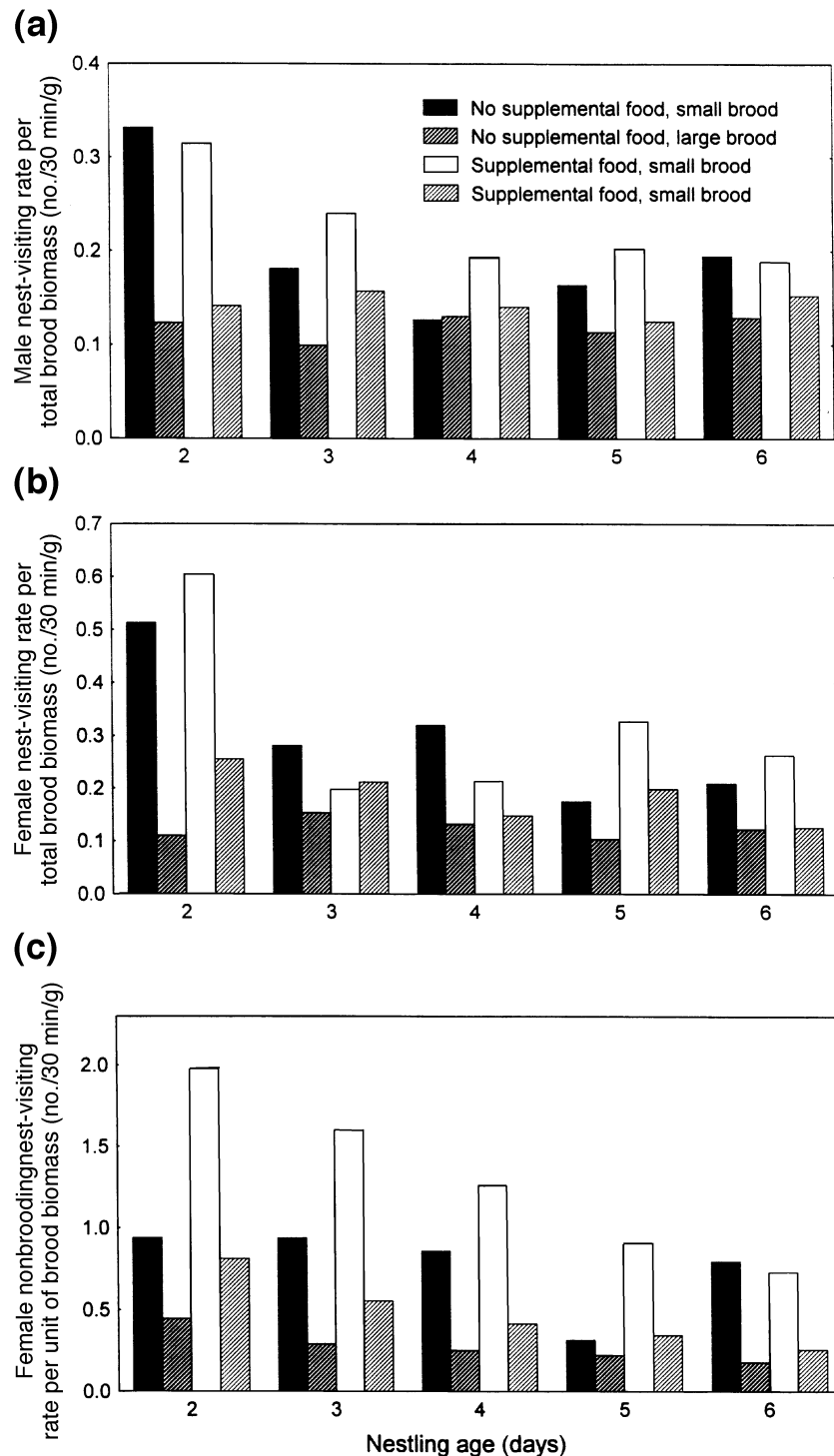
reduced broods. Initial brood sizes for these treatments were set at two and six nestlings, respectively. Any partial nest loss necessarily led to a decrease in mean brood size. As expected, in both groups the mean brood size decreased as the nestlings got older; however, the decrease was significant for enlarged broods ($F_{[4,88]} = 4.48$, $p = 0.0015$) but not for reduced broods ($F_{[4,88]} = 1.37$, $p = 0.2525$) (Fig. 4).

There were no significant effects of brood size or food sup-

plementation on mean nestling masses or nestling size, both measured at 6 days of age.

Discussion

An increase in food abundance had no significant effect on parental care at these two brood sizes. These results are partially consistent with our previous results (Lozano and Lemon

Fig. 4. Effect of food abundance and initial brood size on nestling survival. Open symbols denote no supplemental food and solid symbols supplemental food; squares denote reduced broods and circles enlarged broods.
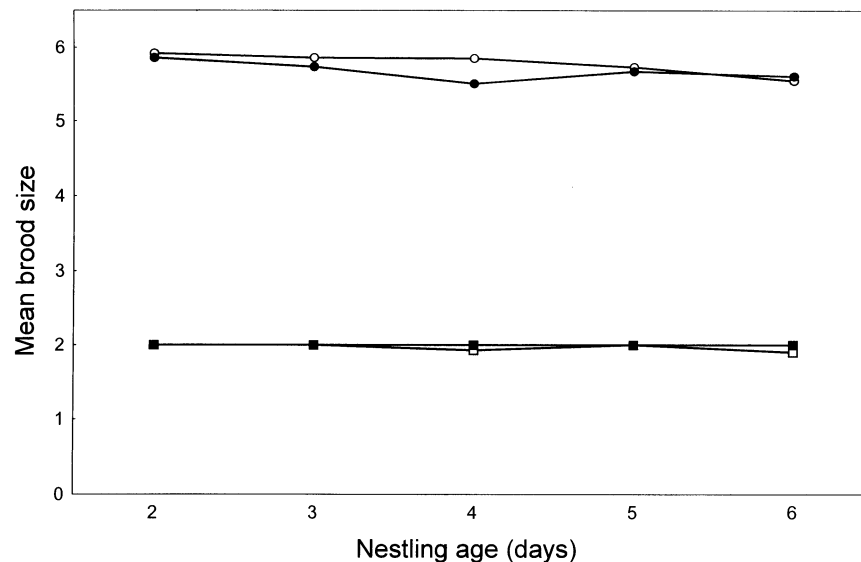
1995) in that food abundance did not affect male care, but the lack of a significant effect on maternal care was unexpected. In a previous study (Lozano and Lemon 1995) we found that when brood size was standardized at four nestlings, higher food abundance increased maternal care. In this study, supplemental food increased some measures of parental care only among enlarged broods, but these results were not statistically significant. We can only surmise that the effects of food abundance and brood size interact, so that at extreme brood sizes the effect of food abundance on parental care is lower than at normal brood sizes. However, more experimental studies are needed, so the question of how food abundance affects the relative contributions of the two sexes remains open.

In contrast, parental care was significantly affected by brood size and nestling age, congruent with findings from other species and with theoretical expectations. The interaction effects of nestling age and brood size with sex were not significant, which indicates that the effects did not differ between the sexes. For both sexes parental care generally increased with nestling age and brood size (e.g., Carlisle 1985; Curio 1987; Montgomerie and Weatherhead 1988; Markman et al. 1995). However, the brood size effect was not linear: the nest-visiting rate at nests with six nestlings was not 3 times those at nests with only two nestlings.

Parental care per nestling did not differ between the sexes, and was lower for both sexes at nests with large broods than at nests with reduced broods (Fig. 2). The latter result could be a consequence of two mechanisms. First, the requirements of large broods may be beyond what parents can provide, in accordance with Lack's (1947) hypothesis that brood size is determined by the maximum number of young that can be fed by the parents. The decreased nestling survival among enlarged broods (Fig. 4) also lends support to this hypothesis. Second, provisioning rates for reduced broods may be relatively higher because of the greater needs of these nestlings. Smaller broods lose heat faster, which means that before nestlings acquire the ability to thermoregulate, females have to

spend more time brooding, and afterwards nestlings may need to maintain a slightly higher metabolic rate (Dawson and Evans 1957; Dunn 1975; Verbeek 1995). This idea is supported by the fact that the provisioning rate per unit of brood biomass was still higher in reduced broods, and highest for 2-day-old nestlings (Fig. 3).

Present models view biparental care as one of several possible equilibrium states reached between two individuals whose parental contributions are interdependent (Chase 1980; Houston and Davies 1985). Several outcomes are possible depending on how individuals react to their partner's parental contribution. This interdependence requires that each parent must, directly or indirectly, be able to monitor its partner's contribution, and that any other external factor must affect the parental effort contributed by the sexes equally. The two parents cannot simultaneously use each other's contribution to regulate their parental effort and also respond independently to some other, external factor. The required interdependence of male and female effort cannot be maintained if only one parent adjusts its parental effort based on factors other than its mate's contribution.

When the sexes were analyzed separately, there were some differences between them. For instance, male care was greater in larger broods, and only in large broods did it increase with nestling age. In contrast, maternal care was higher in larger broods, and, independently of brood size, increased with nestling age. For both sexes parental effort per nestling was higher in smaller broods and increased with nestling age. Parental effort per unit of brood biomass was greater in smaller broods for both sexes; decreases with nestling age occurred in both sexes, but were significant only among females. However, when the sexes were analyzed together, the effects of nestling age and brood size on parental care did not differ significantly between the sexes.

The only major distinction between the sexes is that only for female care were there significant differences between the two years of the study. In 1994, females visited their nests more but brooded less than in 1995, probably because 1994

was more rainy than 1995. Only females brood, so it is perhaps not surprising that climate has an important effect on female care but no detectable effect on male care. These results also highlight the trade-off faced by females between providing two types of parental care: brooding and nestling feeding. It is likely that parental care is also regulated by factors besides those manipulated in our experiment, and some of these may affect the sexes differently.

Evidence from other species indicates that the parental contributions of males and females are not necessarily regulated by the same factors, or at least not to the same extent. For example, in pied flycatchers (*Ficedula hypoleuca*), Moreno et al. (1995) found that brood size affects energy expenditure in males but not females. In mountain chickadees (*Parus gambeli*), the contribution by males relative to females increased with brood size (Grundel 1987). In northern mockingbirds (*Mimus polyglottos*), the relative contribution by males increased with nestling age (Breitwisch et al. 1986). In great tits (*Parus major*), experimentally elevated ectoparasite loads led to increases in male, but not female, effort (Christe et al. 1996). Therefore, the fact that male care and female care are regulated differently is not new. However, the implications of these results for current models of maintenance of biparental care have been generally overlooked.

Markman et al. (1995) suggested that parental contribution systems could be better explained by considering the benefits to males and females of parental and nonparental activities, rather than by current models of biparental care. The benefits of providing parental care can differ drastically between the sexes depending on the occurrence of extra-pair paternity. In yellow warblers, for example, extra-pair paternity can vary within one population from 25.9% in one year to 43.2% in the following year (Yezerinac et al. 1995). This means that a large portion of parental effort in males has no direct bearing on their fitness and is, in effect, wasted, whereas females always allocate parental care to their genetic offspring. Consequently, maternal care is under stronger selection than paternal care, and we should expect female care to be regulated by a relatively wider array of factors, and females to be more responsive than males to the needs of their offspring.

Males should avoid caring for unrelated young, so paternal effort should correlate with paternity (Trivers 1972). Interspecific comparisons using 52 bird species show that feeding of nestlings by males is negatively correlated with the frequency of extra-pair paternity (Møller and Birkhead 1993). In contrast, intraspecific studies in socially monogamous and polygynous species have repeatedly failed to show any relationship between paternal care and extra-pair paternity (e.g., Frederick 1987; Gavin and Bollinger 1985; Leonard et al. 1995; Westneat 1995; Westneat et al. 1995; Yezerinac et al 1996). This apparent contradiction may be resolved if we consider that the rate of extra-pair parentage would be lower if males were able to detect it, and nonexistent if males had the ability to distinguish between within-pair and extra-pair young. There are some interesting scenarios in which males would benefit from knowingly caring for unrelated young (e.g., Soler et al. 1995; Zahavi 1995; Freeman-Gallant 1997), but otherwise, in biparental species, the benefits of extra-pair paternity could not accrue to females if males were able to adjust their parental effort according to their paternity.

In 1982, in support of empirical studies, Wittenberger wrote "No theory currently exists for predicting how parents should adjust their allocation as conditions change." More recently, Markman et al. (1995) stated that present models of biparental care are not sufficient to explain sex-related patterns of parental care. In our experiment we failed to show differences in the way male and female care is regulated. Nonetheless, data from other species and theory indicate that the costs and benefits of providing parental care differ between the sexes, so it is unlikely that biparental care can be maintained solely by a partial compensation response. However, more complex models would necessitate having determined the relationship between social mating systems and genetic mating systems, which is an issue of major importance facing behavioral ecology today.

Acknowledgments

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