

Chapter 5

Short-term regulation of food-provisioning rate and effect on prey size in Blue Tits

(Parus caeruleus)

Fabrizio Grieco

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ABSTRACT

The short-term regulation of parental provisioning rate (PPR) in Blue Tits was investigated by videotaping the parents at the nest. An additional feeding experiment allowed a comparison between the behaviour of parents raising their brood under normal and supplemented feeding conditions. Videotaping revealed that parents changed their PPR as an immediate response to the absence of chicks' food-begging behaviour. When chicks did not beg for food, the parents solicited them with a particular call (feeding call, FC) to make them open their beak. Parents significantly increased the time away from the nest immediately after performing feeding calls. Provisioning rate returned to the usual levels as soon as chicks started begging again, but supplemented parents took a shorter time to do so compared with controls (i.e., parents not provided with additional food). Changes in PPR had effects on both type and size of prey brought to the brood. Females often responded to low brood demand by returning to the nest without food. Food-supplemented parents, not control, took larger larvae when they stayed longer away from the nest. This suggests that parents in the supplemented group could use more time to reach good feeding sites or, more probably, increase their prey selectivity. Blue Tits continually monitored the begging behaviour of the offspring and responded accordingly by adjusting their feeding rate, with immediate consequences for prey choice.

INTRODUCTION

Life-history theory predicts that parental effort is regulated so that the costs and benefits of current reproduction are balanced to maximise lifetime reproductive success (Stearns 1992; Roff 1992). Parents must make decisions throughout the breeding cycle about how much effort to put in reproduction and how much in self-maintenance. When the offspring are well fed, it does not pay to maintain a high feeding effort; conversely, hungry offspring need an increased feeding rate. In birds, a number of observational and experimental studies found a relationship between chick demand and parental effort, primarily in terms of parental provisioning rate (PPR; e.g. Henderson 1975; Bengtsson & Rydén 1983; Hussell 1988; Stamps *et al.* 1989; Dijkstra *et al.* 1990; Yasukawa *et al.* 1993; Leonard and Horn 1996; Price and Ydenberg 1995). Experimental manipulation of brood size causes changes in feeding rate (Nur 1984; Smith *et al.* 1988; Wright & Cuthill 1990; Conrad and Robertson 1992; Rytönen *et al.* 1996). Food-begging behaviour of nestlings appears to be the main signal that parents use to assess the current need of the offspring. Besides the debate on whether begging behaviour is an honest signal of need (Godfray 1991, 1995; review in Kilner and Johnstone 1997), parents do respond to begging levels. Experimental manipulations of begging intensity using recorded vocalisations have often shown an increased provisioning rate relative to unmanipulated situations (Harris 1983; Bengtsson and Rydén 1983; Ottosson *et al.* 1997, Burford *et al.* 1998; Price 1998). Most of the studies above do not report the exact moment when the parents react to the artificial or natural stimulus. In other studies, however, there is evidence for an immediate response by the parents. Captive zebra finches (*Poephila guttata*) increased the frequency of regurgitation as soon as begging calls were played (Muller & Smith 1978). In a study on tree swallows *Tachycineta bicolor*, parents responded to increased begging intensity by immediately reducing their time to the next visit to the nest (Leonard and Horn 1996).

Besides visiting rate, size and type of food items are also important components of provisioning effort. If a parent bird is able to deliver large food loads to the nest, fewer foraging bouts per unit time are needed to meet the brood's requirements. This is of course strongly influenced by the quality of both the territory

(e.g. Royama 1966, van Balen 1973) and the forager. However, prey size is also related to the time budget of the forager. In order to obtain a larger item, thereby to increase selectivity, more time is needed as more small items will be ignored during the foraging bout (see Lessells & Stephens 1983 for central-place foraging). Selectivity is also reflected in the type of prey brought to the nest. This is due to the fact that nutritional quality of available prey types is not uniform across the environment. For instance, prey types that are common in the environment and lead to maximisation of energy gain may not be the ones that serve as protein source (e.g. Krebs & Avery 1984). Therefore, if foraging time is limiting, as in most cases in nature, parents may find it difficult to find the food type that maximises the long-term growth of the offspring. Indirect evidence for this comes from switches in prey type following experimental manipulation of brood size (e.g. Tinbergen 1981; Bañbura *et al.* 1994; Wright *et al.* 1998). Models of Lucas (1983; 1985) predict an increase in selectivity with foraging bout duration, and some field and laboratory studies support this (e.g. Martindale 1982; Lucas 1987). Changes in prey choice as response to changes in prey density, time constraints and satiation are very rapid (Lucas 1990), suggesting that they could be detected in parents responding to different levels of begging of the brood.

During a study of foraging in Blue Tits *Parus caeruleus*, I extensively videotaped the parents at the nest to collect data on provisioning rate and prey choice in different feeding conditions. This gave the opportunity to monitor changes in provisioning rate and prey quality and/or size after changes in parent-offspring interactions. In this paper, I have focused on the instances when the chicks did not beg for food rather than to changes in begging intensity. I have tried to answer the question of whether parents react immediately to the absence of begging by increasing the time spent away from the nest and thereby slowing down PPR. I have then looked at whether a reduction of provisioning rate was accompanied by changes in type and/or size of meals brought to the nest. Moreover, a supplemental feeding experiment was carried out where Blue Tit parents were offered insect food during the nestling-rearing phase. The parents could therefore eat the supplemental food or give it to the young. In any case, this was expected to increase the time available to the parents for searching natural food for the offspring (Martin 1987), with two possible

outcomes were predicted. The rate at which the parents feed the offspring might increase, as reported by Markman *et al.* (1998) for sunbirds. On the other hand, the number of total feeds might not change or even decrease, with a consequent increase in the time gap between two feeding visits. This could potentially reduce the time constraints on food selectivity (Lucas 1983, 1985), and therefore show effects on size and/or quality of food brought to the nest (Hurtrez-Boussès *et al.* 1998). The feeding experiment provided the opportunity to establish whether parents modify their response to the begging behaviour according to the food resources they experience during brood raising.

METHODS

This study was carried out in 1998 and 1999 on the Blue Tit population breeding in nest boxes in the Hoge Veluwe National Park, central Netherlands. The study area comprises of 400 nest boxes located in a mixed forest dominated by European Oak *Quercus robur*, and conifers *Pinus* spp. (van Balen 1973).

Feeding Experiments

Mealworms (*Tenebrio molitor*, family *Tenebrionidae*) and larvae of wax moth (*Galleria mellonella*, family *Pyrilidae*) were offered to adult Blue Tits during breeding, from the day of hatching to the day of fledging of the young. Food consisted of a mixture of the two species in the first six days after hatching, and only mealworms afterwards. The quantity of food supplied daily corresponded to about one half of the brood's daily requirement as reported by Gibb & Betts (1963). For a 12-chick brood, it increased linearly from 1.0 g at day 0 to 20 g at day 10, and then levelled off until fledging date. Adjustments in food quantity were made for smaller and bigger broods. The larvae were placed in small trays (5.5×3.5×4.5 cm) inside the nest boxes so as to prevent birds other than the focal adults from consuming them. Feeding trays were replenished each day according to the scheduled amount. Half of the nest boxes were food-supplemented, while the other half (with a feeding tray as well) were not and served as a control. Food-supplemented and control boxes were

chosen randomly within pairs in order to have the same range of hatching date. Effort was made to assign different treatment levels to boxes in similar habitats.

All the nest boxes were checked daily from the expected date of hatching to the date of fledging of the young. The adults were caught, sexed and colour-ringed when the chicks were seven days old.

Videotaping

Parental behaviour during provisioning of offspring was filmed in 39 nests (18 in 1998 and 21 in 1999), once or twice each, during the time the chicks were three to 13 days old. Of the 75 birds filmed (three males were never filmed as they presumably abandoned the nest), 10 (five females and five males) were filmed in both years. Of these, six were under different treatments in the two years (e.g. control in 1998, food-supplemented in 1999). Even for the four birds that were in the same treatment group in both years, the effect of pseudoreplication should be negligible as the main analysis of provisioning rate was done on breeding pairs (values were averaged over the two adults in each pair). A video camera handy cam SONY CCD-TR825E was placed facing down from the top of the open nest box. During filming, a wooden box covered the video camera and a small lamp placed behind it provided more light in the nest. To have the birds more habituated to the video camera and the light, a dummy wooden box with a small light turned on was placed on the nest box one hour prior to filming. All videotaping sessions (n=75) started in the morning between 0800 and 1200 hours and lasted 90 minutes. In none of the years the starting time of videotaping significantly explained variation in either number of feeds brought in one hour or size of prey. Hi8 videotapes were copied to extra-high grade VHS tapes and these were observed. The adults could be identified from colour ring combinations. If they had not yet been ringed, they could be identified from individual (not sexual) morphological features (e.g. irregularities of the head and face plumage). In such cases, final identification of sexes was done by comparing plumage features in the videos made before and after the date of ringing. Sex identification could also be done through behaviour, i.e. only females brood the young and clean up the nest. Furthermore, the video camera boosted the between-sex difference in blue colour of the bird's crown, probably due to its higher sensitivity to near-UV radiation than the

human eye (for ultraviolet sexual dimorphism in Blue Tits see Andersson *et al.* 1998; Hunt *et al.* 1998). For each visit, I recorded the time when the adult entered and left the nest box. Prey items were classified as insect larvae, arthropods (including adults and pupae), and unidentified items. The latter were divided into 'large' and 'small', according to whether they were larger than the bird's beak width. The size of larvae was estimated from the screen by the size of their head relative to the width of the bird's beak. During a feeding visit, the parent gave a short, low-pitch call (feeding call, FC) if the chicks did not beg for food, with the apparent aim of making them open the beak. By imitating this call the observer could make the chicks open their beaks when opening the nest box. The feeding call has previously been investigated in several passerines, including the great tit (Messmer & Messmer 1956; Khayutin & Dmitrieva 1978), but not the Blue Tit. The FC was scored without detail on per-visit frequency. In a very few cases (27 out of 3325 visits) the prey taken to the nest was so large relative to the chicks' gape that feeding them was difficult, causing the parents to give FCs even if one or more chicks had opened their beak. Those instances were excluded from analysis. In only one visit the parent did not give FCs when the chicks did not beg for food, and left the nest with the prey in its beak. In that instance, it is likely that the adult was scared by the video camera.

Definitions

Between-feed interval (BFI) was the time lag between two subsequent feeds, i.e. the difference between the time the parent entered the nest box and the time it had left the box in the previous visit. In a small proportion of visits (8 %, quartiles 0.0 – 26.2%) food-supplemented parents fed the offspring extra-food items previously taken from the tray. These visits carried no information about the time taken to capture and deliver natural prey, therefore were excluded from the analysis. Feeding call rate was the proportion of all feeding visits (including those with extra-food in supplemented nests) that the parent gave at least one FC. Extra-food visits were included in this calculation because FC-rate was meant to reflect the general level of satiation of the brood.

For FC-visits, I considered three adjacent between feed-intervals (Fig. 1): B, immediately before the visit, A1, immediately after the visit, and A2, after the first

visit where the chicks resumed begging behaviour. Usually A2 followed A1 immediately as in Fig. 1, however if the chicks were well fed they resumed begging a few visits later, causing A2 to be located further. In such instances the parent performed FCs in two or more subsequent visits, thus some BFIs could be considered as occurring both immediately before and after an FC visit. These ambiguous intervals were excluded from calculations. Although these were 40.9% of all BFIs that could be considered of type A1 ($n=357$), including them as A1-type BFIs in the analysis did not change the results qualitatively (second paragraph in the Results section), as shown by preliminary analysis of the 1998 data set.

For any videotaping session, and for each parental sex, I calculated the mean of intervals B, A1 and A2. In an additional analysis, I also considered three adjacent intervals after A2 (A3, A4 and A5). These were all characterised by the absence of feeding calls by the parents at the visit concerned.

Data Analysis

To test whether FC visits by male and female parents were distributed independently along the sequence of visits in a video session, I considered only visits that were followed by a visit by the other parent. Successive visits by one parent were therefore ignored. For each session, I counted the non-FC visits by one parent that were followed by (i) a non-FC visit and (ii) an FC visit by the other parent. The same was done for FC visits by the first parent. Only those nests with 10 or more FC-visits ($n=6$ nests) were included in the analysis. The counts produced a 2×2 table for each session, where the proportion of counts of a certain event (e.g. giving an FC after the other parent gave one) were considered as probability that the event would occur. Changes in proportions were tested with a Chi-square test. A combined test used the P -values relative to each of the n tables according to the formula: $P_c = -2 \sum \log_{10} P$ (Sokal & Rohlf 1997). The combined P_c was then compared with critical Chi-square values with $2n$ degrees of freedom. FC-visits were much less numerous than non-FC visits. To have greater numbers in the tables, counts from different sessions were summed up for each nest. This could be done since the proportion of FC-visits followed by FC-visits by the other parent did not change with chick age ($r=-0.09$, $P=0.72$, $n=17$ sessions with 5 or more FC visits).

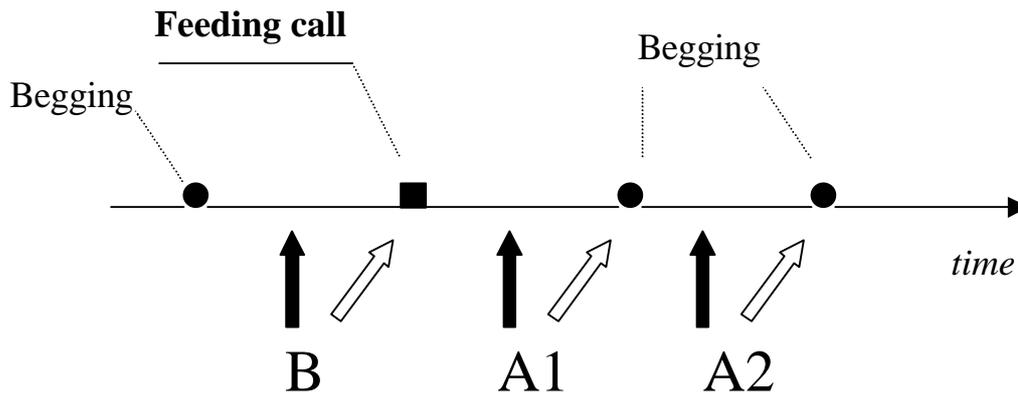


Figure 1. Sequence of visits by parent Blue Tits and behavioural variables in relation to chick-feeding behaviour. Dots represent parental visits when the chicks were begging for food, the square represents a visit when the chicks did not beg and the parent gave a feeding call. The main analysis refer to the between-feed intervals immediately before an FC visit (B), the interval after an FC visit (A1) and the next if chicks resumed begging (A2). If feeding calls were given in more subsequent visits, the related A1 intervals were ignored. Arrows indicate the between-feed interval (black arrow) and the prey brought at the end of it (white arrow). Intervals A3 to A5 immediately follow A2 and were used in a secondary analysis.

Between-feeds intervals and prey size were analysed with general linear models as in Statistica v. 5.5. for Windows (StatSoft 1999). The individual bird or nest were treated as the observation unit. When two sessions per nest were available, one of them was chosen at random and included in the analysis. The size of larvae delivered to the nest increased markedly with date because of their growth during the season (F. Grieco & A. J. van Noordwijk, unpublished data). To express prey size independent of date, I calculated the residual of prey size (RPS) from its regression on date. This was done for the two years separately (regression equations, 1998: $PS = -0.143 + 0.017 \cdot \text{date}$, $R^2 = 0.55$; 1999: $PS = 0.056 + 0.016 \cdot \text{date}$, $R^2 = 0.66$). Values of BFIs were right-skewed distributed, therefore they were log-transformed prior to analysis, while FC rates, expressed as proportions, were arcsine-transformed. Date, chick age and brood size on the day of filming were treated as covariates, and were excluded from the model if their effect was not significant. To test for within-nest changes in BFIs and RPS in the sequence B - A1 - A2, I used repeated measures analysis of variance, where the sequence of intervals B, A1 and A2 was the repeated measures factor. Planned comparisons were used to test for changes between pairs of variables (e.g. B

vs. A1). Changes in prey type along the sequence B - A1 - A2, were tested with Chi-square tests on prey type counts. The data set also included a few visits with no prey (especially for female parents). Given that a certain prey type may reflect the use of a particular feeding site, the data from individual birds did not represent statistically independent data points. For each session and for each parent, I numbered all intervals of a certain type (B, A1 and A2) from 1 to n (where n was the number of intervals available). One of the n intervals was chosen by generating a random number between 1 and n . I then considered the type of prey (or 'no prey' if that was the case) brought at the end of the interval concerned. In this way the prey item brought by the individual parent was represented once for each BFI type.

Ethical Note

Permission to catch the birds was obtained by the National Park “The Hoge Veluwe” and by the Ringing Station of the Netherlands. The videotaping set up did not cause any breeding pair to abandon the nest. The parents returned to the nest within 502 ± 428 (SD) s (range 189 – 2167 s) from the start of filming. The food-provisioning rate in presence of video cameras (35.9 ± 16.3 (SD) feeds/h for unmanipulated pairs) was similar to that gathered from observations at the nest without video cameras in 1997, and within the natural range in habitats rich in caterpillars (Gibb & Betts 1963; Nur 1984; Cramp & Perrins 1993)

RESULTS

Rate of Feeding Calls

Parents gave feeding calls in a small proportion of feeding visits (Table 1). Feeding call rate calculated over a 1.5-hour time decreased strongly with age and number of chicks (ANCOVA: effect of chick age, $F_{1,34} = 29.17$, $P < 0.00001$; effect of brood size, $F_{1,34} = 14.74$, $P < 0.001$). A similar decline of FC rate with nestling age was reported in the great tit (Bengtsson & Rydén 1981). This could be a consequence of the higher food requirements in older and bigger broods. After controlling for chick age and number, food-supplemented parents gave, on average, slightly more FCs (Table 1; ANCOVA, effect of treatment: $F_{1,34} = 4.41$, $P = 0.04$). An interaction between

treatment and brood size was found (ANCOVA: $F_{1,34} = 5.01$, $P = 0.032$), indicating that the effect of increasing number of chicks on FC rate differed between the two treatments. Separate analysis of FC rate revealed that the effect of brood size was highly significant in control broods (ANCOVA: $F_{1,17} = 19.94$, $P = 0.0003$), and not significant in supplemented broods ($F_{1,16} = 1.19$, $P = 0.29$). Thus, food supplementation reduced the influence of brood size on the rate at which parents solicited the chicks, which was inversely related to how often the chicks begged for food.

Male and female parents did not give feeding calls independent of each other. For each nest, I considered only visits by a parent that were followed by a visit by the other one, regardless of the order (male after female or *viceversa*). Counts of visits with or without FCs, and for the first and the second parent produced a 2x2 table for each nest. When the first parent did not give an FC, the probability that the other gave one was 0.10 (quartiles: 0.07 - 0.14). Conversely, this probability was 0.47 (0.21 - 0.54) when the first parent did give an FC ($n = 6$ nests, number of visits ranging 10 to 109 in any category). The difference was significant (combined test, $\chi^2_{12} = 25.4$, $p = 0.013$).

Feeding Calls and Time Away From the Nest

I first looked at whether parents significantly increased the time spent away from the nest immediately after the visits where they gave a feeding call. In a model with experimental treatment, parental sex, repeated measures factor (sequence of intervals in the order B - A1 - A2) and their interactions as explanatory variables there was no effect of parental sex on the duration of feeding intervals (repeated measures ANOVA: $F_{1,36} = 1.05$, $P = 0.31$). Therefore, BFIs of each type were averaged over the two parents. There was a significant difference in the average duration among the three types of BFI under consideration (effect of repeated measures factor; $F_{2,54} = 9.65$, $P = 0.0003$). In particular, the duration of BFI increased markedly after the parent gave an FC (B vs. A1 in Fig. 2; ANOVA planned comparison: $F_{1,27} = 31.47$, $P < 0.00001$), indicating that the parents slowed down their PPR immediately after the chicks showed no food-begging behaviour. Feeding intervals became shorter after the chicks resumed begging (A1 vs. A2 in Fig. 2; ANOVA planned comparison: $F_{1,27} =$

Table 1. Total feeding visits, visits where the parent gave feeding calls and feeding call rate in the two experimental treatments.

| | Visits | FC-Visits | Feeding call Rate* Median (quartiles) | <i>n</i> |
|-------------------|--------|-----------|--|----------|
| Control | 1043 | 102 | 0.058 (0.000; 0.248) | 20 |
| Food-supplemented | 766 | 125 | 0.063 (0.050; 0.280) | 19 |

*Feeding call rate is calculated for each nest, over a 1.5-h videotaping session. When two sessions were available for a nest, one was chosen randomly and included in the calculations. *n*= number of nests.

5.36, $P=0.028$), so that the parents returned to levels of PPR comparable to those before giving FCs (B vs. A2; ANOVA planned comparison: $F_{1,27}= 2.39$, $P=0.13$).

On average, food-supplemented parents stayed away from their nest as long as control parents (repeated measures ANOVA: $F_{1,27}= 0.88$, $P=0.36$). However, there was a difference in the way parents of the two experimental groups responded after giving FCs, as suggested by the interaction between treatment and repeated measures factor ($F_{2,54}= 6.43$, $P=0.003$). Control parents increased BFIs more than supplemented parents after giving FCs (Fig. 2). This was due to the BFIs of type B being much shorter in control than supplemented nests (ANOVA planned comparison: $F_{1,27}= 7.34$, $P=0.011$). The difference reflected the lower provisioning rate in food-supplemented parents found in previous work (Grieco 1999, F. Grieco & A. J. van Noordwijk, unpublished data).

When the chicks resumed begging, control parents stayed away from the nest for long time, so that A2 was as long as A1 (ANOVA planned comparison: $F_{1,27}= 0.54$, $P=0.47$), but still longer than B ($F_{1,27}= 16.24$, $P=0.0004$; Fig. 2). On the contrary, food-supplemented parents returned to the nest sooner, so that type-A2 BFIs were similar to those of type B (Fig. 2; ANOVA planned comparison: $F_{1,27}=2.40$, $P=0.13$). Thus it appears that food-supplemented parents resumed the usual high feeding rate much sooner than controls. This was confirmed when I extended the analysis to three more intervals after A2. Table 2 shows comparisons between the B interval and each of those after A2. For control nests, A3 intervals were

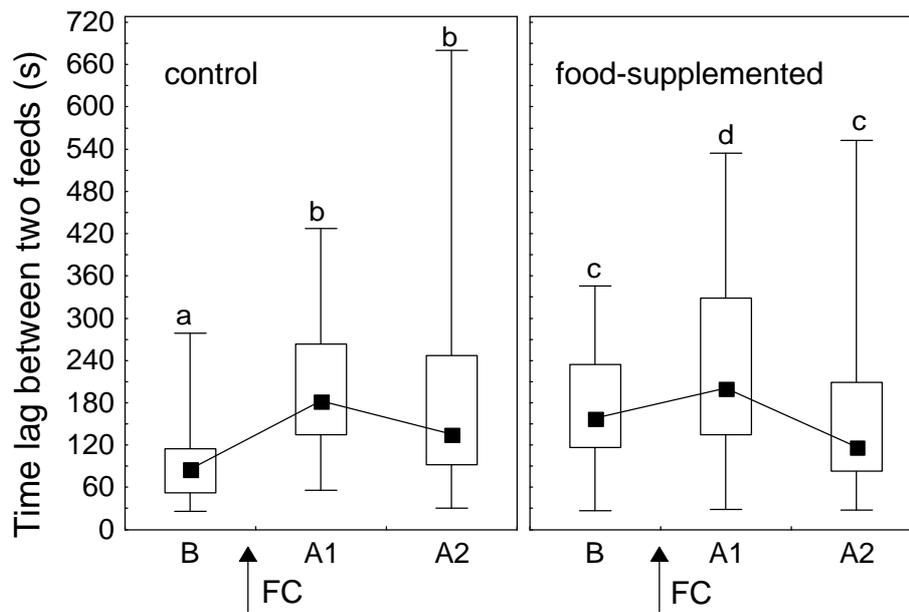


Figure 2. Duration of between-feed intervals at three visits by the parents (see black arrows in Fig. 1). (B) BFI before a visit where the parent gave the feeding call, (A1) BFI after an FC visit, and (A2) BFI for the first visit after the one where the nestlings resumed begging. Nests were included where BFIs of all three types were available. Filled squares: medians; boxes: 25%-75% ; bars: range. Different letters on bars indicate significant differences between samples in planned comparisons: a-b, $p < 0.0005$; c-d, d-c, $p < 0.05$.

still longer than B, and even A4 tended to be so. This suggests that control parents returned to the usual provisioning rates after the third or fourth visit after an FC visit. Food-supplemented parents, on the other hand, did not change the time away from the nest in that sequence, confirming that they had returned to the high feeding frequency earlier on.

Effects on Prey Type and Size

Figure 3 shows the type of prey items delivered immediately before and after giving feeding calls. During the visits when the parents gave FCs, the parents always brought a meal to the nest. In most instances this was a larva (row B in Fig. 3). The nestling diet differed among the three types of BFIs, but only in female parents (Chi-square test: females, $\chi^2_6 = 17.57$, $P = 0.007$; males, $\chi^2_6 = 8.14$, $P = 0.23$; after grouping counts of

Table 2. Comparisons of duration of between-feed intervals (in seconds) between immediately before giving a feeding call (B) and each of three intervals after A2. Changes are the differences between A3, A4 and A5 and B (positive values indicate that the interval concerned is longer than B). Matched pairs *t*-tests are performed on log transformed values.

| B | Control | | | Food-supplemented | | |
|----|------------------------------|----------|------------|------------------------------|----------|------|
| | Change \pm SD (<i>n</i>) | <i>t</i> | P | Change \pm SD (<i>n</i>) | <i>t</i> | P |
| A3 | +152 \pm 232 (16) | -4.59 | 0.0004 *** | -29 \pm 117 (13) | 1.22 | 0.25 |
| A4 | +209 \pm 330 (14) | -2.04 | 0.06 | +77 \pm 283 (10) | 0.25 | 0.81 |
| A5 | +77 \pm 195 (13) | -0.40 | 0.70 | +56 \pm 265 (8) | 0.26 | 0.80 |

small and large unidentified items). After giving FCs, females took relatively fewer larvae, more unidentified items and more often no items at all than before (B vs. A1 in Fig. 3; Chi-square test: $\chi^2_3 = 14.28$, $P = 0.003$). After the chicks started begging again, females tended to bring more larvae and other arthropods and fewer items that were not identified, but the difference was not significant (A1 vs. A2 in Fig. 3; Chi-square test: $\chi^2_3 = 7.47$, $P = 0.06$).

The reduced feeding effort after an FC visit also led to rapid changes in the size of prey delivered. The size of larvae was not affected by parental sex in a model with treatment, parental sex and repeated measures factor and their interactions as explanatory variables, therefore the average value of RPS for each nest was used. There was a general tendency of RPS to increase after the parent gave an FC (Fig. 4), but I found no within-subject change in prey size along the sequence of feeding visits (repeated measures factor: $F_{2,38} = 1.09$, $P = 0.35$). The greater variances in prey size brought at the end of intervals A1 and A2 (Fig. 4) was due to the higher proportion of large items that were underrepresented in the B sample. For instance, larvae with RPS greater than 0.1 were brought by 32.3% and 26.9% of the pairs at the end of A1 and A2 intervals respectively, and by only 12.1% of the pairs at the end of B intervals. This suggests that the reduced feeding effort could somehow lead birds to have access to larger larvae. Food-supplemented parents brought slightly larger larvae than controls, but the difference was not significant (repeated measures ANOVA:

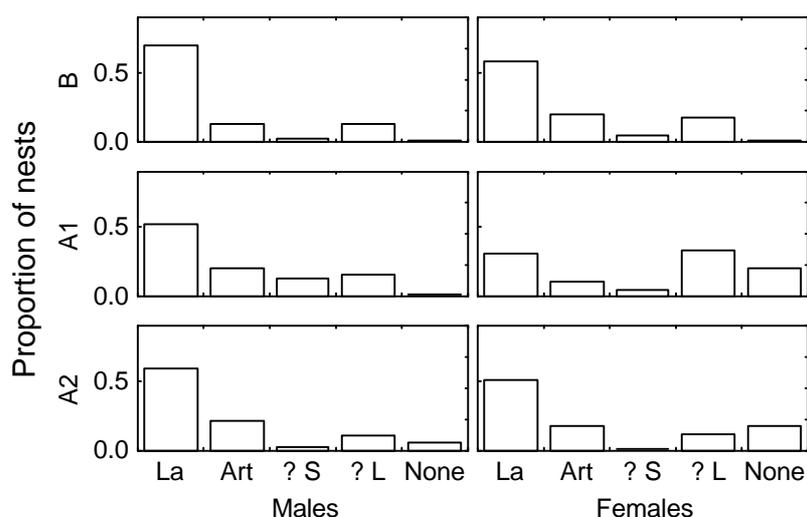


Figure 3. Composition of prey delivered to the nestlings at three visits by the parents (see white arrows in Fig. 1): (B) a visit where the parent gave the feeding call, (A1) a visit after an FC visit, and (A2) at the first visit after the one where the nestlings resumed begging. Each nest is represented by one feeding event for each type B, A1, A2, randomly chosen among those available (more intervals of one type were usually available in a videotaping session). Prey types: La, larvae; Art, adult arthropods; ? S, unidentified, smaller than bill width; ? L, unidentified, larger than bill width; None, no prey brought to the nest.

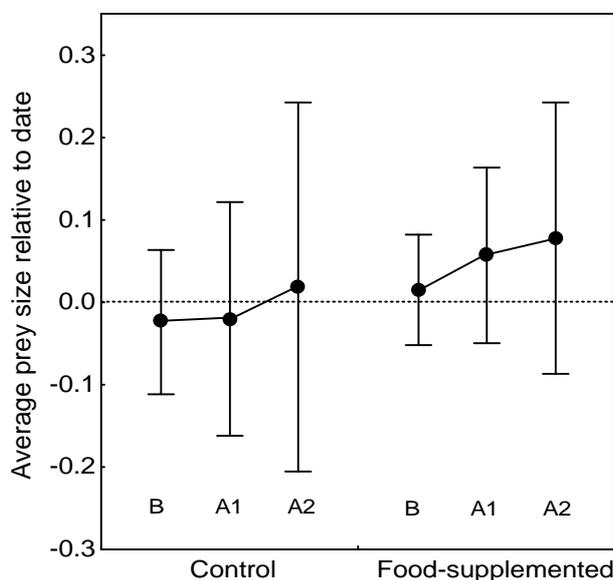


Figure 4. Average (\pm SD) prey size, at three feeding visits: (see white arrows in Fig. 1): (B) when the parent gave the feeding call, (A1) a visit after an FC visit, and (A2) at the first visit after the one where the nestlings resumed begging. Nests were included where visits of all three types were available. Prey size is expressed as deviation from the value expected at the date when filming was done.

Table 3. Paired comparison between values of size of larvae delivered by parent Blue Tits immediately before (B) , after (A1) performing feeding calls and after the first subsequent visit (A2) where parents did not give FCs (see Fig. 1). Prey size is expressed as deviation from the value expected at the date when filming was done.

| BFI types considered | | mean \pm SD | | number of pairs | <i>t</i> | <i>P</i> |
|----------------------|------|--------------------|--------------------|--------------------|----------|----------|
| (1) | (2) | (1) | (2) | | | |
| B | - A1 | -0.041 \pm 0.098 | +0.005 \pm 0.140 | 30 | -1.959 | 0.06 |
| A1 | - A2 | +0.024 \pm 0.126 | +0.052 \pm 0.189 | 21 | -0.690 | 0.50 |
| B | - A2 | +0.002 \pm 0.087 | 0.033 \pm 0.140 | 23 | -0.87 | 0.39 |

$F_{1,19}=1.67$, $P=0.21$; the effect of treatment was significant when all measurements of larvae brought during a videotaping session were considered; F. Grieco & A. J. van Noordwijk, unpublished data). However, the lack of statistical evidence for the change in RPS along the sequence of visits could be due to the repeated measures design. In fact, only observation units (i.e., nests) were included where prey values were available for all three types of intervals (B, A1 and A2). For several sessions, one or more values in the sequence were missing because prey size could not be measured at the end of a certain visit (either size was not measurable or prey was not a larva). These sessions were not included in the analysis, reducing the sample size. I therefore compared RPS in sets of pairs, i.e. B vs. A1, A1 vs. A2, and B vs. A2. The results of the three comparisons are shown in Table 3. Parents returning after giving an FC brought a larva slightly larger than in the immediately preceding visit (B vs. A1, Table 3). The difference in RPS was significant in larvae brought by food-supplemented parents (Paired *t*-test on RPS at the end of B vs. A1: $t_{16} = -2.214$, $P=0.04$), not by controls ($t_{12} = -1.066$, $P=0.31$). The size of larvae taken at the end of interval A2 did not decrease relative to those brought at the end of A1 (Table 3), contrary to what would be expected from the shortened BFI at least for supplemented parents ($t_{11} = -0.48$, $P=0.64$). Nor was there a significant change in size of larvae in the following visits. For instance, the RPS of larvae brought at the end of intervals A1 and A2 was similar to that at the end of A4 and A5 (Paired *t*-test with RPS at the end of A1 and A2, and of A4 and A5 pooled respectively: $t_{18} = -0.92$, $P=0.37$). Therefore, I

could not find evidence, for either supplemented or control nests, that prey size decreased when the parents resumed a high feeding frequency.

DISCUSSION

Short-Term Regulation of Provisioning Rate

Parent Blue Tits regulate their time spent away from the nest as response to changes in the interaction with the brood. A strong increase in the time to the next visit occurred after the parent gave a feeding call. The question is now whether it was the offspring behaviour (absence of begging) or the feeding call *per se* that induced changes in provisioning rates. Such question may be answered if there were cases when the parent did not give FCs after the chicks did not beg for food. Unfortunately this is not the case, however an increase of the time spent away was apparent even when FCs were not given. Sometimes the male entered the nest box with a food item when the female was brooding and delivered it to her without giving any FCs. In two nests, the female ate the prey in some of those instances. Curiously, the male stayed away for long time before the next visit (13 and 18 minutes, longer than the average BFI for those males, approx. 1 and 4.5 minutes respectively). These few cases do not allow to draw firm conclusions, however it seems (as it is reasonable to guess) that the parent is reacting to the behaviour of the brood or its partner, nor to its own behaviour.

The response to the absence of begging was much stronger in control than food-supplemented parents. This was due to the usually short feeding intervals for control parents, which reflected the higher provisioning rate in this group (Grieco 1999; F. Grieco & A. J. van Noordwijk, unpublished data). On the contrary, food-supplemented parents usually stayed away for longer time, and did not slow down their provisioning rate as much when the offspring stopped begging (Fig. 2). This may indicate that there was some upper limit for the time the parents could spend away from the nest. Leaving the brood for a longer time may be costly in terms of predation risk (e.g. Martindale 1982; Martin 1987; Soler & Soler 1996), or cooling of the nestlings (e.g. Betts 1955; Haftorn 1973). The fact that female Blue Tits significantly

returned more often empty-billed when the chicks stopped begging may mean that this cost is reduced with the presence of the parent, even if it does not bring a food item (Houston & McNamara 1985).

When the parents returned to the nest (i.e. end of A1 in Fig. 1), they could either find the chicks well nourished and quiet, or otherwise again begging for food. In the latter case, the parents reduced the time spent in the next foraging trip. Therefore, the parents resumed a higher visiting rate as soon as the chicks started begging again. However, this response was clear only in food-supplemented nests. Control parents took a few more visits to resume the usual provisioning rate. A plausible reason for the slower response of control parents might be that returning to high feeding rates was limited by the performance of other, non-parental activities such as self-feeding. This is a reasonable assumption since food-supplemented parents had access to an extra-food source and consumed a great proportion of it, instead of giving it to the chicks. Those parents took on average 16 extra-food items per hour, but delivered only 15% of them (range 0 – 100%) to the offspring. The remaining proportion was assumed to be wholly consumed by the adults (they usually took an item away when leaving the nest). Observations at the nest made in 1998 support the view that the adults consumed the food taken away. If self-feeding implied an important time constraint, a reduced chick-feeding effort would cause birds to spend significant part of time looking for their own food. Control parents would need to spend more time self-feeding, and therefore would return to a high provisioning rate with some delay compared to parents enjoying an extra food resource.

The immediate changes in the between-feed intervals after FC visits lead us to the conclusion that the parents continually updated their estimate of offspring condition and adjusted their provisioning rate accordingly. Moreover, the magnitude and the duration of these short-term changes were affected by the state of the parent.

Provisioning Rate and Prey Choice

Female Blue Tits responded to the interruption of begging by visiting the nest with no meal at all. On the other hand, male parents kept on bringing a large proportion of caterpillars, while empty-billed visits were extremely rare. Thus, male and female parents differed in the strategy adopted to cope with the reduced need of the offspring.

Male Blue Tits maintain a constant proportion of food components between years, while females vary those components, for instance by bringing more non-caterpillar prey in bad years (Bañbura *et al.* 1994). Female Blue Tits, therefore, appear to be more flexible than males in the response to brood demand and food availability, both in short- and in long-term scales.

The reduced provisioning effort may have caused a change in prey choice in terms of size of items *within* a type. A slight, though not significant increase in the size of larvae was found between the visit when the parents gave a feeding call and the subsequent one. The parents appeared to bring large larvae that were underrepresented in the previous visit when they returned sooner to the nest. The increase in prey size was significant in food-supplemented, but not in control parents. If we assume that longer time away from the nest allows for accessing larger prey, the latter finding is contrary to what would be expected, because control parents increased much BFIs after giving a feeding call. However, the result may be interpreted in the light of the fact that control parents resumed high provisioning rates with more delay than supplemented parents after the chicks started begging again (see above). The fact that control parents did not bring larger larvae after an FC visit is in agreement with the possibility that these used a greater fraction of time for self-feeding than supplemented parents. Control parents would therefore have relatively less time to bring larger food items even though they stay long away from the nest.

The large size of larvae brought when the chicks resumed begging (prey at the end of A2 and subsequent intervals) is in contrast with the reduced time spent away from the nest, at least in food-supplemented pairs (compare Fig. 2 and Fig. 4). Apparently this is contrary to the hypothesis that more time could lead to access to large prey. A possible explanation for this is that parents may have returned to the preceding feeding site after catching a very profitable prey. Repeated visits to the same site are known for tits (Smith & Sweatman 1974; Naef-Daenzer & Keller 1999) and provide a considerable foraging gain to the birds. Thus the reward coming from the use of longer searching time (prey at the end of A1 in Fig. 4) might have been carried over to the next visit through repeated visits to the same feeding site.

There are essentially two ways a foraging bird may deliver larger food items to a central place if it stays away from the nest for longer: (1) the forager can travel

further from the nest and, assuming that feeding sites further from the nest are exploited less (Andersson 1981; Naef-Daenzer 2000), it will be more likely to find larger prey, even if the foraging rule (i.e., minimum acceptable prey value, Lessells & Stephens 1983) does not change. A difference in prey size would be simply an artefact of the prey distribution in the environment. Alternatively, (2) a forager can use more time in searching for food, and reject a larger proportion of small or poor quality food items during each foraging bout. In other words, the forager will increase its selectivity. Hypothesis (1) assumes that the time away from the nest is a function of travel time, otherwise this mechanism could not explain the increase in the total time spent away. However, in a parallel study involving direct observations of Blue Tits while searching for food, the time between two feeds was strongly correlated with the time that the bird spent in the tree canopy within a foraging bout ($r = +0.969$, $n = 15$ nests, $P = 0.0008$). This indicates that the variation in BFIs was primarily explained by variation in search time. In contrast, there was no correlation between BFIs and the time employed in other activities than food searching, of which travel time was presumably the main component. From these findings one may conclude that the longer time spent away after an FC-visit was mainly due to the longer food-searching time. Consequently, the tendency for an increase in prey size following the reduction in provisioning rate could be explained by an increase in selectivity. The possible effect of differential allocation of searching time on food selectivity was also suggested by Hurtrez-Boussès *et al.* (1998) where female, but not male, Blue Tits in experimentally-deparasitized nests spent less time in nest sanitation, had longer foraging bouts and were more selective than control, parasitized nests. An increase in food selectivity of the parents is therefore the most likely explanation for the increase in prey size observed after cessation of the begging activity of the brood.

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