



Flexibility in the Foraging Behavior of Blue Tits in Response to Short-Term Manipulations of Brood Size

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Abstract

Previous work suggests that short-term changes in feeding rate are usually produced by the parent-offspring interaction. However, few studies have properly tested this assumption. In this study, we attempt to explore the short-term consequences of daily (within-pair) brood size manipulations (reduced, original, and enlarged) on feeding behavior (provisioning rates, prey size, and prey type) of Mediterranean blue tits *Cyanistes caeruleus*. Total provisioning rates were lowest when broods were reduced in size and greatest when broods were enlarged. Mean prey size was also affected by the brood size changes: parents tended to bring larger prey when confronted with low brood demand reinforcing the view that a trade-off exists between minimizing foraging time and maximizing food quantity. Such differences in feeding frequencies and the load sizes delivered may be explained by changes in the parents' foraging tactic. Increase of brood size compelled parents to work harder and be less selective in prey choice; we found that stressed birds with a high level of feeding responsibility (hungry nestlings) opted to concentrate on more readily available food items (Tortricids). On the other hand, their immediate reaction when faced with a low level of feeding responsibility was to decrease this prey type in the diet, so that the percentage of other preys (Noctuids) in the diet increased. There was no intersexual difference in the way in which parents responded to the manipulation. In sum, our results revealed a flexibility in foraging strategies of blue tits to cope with changing scenarios, which supports the idea that provisioning behavior is largely governed by nestling demand.

Introduction

The classical models of optimal diets and central place foraging (e.g. MacArthur & Pianka 1966; Pulliam 1974; Charnov 1976; Orians & Pearson 1979) predict how a forager should behave to maximize the rate of energy delivery to a fixed location, e.g. a nest. These theories argue that the decision of prey choice would be solely dependent on extrinsic factors like caloric content, encounter rates, or handling time. More recent studies have emphasized the role of within-nest factors in explaining foraging

decisions (e.g. Lifjeld 1988; Bañbura et al. 2004). For instance, the body condition of the forager or the food requirement of the brood may change the optimal foraging strategy. Hence, load size and composition may vary with the number of nestlings present in the nest or their food requirements (i.e. hunger level). Despite the fact that brood size has been the focus of many investigations concerning reproductive effort (e.g. Royama 1966; Nur 1984; Rytönen et al. 1996; Robinson & Hamer 2000; see also Parejo & Danchin 2006 for a review), the consequences of alterations in brood demand on food

selection have been dealt with only rarely (Wright & Cuthill 1989, 1990a; Grundel 1990; Siikamäki et al. 1998). Most brood manipulation studies have used a fixed design, consisting of assigning a treatment to each nest for most of the breeding attempt. As far as we know, few studies (Wright & Cuthill 1990b; Magrath et al. 2007) have examined the provisioning behavior of parent birds in response to daily brood size changes; that is, the flexibility of both pair members to adjust parental effort in relation to brood demand. In this sense, it has been suggested that within nests, and within days, feeding rates may vary in the short-term because of weather fluctuations (Radford et al. 2001), time-of-day (e.g. Cowie & Hinsley 1988) or shortfalls in work rate of the partner (e.g. Wright & Cuthill 1990b). By being able to adjust their provisioning behavior to the new circumstances (e.g. desertion of the mate), parent birds may be able to cope with such unpredictable variations in conditions during the brood rearing period. A similar pattern is likely to occur when the number of nestlings to feed varies suddenly (from one day to the next).

Stephens (1990) recognizes as a single goal of avian parental foraging behavior, returning more food to the nest in less time. Many pathways exist to achieve this goal (Houston 1987). For instance, during a foraging bout, should the parent minimize the amount of time spent foraging or maximizes the amount of food delivered? Either course can yield a maximization of prey quantity relative to foraging effort (Grundel 1992). This ability to maximize provisioning ratio is strongly influenced by the quality of both the territory (e.g. Royama 1966) and the forager (García-Navas et al. 2009). However, prey load is also related to the time budget of the forager. A positive correlation between patch residence time (or load) and distance has so far been corroborated by field and laboratory studies in several species (e.g. Carlson & Moreno 1982; Kacelnik 1984), which is in agreement with the predictions of the marginal value theorem (Charnov 1976). Hence, it is generally assumed that higher feeding rates correlate with smaller prey items (e.g. Nour et al. 1998; Grieco 2002) and that this may be an optimal strategy to maximize short-term interests (i.e. survival of the nestlings) under stressful conditions (Lifjeld 1988). On the other hand, an increase in searching time or foraging distances is frequently associated with larger food items (e.g. Hurtrez-Boussès et al. 1998; see also Tremblay et al. 2005). To obtain a large item, more time is needed as, more small items will be discarded during the search (Grieco 2001). This suggests that

this strategy ('less but good') is more appropriate for periods where provisioning is less intense (low brood requirements). Hence, assuming that nestling demand drives diet choice, we would expect that under demanding brood conditions (hungry young) parents modify their foraging goal maximizing the rate of gain per unit of time, while, when confronted with satiated young, parents shift their foraging goal toward 'quality' maximization (net energy maximizers, Lifjeld 1988). Alterations in the parent-offspring interactions are likely to occur in a very dynamic way and thus, the term over which foraging goals are switched is expected to be very short (Tinbergen 1981).

In this study, we attempt to explore the short-term consequences of daily brood size manipulations on feeding behavior in a species with bi-parental care, the blue tit *Cyanistes caeruleus*. We asked: (1) whether parents modified their provisioning frequency from one day to the next when the brood demand was experimentally reduced or increased; (2) whether parents adaptively changed their criteria for prey choice according to the new scenario (reduced or increased time available for searching for food); and (3) whether males and females differed in their response to family size change (see e.g. Grundel 1987; Moreno et al. 1995).

Methods

Study Area and Basic Reproductive Parameters

The fieldwork was conducted in the 2009 breeding season in Quintos de Mora (Toledo province, central Spain, 39°24'23' N 4°4'19' W), a government-owned game reserve. A nestbox plot (Valdeyerno) located on a riverbank dominated by Pyrenean oak *Quercus pyrenaica* was chosen to perform this experiment. One hundred wooden nestboxes were mounted on tree trunks at heights of 1.5–2.0 m and protected from predators (woodpeckers and mustelids) with wire mesh (Mainwaring & Hartley 2008) and a polyvinyl chloride (PVC) pipe (length: 70–90 mm, diameter: 40 mm) fixed to the hole entrance. Frequent checks of the nestboxes provided data on laying date (1 = 1st Apr.), clutch size, hatching date, hatching success, and fledgling success for all breeding pairs. Adult birds were trapped while feeding nestlings of 8 d old. All birds were sexed according to the presence/absence of a brood patch and marked with a numbered metal ring. To facilitate further identification of each pair member, females were also fitted with colored plastic bands.

Experimental Manipulation

The brood size of 15 nests was manipulated experimentally. We transferred nestlings between nest dyads, selected so that they had hatched on the same date. Experimental manipulations were conducted between 4 and 17 of May. Nestlings were identified with colored plastic bands before they were transferred to the foster brood. On the first day of manipulation (day 10 post-hatching) both broods were left undisturbed (thus, this day served as a control). The following day (day 11 post-hatching) each nest was assigned to a reduced (minus two chicks) or enlarged (plus two chicks) treatment randomly (so at the same time the brood size of one nest was reduced, that the other was increased). The last day of manipulation (day 12 post-hatching) the treatments were inverted; i.e. the reduced brood increased and *vice versa*. In this way, each brood was subjected to the three treatments (reduced, control and enlarged). By alternating the order of treatments (i.e. some broods were reduced the second day and others on the third day) we precluded the existence of carry-over effects. Sample sizes differ among treatments (enlarged $n = 28$, control $n = 30$, reduced $n = 30$) because of a video camera (see below) that failed one day.

Monitoring Feeding Behavior

We manipulated broods to contain more (enlarged) or fewer (reduced) nestlings than the natural (i.e. unmanipulated) brood size, which ranged from 4 to 9. The provisioning behavior of parents was monitored to explore whether they modified their feeding patterns (provisioning frequency, prey size, and prey type) in response to the family size change. Feeding events were filmed by means of infrared video cameras (SONY handy-cam DCR-SR290E, SONY Corp., Tokyo, Japan) placed at the back of the nestbox and covered with a wooden enclosure. Using this set-up, it was possible to record parental provisioning rates and to identify the prey items delivered to the young. One day prior to filming, the front of the nestbox was substituted for another one with a PVC pipe of lesser diameter (35 mm) than the original, thus reducing the nestbox entrance, such that birds entered the nest slowly, thereby facilitating prey identification. All videotaping sessions took place between 16:30 and 18:00 h. The first half-hour of recording was discarded as birds take time (10–20 min) to resume feeding

activity after the disturbances that the video camera installation entails. Thus, 60 min of film (from 17:00 to 18:00 h) were analyzed per nest per treatment. Recordings were visualized frame-by-frame using the program ADOBE PREMIERE ELEMENTS 7.0 (Adobe Systems Inc., San Jose, CA, USA). For each feeding event the following parameters were noted: time of entry, sex of the parent, number of prey (i.e. single or multiple load), type of prey, and length of prey. The length of prey was measured with a ruler (± 0.1 mm) using a scale bar attached above the hole entrance as a known reference. Within each taxonomic category, items of prey were classified to three ordinal categories of body size [1 = *small* (length < 1.5 cm for caterpillars; < 1.5 cm for adult insects (moths, Hymenoptera, Orthoptera) and abdomen diameter < 0.2 cm for spiders); 2 = *middle* (length 1.5–2.5 cm, 1.5–2 cm and diameter 0.2–0.6 cm, respectively); 3 = *large* (length > 2.5 cm for both caterpillars and adult insects and diameter > 0.6 cm for spiders)] to make individual prey volumes comparable among taxa (see Bañbura et al. 2001). The adults could be identified by ringing details or according to their behavior (only females brood the young and take part in nest sanitation activities such as fluffing the nest structure looking for ectoparasites). Prey items were classified into two main groups: Lepidoptera larvae and 'others'. We further distinguished between caterpillars of the three major Lepidoptera families: Noctuidae (mainly *Orthosia* spp., *Dryobotodes* spp. and *Dicycla* oo), Tortricidae (*Tortrix viridana* and *Archips xylosteana*), and Geometridae (mainly *Erannis defoliaria* and *Operophtera brumata*) which are widely represented in our study area (Notario et al. 2007; García-Navas pers. obs.) and constitute the main food source of blue tits (Cramp 1998). Larvae belonging to other Lepidoptera families (Notodontidae, Lycanidae) were grouped into a separate fourth category. The second group ('others') included spiders (Aranea), pupae [both types of prey accounted for 33.3% of this group] and diverse food items (including Hemiptera, Hymenoptera, Orthoptera, vegetable tissue, fungus, eggshell, moths, and cocoons) that were lumped into a broad category called miscellaneous.

Caterpillar abundance increased gradually until it reached the moment of maximum availability (caterpillar peak date = 14th May); from this date caterpillar availability declined rapidly. There were differences in the availability of different prey species; Tortricids were 4-fold more abundant than Noctuids, the caterpillar species predominant in the

nestling diet (García-Navas & Sanz, submitted manuscript).

Statistical Analyses

In total, 1243 feeding trips were identified and used for analyses of feeding behavior.

To test for within-nest changes in feeding frequency and prey size with respect to brood demand we used repeated measures ANCOVA, where the sequence of treatments control, enlarged and reduced (or control, reduced, and enlarged) was the repeated measures factor. Nest identity and parental sex were included as a random effect and fixed factor, respectively. The inclusion of parental sex as a factor allowed us to determine if the magnitude of responses to brood size change differed between the sexes over the short-term. Hatch date was included as a covariate to assess the existence of a seasonal variation in the capacity of parents to cope with daily changes in brood demand. Parental sex and date were excluded from the model if their effect was non-significant. Pair-wise comparisons were used to test for changes between treatment dyads (e.g. control vs. enlarged). To test for the effect of the treatment on prey types, we calculated the mean delivery rate of each prey type delivered for each bird. First, we assessed the effect of the brood size treatment on the number (count data) of caterpillars brought to the nest. In a second step, we explored the consequences of the manipulation on different prey categories (Tortricids, Noctuids, Geometrids, spiders, pupae). Given the non-independence of these effects, we used repeated measures analyses of variance (RMANOVAs) which tested the changes in prey types simultaneously (overall Wilks' lambda statistic), as well as performing univariate tests on each prey type separately within the same model. In these cases, the assumption of sphericity was tested (Mauchly test), and Huynh-Feldt corrected degrees of freedom used if this assumption was not held. A similar analysis (effect of the treatment on prey choice, i.e. diet composition) was performed by using proportions (percentage of each prey type) instead of count data. We also compared the proportion of multiple-prey feeding events (two or three food items per load) among treatments. Previously, proportions were arcsine square root transformed before analysis to attain homoscedasticity and normality. Statistical analyses were performed with SPSS v.15 (SPSS Inc., Chicago, IL, USA) and STATISTICA 6.0 (Statsoft INC., Tulsa, OK, USA). All values presented are mean \pm SE, unless otherwise stated.

Results

Provisioning Rates

There was no effect of parental sex on feeding rates ($F_{1,26} = 1.77$, $p = 0.19$). This measure of parental effort differed between the three treatments ($F_{2,54} = 17.36$, $p < 0.001$, Fig. 1). The number of feeding events increased markedly after brood enlargement (enlarged vs. control; Wilcoxon matched-pairs signed-ranks test, $n = 28$, $Z = 2.31$, $p = 0.02$) whereas parents fed their young less when the brood size was reduced (reduced vs. control; Wilcoxon test, $n = 30$, $Z = 3.35$, $p < 0.001$). A similar result was found when performing the repeated measure ANCOVA separately for males and females (males: $F_{2,26} = 8.59$, $p < 0.01$, females: $F_{2,26} = 9.20$, $p < 0.001$). When considering the number of feeding events per chick we also found statistically significant differences among treatments ($F_{2,54} = 35.45$, $p < 0.001$) indicating that parents were able to fully compensate for the brood size enlargement (enlarged: 3.96 ± 1.54 , control: 2.23 ± 0.99 , reduced: 1.27 ± 0.81). The magnitude of the response to brood size change decreased slightly with the progress of the season (treatment \times date: $F_{2,52} = 2.95$, $p = 0.06$).

Size of Prey Items

The mean size of prey items was significantly affected by the manipulation of brood size ($F_{2,52} = 6.64$, $p < 0.01$, Fig. 1). *Post hoc* comparisons revealed that the blue tits responded to the reduced brood demand by increasing the prey size (reduced vs. con-

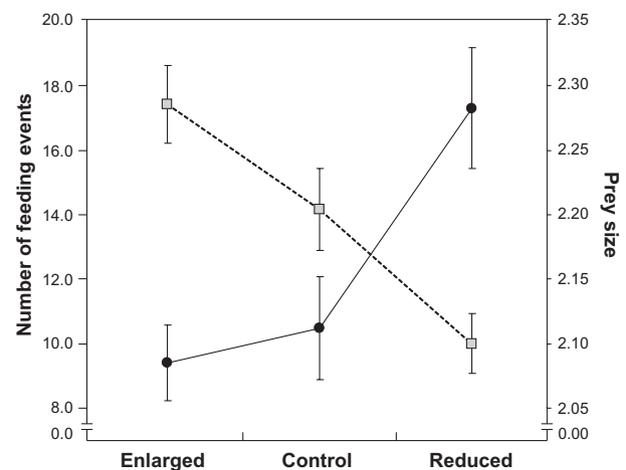


Fig. 1: Differences in feeding frequency (number of feeding events per hour; squares and discontinue line) and prey size (see Methods; circles and continue line) in relation to brood size treatment. Number of broods enlarged = 14, control = 15, reduced = 15. Mean \pm SE are given.

trol; Wilcoxon test, $n = 30$, $Z = 0.09$, $p > 0.50$). On the other hand, the mean size of prey provided when the constraints were harsher (enlarged broods) did not differ significantly from those provided under natural (i.e. original brood size) conditions (enlarged vs. control; Wilcoxon test, $n = 28$, $Z = 2.31$, $p = 0.02$). The size of prey items differed between sexes ($F_{1,26} = 5.12$, $p = 0.03$; males: 2.11 ± 0.14 , females: 2.19 ± 0.14) but the interaction of manipulation and sex was non-significant (treatment \times sex: $F_{2,52} = 1.65$, $p = 0.20$) indicating that males and females reacted in a similar way (tending to provide larger loads when the brood demand was low) to the brood size change. There was also no significant effect of calendar date on the level of response to the manipulation (treatment \times date: $p > 0.1$).

We also found a significant effect of the treatment when visit rates and load sizes were combined to get an estimate of overall energy per unit of time (biomass intake per nestling: $F_{2,54} = 30.60$, $p < 0.001$, Fig. 2). This means that parents really did compensate for the experimental changes in brood size, in terms of nestling intake rates (Fig. 2). That is, in spite of the reduced size of prey allocated to young when parents were faced with enlarged broods, the greater number of visits per hour per nestling outweighed the fact that each visit contained a smaller amount of food.

We further test for a possible effect of the order in which brood size manipulations were conducted. Broods were separated according to the treatment sequence ('control-enlarged-reduced' and 'control-reduced-enlarged'). There was no evidence for the existence of carry-over effects inherent to our experimental design with regard to feeding patterns (treatment sequence: $F_{1,26} = 0.49$, $p = 0.49$, Fig. 3a) or

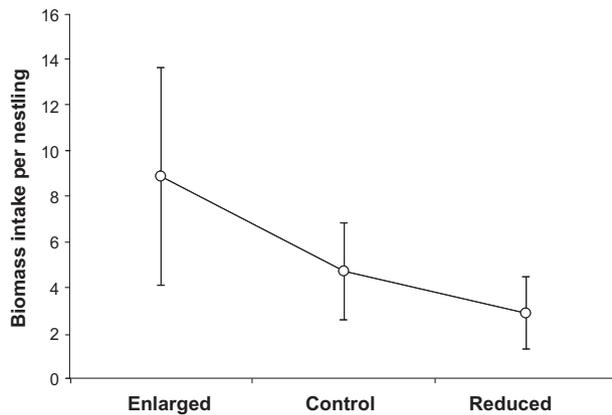


Fig. 2: Differences (Mean \pm SE) in biomass intake per nestling in relation to brood size treatment. Biomass intake is expressed as the result of the combination of feeding rates per nestling and load sizes.

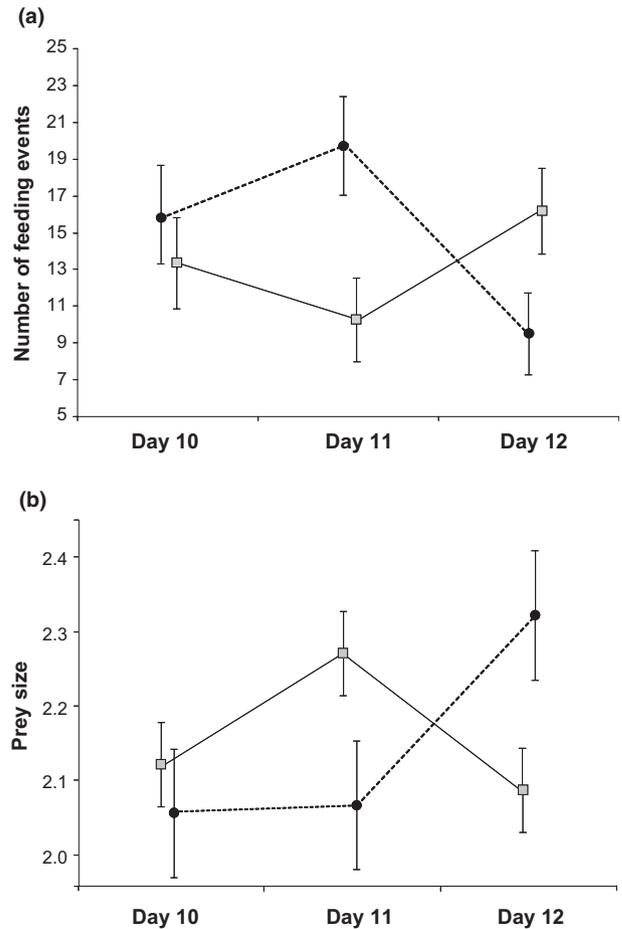


Fig. 3: Mean (\pm SE) feeding frequency (a; number of feeding events per hour) and prey size (b) for day 10, 11 and 12 post-hatching in relation to the order in which brood size manipulations were conducted (circles and discontinue line, treatment sequence: control-enlarged-reduced; empty squares and continue line, treatment sequence: control-reduced-enlarged).

load sizes (treatment sequence: $F_{1,26} = 1.95$, $p = 0.18$, Fig. 3b).

Prey Choice

The blue tit is mostly a single-prey loader; only 6.2% of all food items were brought in multiple loads. The percentage of feedings in which the parents returned with two or three prey items to the nest did not differ between the enlarged treatment and the control (7.8% vs. 6.6%, $p = 0.49$). However, the proportion of multiple-prey loads found after brood reduction (3.5%) was significantly less in comparison with that reported for the original brood sizes ($p = 0.05$). Lastly, we found that males and females differed from each other in the frequency of bringing more than one prey per trip; males were

Table 1: Differences in diet composition [delivery rates (mean \pm SE) and mean proportion (in parentheses) for each prey type] in relation to within-pair manipulation of brood size (BS). Nests were rotated through three different treatments on a daily basis (*enlarged*: plus two chicks, mean BS: 8.47; *control*: unmanipulated, mean BS = 6.47; *reduced*: minus two chicks, mean BS = 4.47)

	Treatment			Test	
	Enlarged n = 28	Control n = 30	Reduced n = 30	E-C	C-R
Lepidoptera larvae	13.03 \pm 1.25 (74.84) ^a	9.96 \pm 1.67 (70.28) ^a	6.80 \pm 0.80 (68.00) ^a	Z = 0.15*	Z = 2.07*
Noctuids ¹	5.82 \pm 0.46 (44.66) ^a	6.18 \pm 0.99 (62.04) ^{ab}	4.76 \pm 0.58 (70.00) ^b	Z = 1.99 ^{ns}	Z = 1.39 ^{ns}
Tortricids ¹	5.82 \pm 1.04 (44.66) ^a	2.71 \pm 0.74 (27.20) ^b	1.53 \pm 0.36 (22.50) ^b	Z = 3.15***	Z = 1.67 [†]
Geometrids ¹	0.36 \pm 0.13 (2.76) ^a	0.75 \pm 0.18 (7.53) ^b	0.27 \pm 0.09 (3.82) ^a	Z = 1.99*	Z = 2.95**
Other preys					
Pupae ²	1.07 \pm 0.23 (24.42) ^a	0.46 \pm 0.18 (10.92) ^b	0.60 \pm 0.16 (18.75) ^b	Z = 2.06*	Z = 0.75 ^{ns}
Spiders ²	0.28 \pm 0.10 (6.39) ^a	0.93 \pm 0.24 (22.09) ^b	0.54 \pm 0.12 (16.87) ^b	Z = 2.55**	Z = 1.70 [†]

Statistics shown are the result of planned comparisons between treatments (enlarged vs. control broods, E-C; reduced vs. control broods, C-R) with respect to mean delivery rate observed for each prey type. Proportions followed by different letters are statistically significant ($p < 0.05$)

¹Percentage with respect the total amount of caterpillars brought to the nest; ²Percentage with respect the total amount of other food items (non-Lepidopteran) brought to the nest.

^{ns} $p > 0.5$; [†] $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

more prone to deliver multiple loads than females (77.9% of the total number of multiple-prey feedings were performed by males, $\chi^2 = 21.22$, $p < 0.001$).

Caterpillars constituted the bulk of the nestling diet at Valdeyerno (70.5%, range: 21.4–100). There was an overall effect of treatment on the number of Lepidoptera larvae brought to the nest ($F_{2,54} = 9.19$, $p = 0.001$). We found statistically significant differences in the occurrence of caterpillars in the nestling diet between enlarged and unmanipulated broods (Table 1). Meanwhile, when parents experienced a decrease in the brood demand the occurrence of caterpillars in the nestling diet diminished significantly in comparison with that reported in natural conditions; i.e. parents feeding broods with the original number of chicks (Table 1). The delivery rate of caterpillars decreased with the advance of the season ($F_{1,26} = 3.98$, $p = 0.05$), but there was no treatment-by-date interaction ($F_{2,52} = 1.89$, $p = 0.16$). Parental sex had no effect on this parameter ($p > 0.5$).

There was a significant effect of treatment on nestling diet composition (RMANOVA, Wilks' statistic = 0.47, $F_{10,100} = 4.54$, $p < 0.001$), brood size treatment mainly affecting the delivery rates of Tortricids ($F_{2,54} = 12.27$, $p < 0.001$), Geometrids ($F_{2,54} = 5.71$, $p < 0.01$), spiders ($F_{2,54} = 4.94$, $p = 0.01$), and pupae ($F_{2,54} = 3.10$, $p = 0.05$). There was no effect of the treatment on the number of Noctuids brought to the nest ($F_{2,54} = 0.96$, $p = 0.39$). Blue tits responded to brood size enlargement by relying more heavily on both Tortricid larvae and pupae (Table 1) and by providing fewer spiders to young (Table 1). On the other hand, when the brood size was trimmed the delivery

rate of Tortricids was slightly lower in comparison with that reported for original (natural) brood sizes (Table 1). There were no date or sex-related differences on diet composition (all p -values > 0.05).

When analyzing prey choice decisions from the relative contribution of each prey type (i.e. percentages) to the nestling diet, we also found an effect of the treatment on the type of prey delivered by parents (see Table 1). For instance, when faced with reduced brood demand (i.e. relaxed time-budgets) parent birds incorporated a higher proportion of Noctuid species in the nestling diet in comparison with natural conditions (Table 1). The relative importance of this and other (spiders) prey in their hierarchy of foraging decisions diminished after brood size enlargement, when parents opted to concentrate on more readily available food items (Tortricids and pupae; Table 1).

Discussion

The results shown in this study indicate that blue tits were able to respond in a short-term manner (from one day to the next) in terms of parental effort and food selection to daily manipulations of brood size. Provisioning rates were influenced by our experiment, increasing when the brood size was enlarged from its original size and declining when the brood was trimmed. Hence, parents provisioning large broods made an effort to increase the number of visits to fulfill the greater requirements of the brood. This pattern, that is parents provisioning more frequently when feeding larger broods to maintain an almost constant level of food provisioning per

nestling, has not been reported previously in studies carried out on this species (Stauss et al. 2005) and on great tits *Parus major* (Naef-Daenzer et al. 2000). However, other authors have found that the increase in feeding rates reported for the enlarged broods was not proportional to the increase in the number of chicks. That is, parents were not able to compensate for additional nestlings (e.g. Nur 1984; Wright & Cuthill 1990b; Rytönen et al. 1996; Laiolo et al. 1998). A possible explanation for such discrepancies may lie in the existence of differences in diversity and distribution of food resources among study areas. For instance, the lack of clumped or sedentary prey items (see more below) could limit the degree of response or leeway of parents to increase their provisioning frequency when they are time limited (i.e. high brood demand).

On the other hand, mean prey size was also significantly related to brood size treatment with parents bringing larger prey in reduced broods and smaller prey in enlarged broods. This indicates that shorter foraging times may have led to a smaller quantity of prey being returned whereas that relaxed time-budgets may have led to an increase in prey size because of reduced constraints on selectivity. Strong evidence for this trade-off between quantity and quality of food comes from an experimental study with starlings *Sturnus vulgaris* in which it was found that high visit rates to larger broods were associated with larger loads per visit and changes in the type of prey delivered (Wright et al. 1998). In a study of pied flycatchers *Ficedula hypoleuca* parent birds took more large prey when they were feeding two well-fed nestlings than when they were feeding five hungry nestlings (Lifjeld 1988). Similarly, Grieco (2001) found in blue tits that short-term changes in feeding rates, apparently caused by changes in the brood's begging activity, changed the size of prey delivered. How do parents manage to increase the size of prey? There are two ways a foraging bird may deliver larger food items to the nest. Foragers may achieve larger prey by foraging at greater distances from the nest in search for less exploited feeding patches (Naef-Daenzer et al. 2000). Alternatively, a forager can spend more time searching for food, and increase its selectivity, i.e. reject a larger proportion of small or low-quality food items during each foraging bout (Lessells & Stephens 1983; Stephens & Krebs 1986). While we did not examine foraging distances in this study, the latter option (i.e. parents gathering larger prey by being more selective) seems more likely in our case taking into account that we rarely observed trees completely depleted in the surroundings of the

nests (García-Navas, pers. obs.). On the other hand, another plausible explanation for the longer trips away from small brood sizes could be linked to the opportunity that it offers for parents to travel further, self-feed or prospect alternative foraging areas, as well as making the return to the nest worthwhile if they come back with a larger load.

It is assumed that tits exhibit a preference for caterpillars whenever possible (see Cramp 1998 and references therein) and that a varied diet is much less advantageous than collecting as much as possible of the same type of food (e.g. Royama 1970; Blondel et al. 1991; Bañbura et al. 1994; but see Tinbergen 1981). A relatively low proportion of caterpillars in the diet is characteristic of suboptimal environments such as suburban gardens (Cowie & Hinsley 1988; Riddington & Gosler 1995), sclerophyllous habitats (Blondel et al. 1991; Bañbura et al. 1994) and forest fragments (Riddington & Gosler 1995). Hence, it is striking that blue tits opted not to increase the proportion of caterpillars delivered (in fact, it was reduced) when they faced a low brood demand and thus their chances to be more selective in prey choice were greater. This result in addition to the fact that spiders (see more below) are nutritionally similar to caterpillars (S.L. Ramsay & K.E. Arnold, unpubl. data quoted in Arnold et al. 2007) is not consistent with the view that a more diversified diet (especially when the occurrence of spiders is high) denotes a poor feeding situation and thus must be considered of lower quality (Blondel et al. 1991; Bañbura et al. 1994; but see also Mägi et al. 2009). In fact, we have found a quadratic relationship between the proportion of caterpillars in the diet and nestling weight (with maximum values around 60–70%) suggesting that a diet with a very high proportion of caterpillars does not necessarily result in nestlings of better condition (García-Navas & Sanz, submitted manuscript).

Looking for differences within prey categories in response to daily brood size changes, we found that when the brood demand rose parent birds increased their usage of *Tortrix viridana* and *Archips xylosteana* (Tortricids). Both *Tortrix viridana* and *Archips xylosteana* are species feeding within a shelter constructed by rolling one or more leaves in a tubular fashion (leaf-rollers). Such shelters are also used to pupate. Thus, curled leaves are indicative of the presence of these species during both the larval and pupal stage. In this sense, Tortricids constitute a more easily detectable food resource than Noctuids and other Lepidoptera larvae (Geometrids, Notodontids) not constructing shelters and feeding externally on the upper or lower leaf surface (i.e. free-feeders). In

addition, the fact that leaf-roller species are sedentary (in comparison with Noctuids and other species with high mobility) and usually present a clumped distribution permits this prey type to be brought back to the nest in runs or multiply per load (e.g. Naef-Daenzer & Keller 1999). This suggests that blue tits may opt to take a high proportion of these species if search times must be short because of time constraints. However, when the constraints are not so harsh the relative profitability of these species becomes lower. Particularly *Tortrix viridana* was underrepresented in the nestling diet as this species is one of the most common Lepidopterans in our study area and along with *Malacosoma neustria* (avoided by tits), the unique species causing severe defoliation during outbreak episodes in our study area. This is in agreement with that noted by Tinbergen (1960) in an extensive study on Dutch great tits where *Panolis flammea* was not exploited as fully as might be expected from the number present on the pinewoods. Similarly, Royama (1970) found that only a few feeding larvae of *Tortrix viridana* were taken to the nest by great tits, even though this species was most abundant and accessible (at least, obvious to human eyes) in their study area. Meanwhile, blue tits seemed to drop this prey type from their diet but the occurrence of Noctuids in the diet remained constant, so their contribution to the diet increased. Noctuids found in the nestling diet are larger and probably contain more water than Tortricids, which may be an important factor in dry and hot breeding seasons, a common feature in Mediterranean environments (Nager & Wiersma 1996). This switch in prey choice as a response to daily brood size alterations is in accordance with an earlier work (Tinbergen 1981) in which it was found that starlings provisioning at artificially increased rates returned with a larger proportion of low-quality prey (leatherjackets larvae) at the expense of the preferred prey, larvae of *Cerapteryx graminis* (Noctuidae).

We also show that when increasing the brood size both the delivery rate and percentage of spiders provisioned to the young decreased. Meanwhile, when the brood demand was artificially relaxed the occurrence of this prey in the nestling diet remained similar to that found for the control treatment. This suggests that the frequency with which this prey was supplied was enough to satisfy the nutrient needs of the nestlings at this phase of their development (day 11 or 12 post-hatching). It is known that spiders contain high levels of taurine (Ramsay & Houston 2003) and this protein is important to

developing young for bile formation and the proper development of feathers (Gosler 1993) and the central nervous system (Ramsay & Houston 2003), as well having downstream impacts on adult behavior and cognition (Arnold et al. 2007). In this sense, several studies of tits (Royama 1970; Cowie & Hinsley 1988; Naef-Daenzer et al. 2000) have recorded a high proportion of spiders during early stages of chick development (5–6 d old). Thus, it is likely that the occurrence of spiders in the nestling diet after brood reduction would be larger if our experiment had been performed in the days of maximum growth rates instead of during the stage in which the development of chicks slows.

Males and females did not differ in the tactic adopted to cope with the new scenario (reduced or increased parental demand). This is in contrast with the findings of Bañbura et al. (2001) who found that male blue tits brought a higher proportion of caterpillars than females and that the caterpillars delivered by the males were also larger in comparison with those brought by their mates. However, these authors suggested that such differences result from the fact that females were more time-constrained because they spent more time at the nest performing nest sanitation and in spite of this, their visit rate was higher. As in our study area, the prevalence of ectoparasites is low (V. García-Navas, J. Ortego & J.J. Sanz, unpubl. data) in comparison with northern populations, the lack of intersexual differences is not especially noteworthy. Similar conclusions have been drawn in previous studies on great and blue tits (Cowie & Hinsley 1988) and other bi-parental care species (pied flycatchers: Moreno et al. 1995; Siikamäki et al. 1998; yellow warblers *Dendroica petechia*: Lozano & Lemon 1998; fairy martins *Hirundo ariel*: Magrath et al. 2007). Nonetheless, it should be stressed that our monitoring period was not long enough to allow us to draw firm conclusions concerning this topic.

In sum, this study shows behavioral flexibility in provisioning strategies of parent birds in response to short-term manipulations of brood size in agreement with previous studies carried out with starlings (Wright & Cuthill 1990b; Wright et al. 1998). The results shown in this study indicate that blue tits make subtle adjustments in their foraging behavior that account for changes in provisioning rates and prey size on a short timescale (see also Grieco 2002). Such differences in feeding frequencies and the load sizes delivered may be explained by changes in the parents' prey choice tactic. Our data suggest that when the time budget is constrained (e.g. larger

broods) parents exploit those preys that are easier to obtain (Tortricids). On the other hand, when the feeding constraints are relaxed (e.g. as in the days in which the brood was experimentally reduced), the occurrence of this prey in the diet decreased dramatically, which suggests that these species do not constitute a preferred prey for blue tits.

This switch in the nestling diet is not trivial in terms of fledgling condition (and thus, post-fledging survival; e.g. Tinbergen & Boerlijst 1990). We have found a decrease in nestling weight as the proportion of Tortricids increased and Noctuids become scarcer in the diet (García-Navas & Sanz, submitted manuscript), which suggests that switches at a fine scale in nestling diet could have fitness consequences in both the short- and long-term. In this sense, regions like the Mediterranean where tits do not solely depend on one species ('multiple caterpillar peak') offer a useful scenario to explore the adaptive response (plasticity) of these birds to alterations in phenology and abundance of different Lepidoptera species and their fitness consequences.

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