

The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*

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Many bird species face seasonal and spatial variation in the availability of the specific food required to rear chicks. Caterpillar availability is often identified as the most important factor determining chick quality and breeding success in forest birds, such as tits *Parus* spp. It is assumed that parents play an important role in mediating the effect of environment on chick development. A reduction in prey availability should therefore result in increased foraging effort to maintain the amount of food required for optimal chick development. To investigate the capacity of adults to compensate for a reduction in food supply, we compared the foraging behaviour of Blue Tits *Parus caeruleus* breeding in rich and poor habitats in Corsica. We monitored the foraging effort of adults using radiotelemetry. We also identified and quantified prey items provided to nestlings by using a video camera mounted on the nest. We found that the mean travelling distance of adults was twice as great in the poor habitat as it was in the rich. Despite the marked difference in foraging distance, the proportion of optimal prey (caterpillars) in the diet of the chicks and the total biomass per hour per chick did not differ between the two habitats. We argue that relationships between habitat richness, offspring quality and breeding success cannot be understood adequately without quantifying parental effort.

As in most other bird species, Blue Tits *Parus caeruleus* face considerable spatial and temporal variation in food abundance. Caterpillars, the preferred prey of tits during the breeding season (Blondel *et al.* 1991, Perrins 1991, Banbura *et al.* 1994, 1999), are abundant only during a brief seasonal peak in any given habitat and their overall abundance varies considerably between habitats (Tremblay *et al.* 2003). For tits, temporal and spatial variation in caterpillar abundance influences many traits related to reproduction, such as the timing of egg laying (Perrins 1970, Zandt 1994, Svensson & Nilsson 1995), clutch size (Nour *et al.* 1998, Blondel *et al.* 1999), chick growth and development (Keller & van Noordwijk 1994, Tremblay *et al.* 2003) and chick survival until fledging (Tremblay *et al.* 2003), and can also directly affect adult body condition (Merilä & Wiggins 1997)

and the energetic cost of parental care (Tinbergen & Dietz 1994, Thomas *et al.* 2001a).

We have shown elsewhere that the relationship between the breeding success of Blue Tits (fledging mass and success of nestlings) and food abundance is not linear, but rather that it follows a saturation curve with both fledging mass and survival reaching a plateau above a certain level of food abundance (see Fig. 1, which is an updated version of figure 3 presented in Tremblay *et al.* 2003). The form of this relationship implies that at relatively high levels of caterpillar abundance (> 500 mg caterpillar frass/m²/day) adults are able to compensate for changes in local food supply. However, at caterpillar abundance < 500 mg/m²/day adults appear to be unable to adjust foraging sufficiently to maintain maximal chick growth and survival to fledging. This non-linear relationship between breeding performance and caterpillar abundance indicates that adults play a crucial role in mediating the interaction between the local environment and the nestlings.

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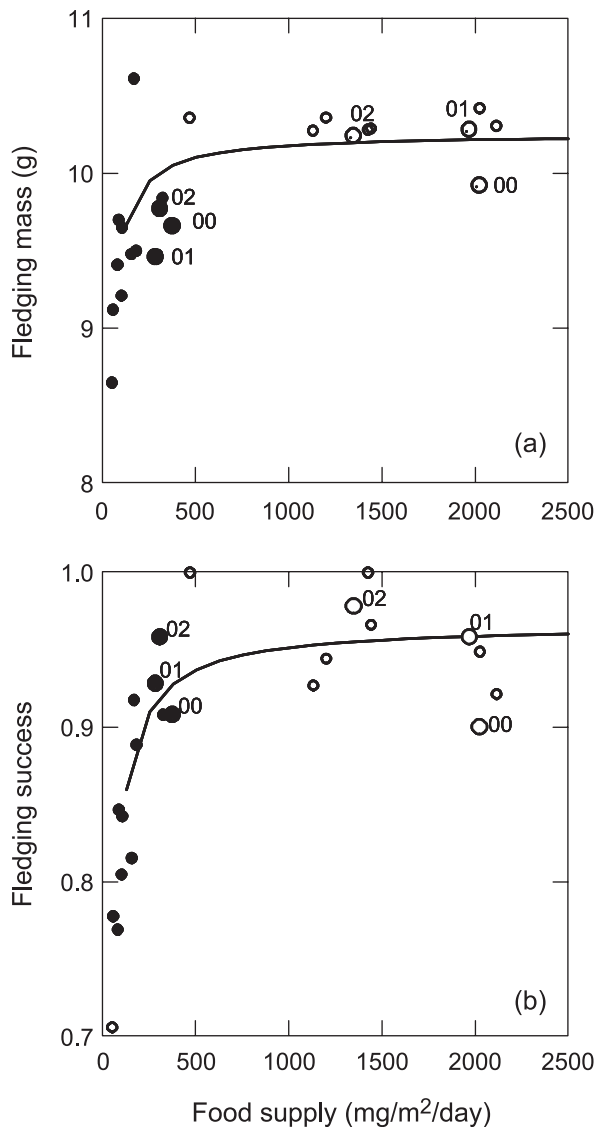


Figure 1. Variation in mean annual fledging mass (a) and mean fledging success (b) with increasing caterpillar frass abundance, for deciduous Muro (○) and evergreen Pirio (●) habitats. Large circles represent data for years that cover this study (2000, 2001, 2002) and curves indicate a saturation function (Michaelis–Menton) fitted to the data (fledging mass, $r^2 = 0.68$; fledging success, $r^2 = 0.82$). This figure is an updated version (data for 2001 and 2002 added) of figure 3 presented in Tremblay *et al.* (2003).

During the rearing period, foraging adults have to return repeatedly to a central point (the nest) and are consequently considered to be ‘central-place foragers’ (Grieco 1999). According to models of central-place foraging, birds start by exploiting patches closest to the nest and then increase their foraging distances progressively to exploit new and more distant patches as resources near the nest become depleted (Naef-

Daenzer 2000). Because food patches closest to the nest should become depleted more quickly in poor than in rich habitats, one would expect that adults would have to compensate for the decline in local food abundance by increasing their foraging range when nesting in habitats of low productivity. Thus, along a gradient from rich to poor habitats, one might expect foraging distances around the nest to increase, particularly in the late nestling period when local food resources would already have been depleted. However, this expansion in foraging range is probably limited by the increased time and energy demands associated with extended flight distances (Andersson 1978, Bryant 1997).

In this study, our objective was to examine how differences in caterpillar abundance between two habitats affect the foraging distances and provisioning rates of breeding Blue Tits on the Mediterranean island of Corsica (Lambrechts *et al.* 1997, Blondel *et al.* 1999, Tremblay *et al.* 2003). One habitat, Muro in the Balagne, offers an extremely high spring peak in caterpillar abundance, coupled with low infestation rates of ectoparasitic blow-fly larvae, *Protocalliphora* spp. (Hurtrez-Boussès *et al.* 1997). This combination of high food abundance and low ectoparasite levels allows breeding Blue Tits to maximize nestling growth and survival irrespective of the interannual variation in caterpillar abundance (Blondel *et al.* 1999, Tremblay *et al.* 2003). The other habitat, Pirio in the Fango valley, offers a far lower spring peak in caterpillar abundance, on average amounting to only 10% of that found at Muro (see Blondel *et al.* 1999, Tremblay *et al.* 2003). This site is also characterized by a high infestation rate of *Protocalliphora* larvae, which acts to reduce nestling growth and fledging mass (Simon *et al.* 2004). At Pirio, nestling growth and survival show a strong positive response to variation in caterpillar abundance (Tremblay *et al.* 2003). We predicted that differences in caterpillar abundance between the two sites would result in differences in the distance at which parents foraged around the nest. We also predicted that provisioning rates for nestlings would decline as foraging distances and search times increase.

METHODS

We conducted this study over the breeding seasons of 2000–2002 in two valleys separated by 25 km in northern Corsica, France. One valley (Muro: 42°33′N, 08°54′E; 350 m elevation) is dominated by deciduous Downy Oak *Quercus pubescens* forest where Blue

Tits typically hatch and raise chicks in April and May. The other valley (Pirio: 42°34'N, 08°44'E; 200 m elevation) is dominated by evergreen Holm Oak *Q. ilex* forest where Blue Tits typically hatch and raise chicks in May and June. For detailed descriptions of study sites and breeding phenology see Lambrechts *et al.* (1997) and Tremblay *et al.* (2003). At both sites, 100–150 concrete nestboxes spaced at roughly 50-m intervals offered artificial breeding sites for Blue Tits. Beginning in March (Muro) or April (Pirio), nestboxes were visited at weekly to daily intervals to monitor nest construction, date of first egg and hatching date. Nestlings were banded at 6 days of age and weighed at 14–15 days when they had reached asymptotic mass (Perrins 1991).

We monitored differences in caterpillar abundance between sites and changes in caterpillar abundance through the breeding season by monitoring frass fall in 15, 0.25-m² collectors placed under the forest canopy (see Zandt 1994 for a review of the technique). We collected samples twice weekly, separated frass from debris and weighed the dried frass to 0.1 mg precision. We used these measures of daily frass production (mg/m²/day) to construct curves of caterpillar abundance through the breeding season, which allowed us to measure peak caterpillar abundance at each site.

In all three years, we used a small video camera (Panasonic model KS 152) mounted in the nestbox to quantify parental visits and to identify and measure prey items brought to nestlings when they were 9–13 days of age. The camera was mounted in the back of the nestbox facing the entrance hole early in the morning and all visits to the nest were recorded on a digital VHS recorder for a period of 6–8 h. We later analysed recordings to count the visits of parents and to identify approximately 85% of the prey brought to the nest over the recording period. We classified prey as either caterpillars and pupae, the preferred prey of breeding Blue Tits (Perrins 1991, Banbura *et al.* 1999), or 'other' prey, which included spiders and a wide range of small insects (Banbura *et al.* 1994, 1999). For caterpillars and pupae, we measured total length (L) and mean width (W) using the diameter of the nest-hole as a reference. These measures allowed us to calculate a volume index for each caterpillar and pupae using the formula $(\pi/4) * L * W^2$ (Blondel *et al.* 1991). We made recordings at eight nests at Muro and 18 nests at Pirio and identified over 1200 prey for each site.

In 2001 and 2002, we used radiotelemetry to measure the foraging distances of one of the two parents at five nests at Muro and at eight nests at Pirio.

When chicks were 9 days of age, we caught one adult at the nestbox. After weighing the bird, we fitted a radio-transmitter (Holohil Systems Ltd, BD-2A) using a figure-eight harness made of monofilament fishing line to position the transmitter in the interscapular region without gluing to the skin. The final weight of the transmitter and harness package was < 0.65 g, which represented 6–7% of the birds' mass and was within the load limits suggested by Caccamize and Hedin (1985). After release, birds were left for 1 day to habituate to the transmitter package. Over the following 2–5 days, we located birds by triangulation during two 30-min periods in the morning and afternoon of each day. To locate the radiotagged individual at a given nest, we stationed two observers, each equipped with a directional three-element Yagi antenna and a radio receiver (Communication Specialists model R1000, 148–174 MHz), 50–75 m to each side of the nest. At roughly 1-min intervals, the two observers took a bearing on the radiotagged bird, synchronizing their bearings by walkie-talkie. We later used the Locate II program (v.1.82, Truro, Nova Scotia, Canada) to calculate the bird's position at each fix, based on the bearings and the UTM positions for the observers, which were measured using a global positioning system (Garmin model GPS48, 12-channel). We calibrated the accuracy of the calculated positions by moving a transmitter between known positions. Accuracy of the x - y coordinates ranged from ± 6 m to ± 55 m (mean = 26.4 m) depending on the intersection angle for the bearings.

Because it is widely reported that breeding tits invest more than 90% of their active time foraging to provide food for their young (Gibb 1950, Van Balen 1973, Smith & Sweatman 1974), we assumed that each position reflected a possible feeding site. The distance between that point and the nest was calculated and was used as an estimate of foraging distance. The range of our transmitter was evaluated at approximately 600 m and fixes exceeding this distance were considered to be outliers and were excluded from the analysis (fewer than 1% of observations).

To test the effect of habitat quality on the foraging performance of Blue Tits, we used a one-way ANOVA including foraging distance, visiting rate, provisioning rate, proportion of caterpillars and mean volume indices as dependent variables, and site as the main effect. Breeding parameters (brood size and fledging mass) for each site were calculated using unmanipulated nests in 2000, 2001 and 2002, grouped by year and compared using a one-way ANOVA with site as the main effect.

RESULTS

Caterpillar abundance, timing of reproduction, and clutch and nestling size

Over the three study years, the peak in caterpillar abundance averaged 303.4 ± 45.9 mg frass/m²/day at Pirió and 1763.3 ± 376.3 mg frass/m²/day at Muro (Fig. 2) (results are given throughout as mean \pm sd). At both sites, Blue Tits timed their breeding such that the nestling period was closely synchronized with the peak in caterpillar abundance. Brood size differed significantly between the two sites (ANOVA, $F_{1,4} = 16.05$, $P = 0.02$), with mean brood sizes being 7.6 ± 0.7 at Muro and 5.8 ± 0.4 at Pirió. Nestling mass at 15 days also differed significantly between sites (ANOVA, $F_{1,4} = 23.69$, $P = 0.008$), with mean nestling mass being 10.2 ± 0.2 g at Muro and 9.6 ± 0.1 g at Pirió. Parents at Muro thus had to provide food for a greater chick biomass ($7.6 * 10.2$ g = 77.5 g) than parents at Pirió ($5.8 * 9.6$ g = 55.7 g). Although chick biomass was 39% higher at Muro, the 581% increase in peak caterpillar abundance resulted in a substantially higher supply/demand ratio at Muro than at Pirió. Whereas parents at Muro foraged in an environment that presented 22.8 mg frass/m²/day per gram of chick, the

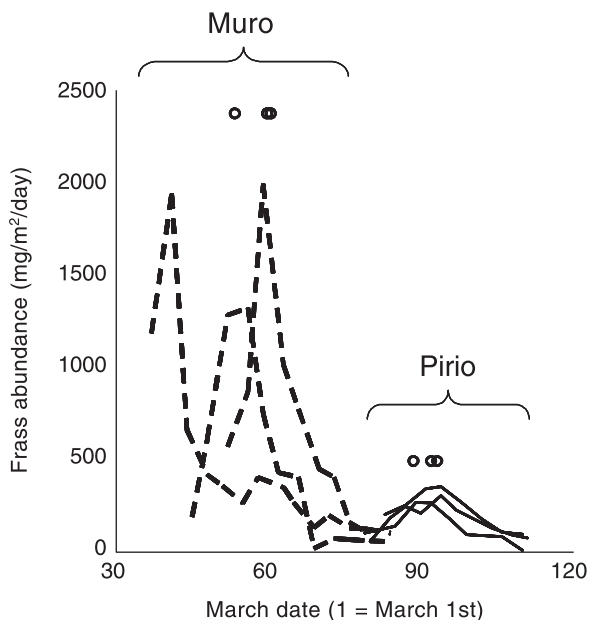


Figure 2. Seasonal variations in caterpillar frass abundance at Muro (broken line) and Pirió (lines). Circles represent peak demand in each habitat for the three study years (estimated as 23 days after laying date to allow for 13-day incubation and growth to 10 days of age).

environment for those at Pirió presented only 5.4 mg frass/m²/day per gram of chick.

Foraging distances

The foraging behaviour of one female (at Muro) and 12 males (four at Muro, eight at Pirió) was recorded successfully.

The use made of space around the nest by foraging parents differed dramatically between Muro and Pirió (mean travelling distances, ANOVA, $F_{1,11} = 5.88$, $P = 0.03$). Figure 3 shows the distribution of positions around a typical nest for each site. At Muro, parents foraged at a mean distance of only 25.2 ± 12.3 m from the nest and commuted to distances greater than 50 m from the nest in only 7% ($6.9 \pm 6.9\%$) of foraging trips. Birds were rarely detected foraging at distances greater than 200 m from the nest. At Pirió, parents foraged at a mean distance of 53.2 ± 22.9 m from the nest and flew to beyond 50 m from the nest in nearly one-third ($30.2 \pm 14.4\%$) of all foraging trips. Birds often flew out to 500 or 600 m from the nest, at which distance they were normally lost from detection, so these data underestimate the mean foraging distances at Pirió.

The flights that parents must undertake while feeding their young is set by the number of feeding trips and the mean travel distance. Although parents foraged closer to the nest at Muro, they made more feeding trips than at Pirió (see below). This resulted in very similar flight distances at the two sites, with parents travelling a mean of 1840 m/h at Muro and 1809 m/h at Pirió.

Parental provisioning rate and caterpillar biomass

Parental provisioning rate and caterpillar biomass provided to nestlings was estimated for a total of 26 nests (eight at Muro and 18 at Pirió).

Caterpillars constituted by far the greatest proportion of prey provided to chicks at both Muro and Pirió and there was no difference in the diet composition between the two sites (arcsine-transformed ANOVA, $F_{1,24} = 1.98$, $P = 0.17$). At Muro, caterpillars represented $82.4 \pm 9.9\%$ of the prey items whereas at Pirió caterpillars accounted for $73.6 \pm 16.2\%$ of prey items. Chicks reared at Pirió received larger prey items (0.19 ± 0.05 cm³) than chicks reared at Muro (0.11 ± 0.04 cm³; ANOVA, $F_{1,24} = 18.31$, $P = 0.0003$).

Parental visiting rate was significantly higher at Muro than at Pirió (36.5 ± 10.5 vs. 17.0 ± 4.5 visits/h; ANOVA, $F_{1,24} = 45.48$, $P < 0.0001$) and this difference

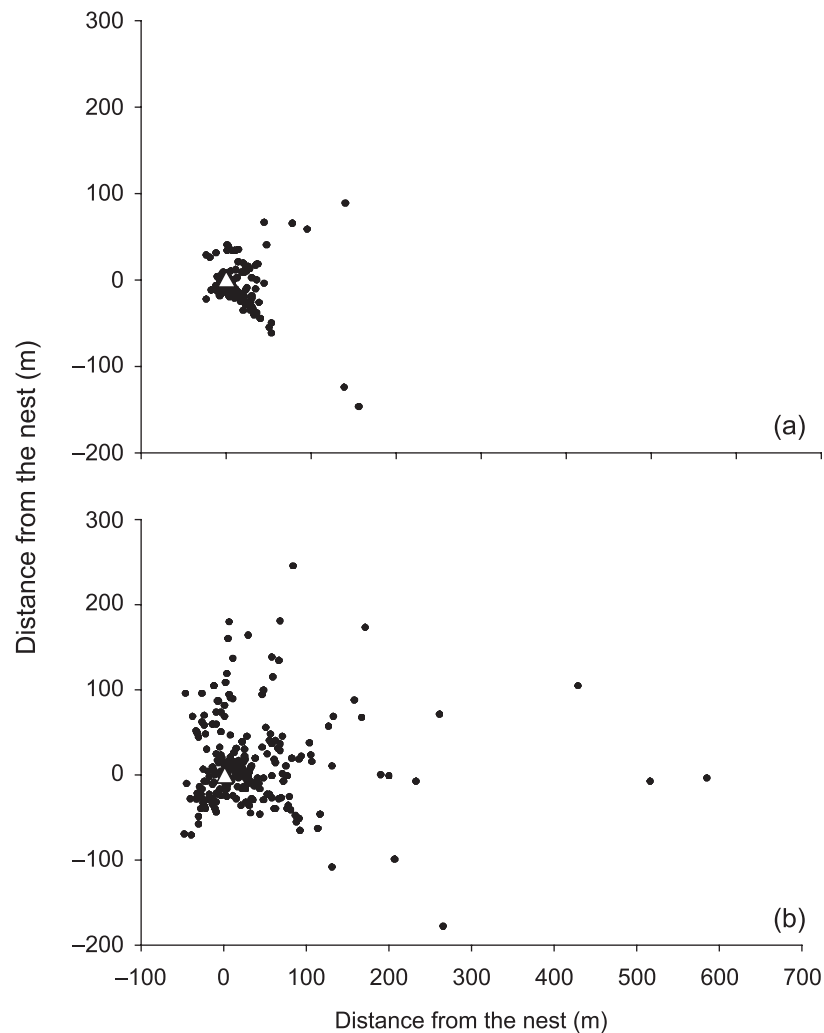


Figure 3. An example of the spatial distribution of positions of foraging Blue Tits for one representative nest at Muro (a) and one at Piriò (b) based on radiotelemetry. Each point represents a bird's position determined by triangulation when foraging to provision chicks of 9–13 days of age. At each site, the nest is indicated by a triangle (Δ). The distribution of points is not always symmetrical around the nest due to local patchiness in prey abundance and tree cover.

was maintained when provisioning rate was considered on a per-chick basis (Muro: 5.0 ± 2.0 visits/h/chick, Piriò: 3.3 ± 1.3 visits/h/chick; ANOVA, $F_{1,24} = 6.56$, $P = 0.017$).

The quantity of caterpillars that chicks receive is a function of the provisioning rate per chick and the mean caterpillar size provided by parents at each site. Although chicks received a 34% lower provisioning rate at Piriò, this was offset by the increase in mean caterpillar size. Chicks received approximately the same biomass of caterpillars at the two sites (Muro: 0.36 ± 0.12 cm³/h/chick, Piriò: 0.39 ± 0.09 cm³/h/chick; ANOVA, $F_{1,24} = 0.34$, $P = 0.57$).

DISCUSSION

Although our study was conducted in only two habitats, the wide range of caterpillar abundance between these two sites offers a good model to test the effect of food abundance on the foraging patterns of Blue Tits. In fact, our results show clear habitat-related differences in the foraging distances and provisioning rates of breeding Blue Tits, which are probably related to the abundance of caterpillars available in the vicinity of the nest. At Piriò, where caterpillar abundance is substantially lower than at Muro, parents expand their foraging radius by a factor of two (50 m vs.

25 m), thus covering approximately four times the surface area (7854 m² at Pirio vs. 1963 m² at Muro). The increase in foraging area roughly parallels the difference in caterpillar density between the two sites during our study (5.81-fold greater caterpillar density at Muro than at Pirio), suggesting that parents seek to maintain access to approximately the same absolute quantity of caterpillars despite substantial variation in density. This confirms the idea that adult Blue Tits adjust their foraging behaviour on the basis of caterpillar density because they are the preferred food for growing nestlings. Caterpillars require shorter handling times, are easier to ingest and contain more water (e.g. 85% for caterpillars, and 73% for spiders: Edney 1977), than other types of small invertebrates, and so allow for maximal chick growth (Banbura *et al.* 1999). It should also be noted that, during our three study years, the peak abundance of caterpillars at Pirio was much higher than the mean generally observed for this poor habitat (Tremblay *et al.* 2003). Consequently, the high abundance of caterpillars probably allowed parents to maximize their use of this preferred food item in a way that differed from years of lower caterpillar abundance (Blondel *et al.* 1991, Banbura *et al.* 1994).

The price that parents pay for foraging over a greater area is an increase in the round-trip distance of individual foraging bouts and a decrease in the provisioning rate for chicks in the nest. The lower feeding rate at Pirio than at Muro (3.3 vs. 5.0 visits/chick/h, respectively) may be due partly to an increase in travelling time, but it probably also reflects an increase in search times associated with lower caterpillar density at Pirio. If parents did not adjust prey size, a decline in provisioning rate would have resulted in a decline in the overall biomass of prey delivered to growing nestlings, with a concurrent fall off in growth rate, fledging mass and possibly survival to fledging. However, our data indicate that parents brought 73% larger caterpillar prey to the nest at Pirio than they did at Muro, thus offsetting the decline in provisioning rate. Nestlings at the two sites received the same caterpillar biomass. Because we have no direct measures of the size distribution of caterpillars at either of our sites, we cannot be sure that the greater size of prey brought to nests at Pirio reflects greater selectivity on the part of the parents or simply larger overall caterpillar size at Pirio. Because the peak in caterpillar abundance occurs about 4 weeks later at Pirio than at Muro (Lambrechts *et al.* 1997, Blondel *et al.* 1999, Tremblay *et al.* 2003), mean temperatures are 2–4 °C higher during the caterpillar growth

period (based on data from Météo-France for Calvi, Corsica). For this reason, we would expect caterpillar growth rates to be faster at Pirio, which might increase the mean size of caterpillars available to foraging Blue Tits when their nestlings reach 10–15 days of age.

It remains to be tested whether Blue Tits select small prey preferentially when caterpillars are abundant and large prey when caterpillar density declines. However, because the preparation time of the adults (Barba *et al.* 1996) and handling times of the chicks (Banbura *et al.* 1999) increase with prey size, it may be that the most efficient strategy for parents is to provide many small prey rather than fewer larger prey (but see Grieco 1999). If this were not the case, under conditions of low caterpillar availability, larger prey may become more conspicuous targets, perhaps even more so in our evergreen forest where the tree canopy is closed and less light is available for foraging Blue Tits. In addition, larger prey may be more profitable for adults that have to fly greater distances to forage. Finally, larger prey contain more water, which could be important during the drier and hotter climate experienced by chicks raised at Pirio.

Although the results confirm our prediction that foraging distances would increase as caterpillar density declined, we also anticipated that the difference in caterpillar density between Pirio and Muro (more than four-fold) would result in an increase in total round-trip flight distances at Pirio, measured in metres per hour. This, however, was not the case. Although the distance travelled during individual foraging bouts did increase, this was offset by the decrease in the number of foraging bouts per hour, to the point at which parents travelled equivalent distances in the two habitats (1809 m/h at Pirio vs. 1840 m/h at Muro). By flying greater distances to forage for larger prey for their chicks, but at a lower rate, parents could theoretically ensure near-maximal chick growth without increasing their overall flight distances. The fact that the biomass provided to nestlings remains constant due to the increase in prey size suggests that foraging parents actively increased their selectivity as caterpillar abundance declined. If they had attempted to provide a constant biomass to nestlings without adjusting prey size, at Pirio parents would be forced to maintain provisioning rates equal to that found at Muro, covering hourly distances of 2740 m rather than the observed distance of 1809 m. However, by investing more time in search of larger prey, it is possible that parents trade off search time against travel costs. We presume that

within-tree movements associated with searching are less energetically costly than flight (Pennycuik 1989, Goldstein 1990), so by increasing prey size (and hence search time) foraging parents are able to hold travel costs constant while still providing adequate caterpillar biomass to their nestlings.

Because overall flight distances remained constant, we would not expect to see an increase in the energetic cost of feeding chicks over the range of caterpillar abundance experienced over the three years of this study. This is in marked contrast to Thomas *et al.*'s (2001) results, which showed a dramatic increase in foraging costs at low caterpillar densities, but agrees with Verhulst and Tinbergen's (2001) observations that daily energy expenditure of breeding Great Tits *Parus major* did not vary with the timing of breeding and caterpillar abundance. Telemetry data, for our two sites, confirm that over a considerable range of caterpillar abundance (300–1700 mg frass/m²/day), parents are able to adjust foraging so as to maximize chick growth and survival, representing the plateau of the saturation curve (Fig. 1). As we have pointed out elsewhere (Thomas *et al.* 2001, Tremblay *et al.* 2003), when caterpillar abundance is extremely low, parents are unable fully to compensate for the decrease in food supply, which explains the steep slope observed in the relationship between food supply and either breeding success or metabolic rates. In fact, Banbura *et al.*'s (1994) results suggest that when caterpillar abundance is low (peak frass abundance of 165 mg/m²/day), adult Blue Tits diversify prey items brought to the nest, increasing the proportion of spiders by up to 50% and decreasing the proportion of caterpillars (less than 30%) in their nestling diet. Moreover, when the mean caterpillar volume is smaller than that of spiders, Great Tits opt for the latter, apparently preferring size over prey type (caterpillars or others). Spiders can also represent more than 75% of nestling diet, early in the season, before the emergence of caterpillars (Naef-Daenzer *et al.* 2000). As spiders are less digestible than caterpillars (Banbura *et al.* 1999), this reduction in the quality of prey brought to the nest could explain the decrease in breeding success (number and mass of fledglings) when caterpillars become scarce (Tremblay *et al.* 2003).

From our observations that caterpillar provisioning rates and the proportion of caterpillars in the nestling diet were similar at the two sites, we expected that nestlings reared in the poor habitat should reach a similar fledging mass to those reared in a rich environment. However, this was not the case. As parental care did not differ between the two sites, this dis-

crepancy in chick fledging mass could indicate either that growing conditions are worse at Pirió than at Muro or that the smaller size of birds in this poor habitat is an adaptive response to the poorer food supply, thus allowing a reduction of reproductive costs (Blondel *et al.* 2002). Although our results do not allow us to differentiate between these two hypotheses, we suspect that variation in infestation rate of blood-sucking parasites (*Protocalliphora*) might also play an important role in the observed variation. In the poor habitat, nestlings face an extremely high infestation rate, whereas *Protocalliphora* are far less common at our rich site (Hurtrez-Boussès *et al.* 1997). Because low body mass, low haematocrit and depressed aerobic capacity at fledging are associated with high *Protocalliphora* loads (Hurtrez-Boussès *et al.* 1997, Simon *et al.* 2004), we suggest that the parasite loads might be responsible for the slight difference in fledging mass that we found for nestlings at Pirió and Muro in this study. Thus, it would be of great interest to make the same measurements of parental care in the absence of these parasites to verify this supposition.

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