



Time constraint on food choice in provisioning blue tits, *Parus caeruleus*: the relationship between feeding rate and prey size

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Previous work on food-provisioning behaviour in blue tits suggested that the parents could gather larger prey items only by making longer foraging excursions, for example, by being more selective or by reaching more distant (and less exploited) feeding sites. Here, I show that within-nest, within-day variation in size of prey delivered by the parent could be explained by the time since its last visit. In unmanipulated conditions, size of larvae tended to increase with the time spent away from the nest. A significant positive relationship was more likely at high provisioning rates, suggesting that periods of intense feeding limited the size of prey delivered to the brood. To assess the effect of less intense feeding on prey size, I experimentally increased food availability to the tits. The parents could decide whether to eat the extra food or feed it to the nestlings. In both cases, food supplementation could result in longer time lags between natural feedings. Food-supplemented parents consumed the extra food and fed it to their nestlings, made longer foraging trips and delivered larger natural larvae than controls. In this group, size of larvae was more constant during the observation period and was independent of the time since the parent's last visit. This suggests that, below some value of visit rate, prey size is no longer limited by the duration of the foraging trip. The results support the view that tits continually vary visit rate and prey size. There is some evidence that these adjustments are made by changing food selectivity in response to changes in the state of the brood and of the parents.

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In altricial birds, the frequency with which the parents feed the young varies considerably. Feeding rate is influenced by a number of factors, both environmental (prey size and density, van Balen 1973; Naef-Daenzer & Keller 1999; Naef-Daenzer et al. 2000) and life history (brood size, Royama 1966; Klomp 1970; Tinbergen 1981; Nur 1984; Blondel et al. 1991; chick age, Gibb 1950; Kluyver 1961; van Balen 1973; absence or low parental contribution of the mate, Sasvári 1986; Wright & Cuthill 1989). Within nests, and within days, feeding rate may vary because of weather fluctuations (heavy rain causes drops in feeding rate, Keller & van Noordwijk 1994) or time of day (Cowie & Hinsley 1988). However, short-term changes in feeding rate are usually produced by the interaction between the parent and the offspring, feeding rate increasing with the level of begging of the brood (e.g. Tinbergen 1981; Bengtsson & Rydén 1983; Leonard & Horn 1996; Ottosson et al. 1997; Burford et al. 1998; Price 1998; Grieco 2001).

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In a study of blue tits, short-term changes in feeding rate, apparently caused by changes in the brood's begging activity, changed the size of prey delivered (Grieco 2001). The absence of begging caused the parents to stay away from the nest for longer and return with larger larvae than at the previous visit. Similar patterns were found in starlings, *Sturnus vulgaris*, by Tinbergen 1981. These findings suggest that large prey could be gathered only by making longer foraging excursions. An association between prey size and foraging trip duration could be the result of at least two, not mutually exclusive, processes. First, the parent can gather larger prey by increasing its selectivity. In animals that bring one food item per trip (single-prey loaders), this requires longer searching times, because the forager has to reject all prey below a critical value (minimum acceptable prey value, see also Orians & Pearson 1979; Lessells & Stephens 1983; Stephens & Krebs 1986). The more selective the forager, the higher the critical prey value will be, and the longer the forager will have to search. A change in food selectivity is optimal when the parent changes the duration of its foraging excursions. For instance, in the presence of predators

around the nest (Martindale 1982), the parent bird should make shorter trips, and decrease its selectivity (Houston & McNamara 1985b; Lucas 1983, 1985).

Second, the different distribution of prey across the birds' feeding range may produce a correlation between prey size and foraging trip duration. Feeding sites closer to the nest are more exploited than those further away (Naef-Daenzer 2000, so that they generally contain prey at lower density (Andersson 1978, 1981) and of smaller size (tits tend to catch large caterpillars among those available: Tinbergen 1960; Gibb & Betts 1963; Naef-Daenzer 2000). As a result, the parents foraging further from the nest could deliver larger food items. Thus, assuming the environment to be constant (for instance within a day or shorter time interval), the parents may get access to larger prey by increasing either search time or travel time, or both. We therefore expect to observe, even in a matter of a few hours, significant variation in prey size that can be explained by changes in feeding rates.

In this study, I investigated the relationship between the time spent away from the nest and the size of prey delivered to the brood. To do this, I looked at the variation in both variables in 1.5-h periods. Because I wished to compare the size of a sufficient number of food items of similar type, I focused on the relationship between feeding intervals and size of larvae, which are the most common nestling food in my study area, and ignored other prey items, including supplementary food. Because of the mechanisms of regulation of visiting rate and their effects on prey size (Tinbergen 1981; Grieco 2001), the alternation of periods of intense and less intense provisioning should result in a positive correlation between prey size and the time since the last visit, even within periods as long as 1 h (Fig. 1). However, there may be a range of conditions where this relationship is not apparent. If the parents feed the brood at slow rates they would in any case have sufficient time to get access to large food items. At low feeding rates, prey size would not increase with foraging trip duration (Fig. 1). This is because prey size cannot increase above a certain limit set either by the environment (i.e. the size distribution of prey) or by the parent's preference. The latter mechanism is likely since nestlings, especially young ones, cannot process large food items (van Balen 1973; Perrins 1979), so the parents will not look for them.

To test whether the parents could have access to larger prey when they have more time for foraging, I attempted to reduce the proportion of short foraging excursions by offering them additional food. The effect of food addition on visiting rate could be either direct or indirect. In the direct effect, the parents give extra food to the nestlings, and decrease their visit rate as a response to reduced begging (Grieco 2001; see also e.g. Bengtsson & Rydén 1983; Leonard & Horn 1996). Therefore, the average time between feeds as well as natural prey size will increase (I do not consider visits with extra-food items, because they do not carry information on the time necessary to find prey). In the indirect effect, the parents consume the food themselves, and so could save time otherwise spent self-feeding (Martin 1987). At this point, two scenarios are

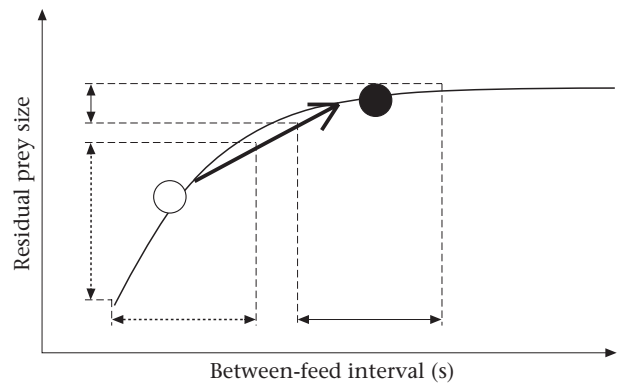


Figure 1. The hypothetical within-nest, within-day relationship between RPS (prey size independent of date) and the time the parent spends away from the nest (between-feed interval, BFI). The parent bird moves along this line when provisioning the offspring. Smaller prey are delivered at the end of short than long BFIs, because of the lower selectivity or the shorter travel distance (see text). Because of the size distribution of prey in the environment or selected by the parent, prey size does not increase further above some value of BFI. Circles show the expected effect of food supplementation on average prey size and the time the parent spent away from the nest before delivering the prey item. ○: Controls; ●: food-supplemented parents. The horizontal and vertical arrows indicate short-term (e.g. within 1.5 h) variation in BFIs and size of prey delivered by control (dashed arrows) and food-supplemented (full arrows) parents, respectively. Food-supplemented parents are expected to bring larger larvae, but of more constant size than controls.

likely. First, the extra time is spent bringing additional feeds (see the effect of food addition in Markman et al. 1998), so that the average time between feedings and prey size will not change. Second, the extra time is spent making longer foraging excursions (to reach further feeding sites, or to search for longer), so that the average time between feedings will increase. As shown by Tóth et al. 1998 for great tits, *Parus major*, a reduction in self-feeding may increase the time allocated for food provisioning and affect the prey choice strategy. Thus, the feeding experiment could increase the between-feeds intervals and prey size by acting on the parent's state. Because the food-supplemented parents would be able to gather large prey more often, variance in prey size should decrease, so that prey size would be less dependent on the duration of the foraging trip (Fig. 1).

METHODS

I did the study in 1998 and 1999 on the blue tit population breeding in nestboxes in the Hoge Veluwe National Park, central Netherlands, in the breeding seasons of 1998 and 1999. The study area includes 400 nestboxes in a mixed forest dominated by European oak, *Quercus robur*, and conifers, *Pinus* spp. (for details see van Balen 1973).

Feeding Experiments

I offered mealworms, *Tenebrio molitor*, and wax moth larvae, *Galleria mellonella*, to adult blue tits from the

day the chicks hatched to the day they fledged. Food consisted of a mixture of the two species in the first 6 days after hatching, and only mealworms thereafter. The quantity of food supplied each day corresponded to about one-half of the daily brood requirement (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. I adjusted the food quantity for smaller and larger broods (ca. 1 g per additional nestling; see Grieco *in press* for details). The larvae were placed in small trays (5.5 × 3.5 × 4.5 cm) inside the nestboxes to prevent birds other than the focal adults from consuming them. I replenished feeding trays each day according to the scheduled amount. Half of the nestboxes 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 assigned randomly within pairs to have the same range of hatching dates. I also tried to assign different treatment levels to boxes in similar habitats.

I checked all the nestboxes daily from the expected date of hatching to the date of fledging of the young. I checked nestboxes to assess nestling survival (for both experimental groups) and add food (for the fed group). In addition, all nestlings were weighed at 6, 10 and 14 days after hatching. Thus, I carried out the same type of disturbance for the nests of both experimental groups. The adults were caught when the chicks were 7 days old. A small metal door placed behind the nestbox entrance hole was kept open with a narrow stick. A parent entering the nest caused the stick to fall down and the door shut quickly, preventing the bird leaving the nest. During capture sessions, nestboxes were checked every 5–10 min, so that both parents were quickly caught. The parents were then sexed and colour ringed.

Videotaping and Direct Observations

I filmed parental behaviour during provisioning of offspring in 42 nests (21 in 1998 and 21 in 1999), once or twice each, when the chicks were 3–13 days old. Brood size on the day of filming was on average 7.8 (range 2–12). One pair was filmed in both years, although under different treatments (food supplemented in 1998, control in 1999). Of the 81 birds filmed (three males were never filmed as they presumably never attended the brood, even before the first filming session), eight (four females and four males) were filmed in both years. Of these, five were under different treatments in the 2 years (e.g. control in 1998, food supplemented in 1999). Even for the three 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 videocamera handy cam SONY CCD-TR825E was placed facing down from the top of the open nestbox. During filming, a wooden box covered the videocamera and a small lamp placed behind it provided more light in the nest. To habituate the birds to the videocamera and the light, I placed a dummy wooden box, with a small

light turned on, on the nestbox 1 h prior to filming. All videotaping sessions ($N=75$) started in the morning between 0800 and 1200 hours and lasted 90 min. In none of the years did the starting time of videotaping significantly explain variation in either the number of feeds brought in 1 h or the size of prey (effect of starting time on feeding frequency: $F_{1,33}=1.49$, $P=0.23$ in a model with experimental treatment, chick age and brood size as significant predictors; effect on prey size (see below for definition): $F_{1,32}=1.27$, $P=0.27$ in a model with year, treatment, chick age and brood size as significant predictors). Hi8 videotapes were copied to extra high grade VHS tapes. The adults could be identified on the tapes from colour ring combinations, or if not yet ringed, from individual (not sexual) morphological features (e.g. irregularities of the head and face plumage). In the latter cases, I confirmed the sex by comparing plumage features in the videos made before and after the date of ringing. The sexes could also be identified by behaviour, that is, only females brood the young and clean the nest. For each visit, I recorded the time when the adult entered and left the nestbox.

Between-feed interval (BFI) was the time between two feeds, that is, the difference between the time the parent entered the nestbox and the time it had left the box in the previous visit. In a small proportion of visits (see Table 1) food-supplemented parents fed the offspring extra food items previously taken from the tray. Since these visits carried no information about the time taken to capture and deliver natural prey, I excluded them from the analysis. Natural prey items were classified as larvae, adult arthropods (including mainly spiders and pupae) and unidentified items. In this paper I focus on larvae, excluding extra food items. For natural larvae, prey size (PS) was defined as the ratio between the width of the larva's head capsule and bill width, both measured on the screen with callipers to the nearest 0.1 mm. Size could be measured in 66.7% of the larvae brought to the nest ($N=2240$). PS was expressed as beak size units ($1.0=1 \times$ beak width). The size of larvae delivered to the nest increased linearly with date as a result of their growth during the season. In both years, the quadratic term of date did not significantly improve the model of prey size ($\Delta R^2=0.005$, $F_{1,71}=0.99$, $P=0.33$; all video sessions included; see also Naef-Daenzer *et al.* 2000). To express prey size independent of date, I calculated the residual of PS from its linear regression on date (residual prey size, RPS). This value was calculated separately for the 2 years (regression equations: 1998: $PS = -0.143 + 0.017 \times \text{date}$, $R^2=0.55$; 1999: $PS = 0.056 + 0.016 \times \text{date}$, $R^2=0.66$).

Extra food items were larger than caterpillars (mean width of head capsule \pm SD; mealworms: 2.1 ± 0.2 mm, $N=200$; wax moth: 1.8 ± 0.2 mm, $N=200$; caterpillars: 1.6 ± 0.4 mm, $N=84$; dry mass: mealworms: 0.029 ± 0.007 g, $N=200$; wax moth: 0.054 ± 0.029 g, $N=200$; caterpillars: 0.011 ± 0.010 g, $N=84$; caterpillars were collected in the forest). Supplementing with large prey items could affect the search image used by the parents (Tinbergen 1960), resulting in food-supplemented birds searching for larger prey than controls (Allen 1988). However, food-supplemented as well as control parents

Table 1. Composition of the diet of control and food-supplemented nestling blue tits

Prey type	1998		1999	
	Control (9)	Supplemented (12)	Control (11)	Supplemented (9)
Larvae (natural)	0.62±0.13	0.59±0.18	0.62±0.17	0.67±0.15
Larvae (additional)	—	0.10±0.03	—	0.13±0.12
Spiders	0.06±0.07	0.06±0.09	0.14±0.12	0.08±0.07
Other arthropods	0.02±0.03	0.03±0.04	0.05±0.04	0.03±0.02
Unidentified	0.30±0.10	0.22±0.10	0.20±0.08	0.10±0.05
Proportion of additional items*				
Eaten by parents	—	0.83±0.27	—	0.65±0.33
Eaten by nestlings	—	0.17±0.27	—	0.35±0.33

Mean proportions are given±SD. Sample sizes are given in parentheses.

Significance of the effect of treatment on the proportion of prey types (only significant variables included in the models), ANCOVA: natural larvae: $F_{1,37}=0.002$, $P=0.97$; spiders: $F_{1,36}=1.24$, $P=0.27$; other arthropods: $F_{1,38}=0.16$, $P=0.69$; unidentified: $F_{1,36}=10.07$, $P=0.003$, controlled for year, nestling age, and date.

*Proportion of additional food items taken by the parents from the tray during filming.

brought larger prey as the nestlings grew older, independent of the environment (unpublished data), which is unexpected if the parents keep selecting large prey throughout the nestling period. Thus, any difference in prey size between treatment levels is unlikely to be due to this mechanism.

For 15 nests in 1999 I observed the behaviour of parents during filming sessions. Every time the parent left the nest for a foraging excursion, I measured the time it spent hopping along branches (see 'searching movements' in Remsen & Robinson 1990). This was defined as search time. I excluded the time spent flying between branches from search time measurements. My stopwatch was synchronized with the time counter of the video camera, so that search time could be related to the between-feed interval.

Data Analysis

I analysed the variation in BFI and RPS for visits with natural larvae only, from 41 of 42 nests (in one nest there were no data available on prey size). Individual nests were treated as observation units. Whenever two sessions per nest were available, I chose one at random for analysis. The proportion of prey types was arcsine transformed before analysis. I analysed RPS with general linear models in Statistica for Windows version 5.5 (StatSoft 1999). Log-transformed BFI, time at the start of filming, nestling age, brood size and date (expressed as April date, 1=1 April) were treated as covariates. Non significant variables were removed from the models. To test for a between-nest difference in the slope of the regression line of RPS on BFI, I tested the effect of the interaction Nest*log BFI on RPS. For each nest, I calculated the slope of the regression line of RPS on log BFI, and tested the difference of such values between treatment levels. Since log BFI is dimensionless, the slopes are expressed in beak size units.

Ethical Note

Permission to catch the birds was given by the National Park 'The Hoge Veluwe' and by the Ringing Station of The

Netherlands. Apparently, no breeding pair abandoned the nest after I put up the video camera or the dummy video camera box on the nest. However, three food-supplemented nests were attended only by the female, as the males abandoned the nest before the first filming sessions. In those nests, chick body mass and fledging success was not different from the other nests of the same treatment group (mean chick body mass at 14 days ± SD: one-parent nests: 10.4 ± 0.3 g, $N=3$; two-parent nests: 11.2 ± 0.9 g, $N=16$; $F_{1,16}=1.26$, $P=0.28$; mean proportion of young fledged ± SD: one-parent nests: 0.67 ± 0.29, $N=3$; two-parent nests: 0.70 ± 0.19, $N=15$; $F_{1,15}=0.11$, $P=0.75$). Total brood failure occurred in six of the 42 original nests, and was caused either by nest desertion of the parents after they were caught during the ringing sessions, or by *Protocalliphora* outbreaks. In all nests, the parents returned to the nest within a mean ± SD of 544 ± 437 s (range 189–2167 s, $N=41$) from the start of filming. The mean visit rate in the presence of videocameras ± SD was 35.7 ± 15.0 visits/h for unmanipulated pairs with nestlings 3–13 days old ($N=20$), similar to that at nests without videocameras in 1997, and within the natural range in habitats rich in caterpillars (Gibb & Betts 1963; Perrins 1979; Nur 1984; Cramp & Perrins 1993).

RESULTS

Extra Food and Prey Choice

The parents used the whole amount of food offered in 468 (67.7%) of the 691 nest-feeding days and ignored the extra food in 21 (3%) of the nest-feeding days. During videotaping in 1998 and 1999, the adults took a mean ± SD of 19.3 ± 14.6 items/h (range 0–49.3, $N=39$ filming sessions). However, the adults delivered to their young a mean ± SD of only 26 ± 27% (range 0–100%) of food items taken from the tray. This percentage increased with nestling age (Spearman rank correlation: $r_s=+0.41$, $N=37$, $P<0.02$), but not with brood size ($r_s=+0.08$, $N=37$, $P=0.64$).

In unmanipulated nests, larvae were about 60% of the number of prey items brought to the nestlings (Table 1). A large part of the nestling diet consisted of unidentified items (Table 1). Food supplementation changed the composition of the nestling diet since the adults delivered several supplementary food items (over 10% of the total number). The proportion of natural larvae, spiders and other arthropods in the nestling diet did not change with food addition (Table 1). However, food-supplemented parents brought relatively fewer unidentified prey than controls (Table 1). Since many unidentified items were small (their size being comparable to the bird's beak width), it appears that food supplementation caused the adults to deliver on average larger prey items.

Prey Size and Time Away From Nest

Figure 2 illustrates how feeding rate was associated with prey size. Figure 2a shows the sequence of feeding visits in a videotaping session. In this example, both the time since the last visit and RPS increased during filming (in other nests the pattern was sometimes different). Regressions of RPS on log-transformed BFI for each nest (Fig. 2b) revealed an association between these factors. The interaction between nest and log-transformed BFI was significant (ANCOVA: $F_{40,685}=1.76$, $P=0.003$), indicating that nests differed in the slope of the regression of prey size on BFIs. Food-supplemented nests showed lower slopes ($\bar{X} \pm \text{SD}=0.004 \pm 0.057$ beak size units, $N=21$) than controls (0.045 ± 0.053 beak size units, $N=20$; $F_{1,39}=5.64$, $P=0.023$; time of day, nestling age, brood size and date not significant; Fig. 3), indicating that prey size increased less strongly with time spent away from the nest.

In control nests, the interaction Nest*log BFI was almost significant ($F_{19,385}=1.59$, $P=0.056$), indicating that nests tended to differ in the slope of the relationship between prey size and foraging trip duration. Although the majority of slopes were not significantly different from zero (Fig. 3), in control nests there were more positive slopes than expected by chance (16 of 20, four significant (all positive); goodness-of-fit test: $\chi^2_1=7.20$, $P=0.007$; Fig. 3). In contrast, in food-supplemented nests the slopes of the regression lines of RPS on log BFI did not differ from each other (ANCOVA: interaction Nest*log BFI: $F_{20,301}=1.36$, $P=0.14$; Fig. 3). Food-supplemented nests showed negative and positive slopes in similar proportions (nine and 12 (one significant) of 21, respectively; goodness-of-fit test: $\chi^2_1=0.43$, $P=0.51$; Fig. 3). On average, control parents brought more natural feeds per time unit than supplemented parents (ANCOVA: $F_{1,36}=12.94$, $P=0.001$ after controlling for chick age, brood size and date of filming; Fig. 3). The greater number of prey items used to calculate the regression coefficients in control nests could increase the probability of detecting a significant positive coefficient and could be why control nests had more positive coefficients than food-supplemented nests. However, the regression lines of RPS on log BFI were steeper in the former than in the latter group even when the comparison was limited to nests

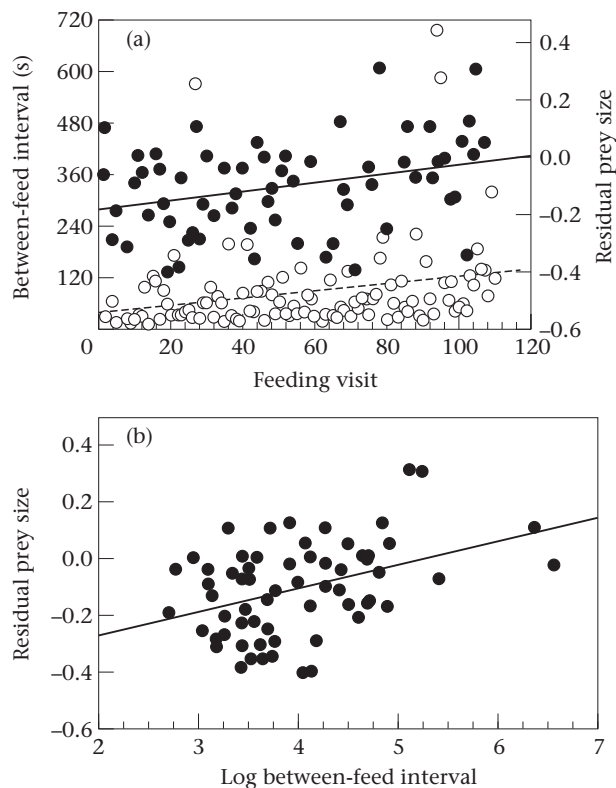


Figure 2. An example of the within-nest, within-day relationship between size of prey brought to the nest and time since the last visit by parent blue tits. Data are from one nest and do not represent a general result. In many nests (for instance, nests with an additional food source), the parents fed nestlings at a lower rate than in this example. Thus, prey size is less constrained by the parental visit rate (see Results) (a). Between-feed interval (\circ ; BFI, the time between one visit and the next by the same parent) and size of the larva brought at that visit (\bullet ; residual prey size, RPS, i.e. prey size independent of date) along the sequence of visits. All BFIs are shown, including those where prey other than larvae were brought. Both BFI and RPS correlate with visit number: log-transformed BFI: $r_{77}=+0.36$, $P=0.002$; RPS: $r_{62}=+0.31$, $P=0.01$. This pattern was not a general feature across nests. In some nests, BFIs and prey size decreased with time since the start of filming, while in others there was no clear trend in any direction (e.g. first increasing, then decreasing). (b). Regression of RPS on log-transformed BFI from the data in (a). $Y=0.516+0.084 \times \log(\text{BFI})$ ($N=63$); $F_{1,61}=12.02$, $P=0.001$. A regression equation was calculated for each videorecording session.

with similar numbers of items used in the calculation of regression coefficients (e.g. nests with 10–30 items: $\bar{X} \pm \text{SD}$; control: $+0.056 \pm 0.057$ beak size units, $N=13$; food-supplemented: $+0.001 \pm 0.034$ beak size units, $N=14$; $F_{1,25}=9.47$, $P=0.005$). Thus, the probability of detecting a positive correlation between prey size and BFI was not simply due to the sample size available for nests in the two experimental groups.

According to Fig. 1, prey size should be associated with BFI only when visit rate is high. Figure 3 shows the relation between the regression coefficients of RPS on log BFI and the visit rate, expressed as the number of natural feeds in 1 h. The interaction between food supplementation and provisioning rate was significant (ANCOVA:

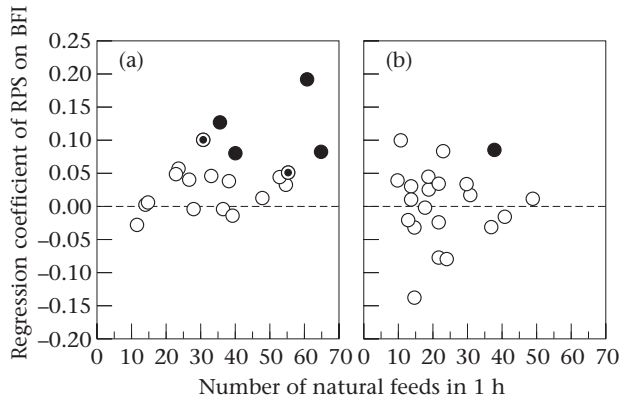


Figure 3. Coefficients of within-nest, within-day regression of residual prey size (RPS, size of larvae independent of date) on the between-feed interval (BFI; time since the parent's last visit) in relation to the feeding frequency of (a) control and (b) food-supplemented parents. The dashed horizontal line represents the regression coefficient equal to zero, that is, full independence of RPS on BFI. Statistical significance of regression coefficients: ○: $P > 0.10$; ⊙: $P < 0.10$; ●: $P < 0.05$.

$F_{1,39} = 8.56$, $P = 0.006$). For control nests, regression coefficients increased with visit rate (ANCOVA: $F_{1,18} = 6.66$, $P = 0.019$; Fig. 3). This was not the case for food-supplemented nests (ANCOVA: $F_{1,19} = 0.02$, $P = 0.88$), which showed less variation in natural feeding frequency. Note that the significant regression coefficients are in the upper right corner of Fig. 3, indicating that prey size increased significantly with the duration of the foraging trip only in nests with high provisioning rates.

At low visit rates, parents should always be able to gather large prey items (unless these are scarce) because they would have enough time to get access to them (BFI would be longer than in nests with high provisioning rates). Food-supplemented parents stayed away from their nest for longer before delivering a natural prey than controls (mean BFI \pm SD; control: 173.6 ± 87.8 s, $N = 20$; food-supplemented: 214.7 ± 68.1 s, $N = 18$) although the difference was not significant ($F_{1,33} = 3.94$, $P = 0.056$ after controlling for chick age, brood size and date of filming; nests attended by only one parent were excluded). Thus, prey brought by food-supplemented parents (feeding the chicks with long BFIs) should be larger than that brought by control parents (feeding the chicks with short BFIs). Food-supplemented parents brought larger larvae to the brood than controls (ANCOVA: $F_{1,33} = 4.57$, $P = 0.04$ after controlling for year, chick age and date of filming; Table 2). The effect of treatment was even larger for nests where at least 10 larvae were measured ($F_{1,29} = 9.03$, $P < 0.005$). As we have seen, prey size was no longer related to the time since the last visit when parents could have access to extra food. Within 1.5-h periods, variation in RPS was higher in control than food-supplemented nests, although the difference was not significant (ANOVA: $F_{1,36} = 3.58$, $P = 0.067$; Table 2). This might indicate that food-supplemented parents brought larvae of more constant size, as predicted in Fig. 1.

Table 2. Average size \pm SD of prey brought to the nest by parent blue tits and average variance \pm SD in residual prey size calculated for each videotaping session

Year	Control	Supplemented
1998	0.71 \pm 0.10 (9)	0.74 \pm 0.13 (11)
1999	0.82 \pm 0.12 (11)	0.95 \pm 0.12 (7)
Variance		
All	0.026 \pm 0.016 (20)	0.018 \pm 0.009 (18)

Prey size is the ratio of the larva's head size to the bird's beak width. Residual prey size is the residual of the larva's size from its regression on date. Number of nests is given in parentheses.

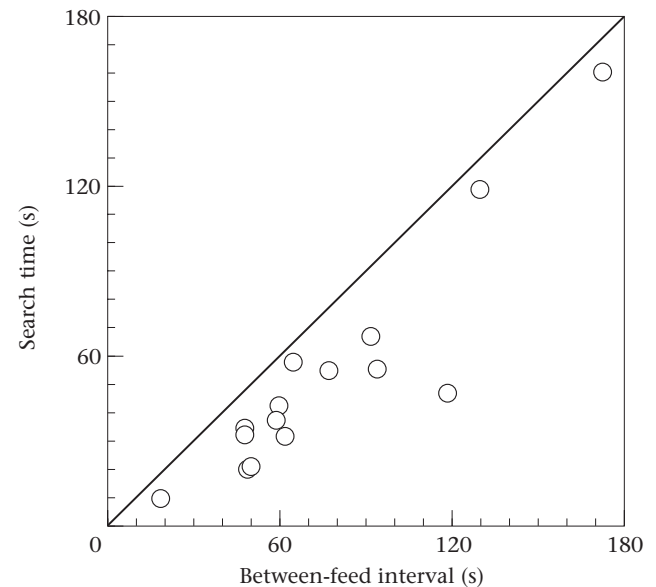


Figure 4. Time spent searching for food before a visit in relation to the time since the last visit. The diagonal line indicates the identity line (search time cannot exceed the total duration of the nest-feeding site-nest trip). Each data point represents a single foraging trip taken randomly from those available for each nest. Search time was measured by direct observation of parents foraging in the trees, while at the same time the videocamera recorded the between-feed intervals (total duration of the foraging trip).

Search Time and Prey Size

Search time was a good predictor of the total duration of the nest-feeding site-nest trip. I found a strong positive correlation between search time and BFI (correlation of log-transformed time intervals: $r_{13} = +0.92$, $P = 0.0004$; each nest was represented by a single foraging excursion taken randomly; Fig. 4). This indicates that the large variation in BFI, which reflects provisioning rate, was due to the variation in search time. However, there was no relationship between the BFI and the remaining time within BFI ($=$ BFI - search time; $r_{13} = +0.26$, $P = 0.34$). If travel time was the main component of this remaining time, only search time, not travel time, could explain the large variation in BFIs.

that the distance of the foraging site from the nest could not explain duration of feeding intervals. I conclude that variation in prey size could not be explained by a mechanism in which the parents collect large larvae when feeding further from the nest. Rather, short-term variation in prey size could be explained by a variation in search time. Because of the small data set for the searching time, I failed to demonstrate a within-session relationship between searching time and prey size. However, the parents that, on average, searched for longer were also the ones that fed the nestlings larger meals (Fig. 5). A difference in search time of 20–40 s, which matches the difference in BFI between food-supplemented and control parents, is that required to produce an increase in prey size of 0.5–0.1 beak size units observed in food-supplemented parents (Table 2), which corresponds to an increase of 10–15% in the size of the larva's head capsule. This would imply that the within-session variation in prey size is due to the parents continually making adjustments in prey selectivity while feeding the young. Thus, what appear as partial preferences in a static representation of prey choice (small as well as large larvae being brought to the nest in a 1.5-h period) are instead dynamic foraging rules that change rapidly (e.g. small larvae brought during intense feeding, followed by larger items being brought during less intense feeding; see McNamara & Houston 1987).

Naef-Daenzer et al. (Naef-Daenzer & Keller 1999; Naef-Daenzer et al. 2000) showed that the time between two feeds is strongly affected by external variables, mainly the average size and density of prey in the environment. Tits foraging in habitats with few and small caterpillars search for longer than when foraging in habitats with many and large caterpillars. From that work it could appear that provisioning rates in tits simply reflect the constraints imposed by the environmental conditions in which the parents feed the young. My data suggest that, besides the presence of strong environmental constraints, the parents make subtle adjustments in their foraging behaviour that account for changes in prey size and feeding rate on a short timescale (see also Grieco 2001). Tits seem to modify their provisioning rule, that is, their selectivity, so that the time taken to deliver a prey item is also affected by the decision of what size (and possibly also type) of prey to look for in a particular moment.

I failed to show that the regression coefficient of prey size on BFI is affected by factors such as nestling age and brood size. This is contrary to what one would expect. For instance, foraging is more intense when parents attend large broods. Therefore, the high proportion of short feeding intervals ending with the delivery of small items should result in a stronger association between RPS and BFI in large broods. The majority (four of five) of the significant positive regression coefficients were found in nests with seven to nine nestlings, that is nests with the modal brood size, while the largest brood was 12. This suggests that the extent to which prey size is limited by the duration of feeding intervals does not depend strictly on 'fixed' factors such as the size of the brood. Rather, it is affected only by the visiting rate, which reflects the

conditions in which the parents feed the young at the moment of filming. Even in large broods the feeding rate might be low. For instance, the quality of the territory or of the parents of large broods may allow feeding with large prey. In addition, the nestlings may be more satiated at some times of day than others. In both cases the current visiting rate may be relatively low, so that prey size will not depend on the duration of feeding intervals. Thus, time limitations of prey size occur, but are a function of the current situation during food provisioning.

Food Supplementation and Prey Choice

Blue tit parents receiving additional food consumed it but also gave a significant proportion of it to the young. This may have had both direct and indirect effects on provisioning rate (see Introduction). Compared with control parents, food-supplemented parents stayed away from the nest for longer and delivered large natural larvae to the brood. In addition, the size of the larvae they brought was more constant during the sampling period, and was independent of the duration of the foraging excursion. As the analysis of prey choice shows, the difference in size of larvae reflects a more general effect of food supplementation, in that the parents reduced the delivery of small (and presumably less preferred) food types. The effect on prey size might be the result of differential prey depletion in the blue tit territories. Since food-supplemented parents could use extra food, they might have depleted their territories less quickly than controls. However, the effect of food addition was already clear early in the nestling period (when the nestlings were 3–6 days old) when depletion of territories was unlikely (F. Grieco & A. J. van Noordwijk, unpublished data). I conclude that the effect of food addition on prey size was due to a change in the parents' prey choice strategy. Food-supplemented parents made longer foraging trips than controls. Since these were more likely to reflect longer searching time than longer travel time, the larger prey items brought by food-supplemented tits should be the result of longer searching time, and therefore greater selectivity. Some direct observations of food-searching parents seem to confirm this (Fig. 5). Since selectivity determines the average searching time, greater selectivity would reduce the overall food delivery rate. This can be compensated for by (1) delivering supplemental food items, which are much less costly to obtain, or (2) increasing the total time devoted to food searching in the forest. The latter could be done only if the time spent on other activities (e.g. self-feeding, brooding or nest cleaning) is reduced. Estimates of the amount of food delivered to each nestling per time unit suggest that both processes were at work (Grieco *in press*).

Other experimental work suggests that a relaxed time budget may reduce the constraints on selectivity. When Hurtrez-Boussès et al. (1998) reduced the density of ectoparasites in blue tit nests, females spent less time in nest sanitation (Hurtrez-Boussès et al. 2000), but made longer foraging excursions and delivered larger prey (J. Blondel, personal communication). This effect was not

seen in males, which do not clean the nest, excluding possible side-effects of the manipulation on prey depletion around the nest (highly parasitized broods may require more food, so that the parents might deliver more food). In a study of pied flycatchers, *Ficedula hypoleuca*, Lifjeld (1988) experimentally increased the hunger level of broods by replacing two well-fed young with five hungry young. The parents responded by taking smaller prey on average, indicating that they increased their feeding rate at the expense of prey selectivity. Tóth et al. (1998) observed that great tits returned to the nest with smaller meals when they had spent some time self-feeding. These studies show that provisioning rules change according to the state of the brood (Lifjeld 1988) and to the trade-offs between food searching and other activities of the parent (nest cleaning, Hurtrez-Boussès et al. 2000; self-feeding, Tóth et al. 1989). Functional explanations for changes in foraging rules have been proposed for both effects. By reducing selectivity or foraging in sites nearer the nest, the parents can adaptively increase their provisioning rate to minimize the risk of starvation of the nestlings (see the model by Houston & McNamara 1985a taken in the context of central place foraging) or to maximize gross energy intake (Lifjeld 1988). However, models such as those described by Houston (1987) suggest that, as soon as the parent's energy budget is brought into a model, the energy that the parent gets from items below the critical prey size becomes important, and can produce different optimal degrees of selectivity. In my study, food addition affected the state of the brood but also reduced the parent's need to self-feed in the forest (Grieco in press). Therefore, the changes in prey size in this study might have been caused by a combination of the processes described above.

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