Patterns of nestling provisioning by a single-prey loader bird, Great Tit *Parus major*

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Capsule Nestling provisioning rates depend on nestling age and number, and on time of season, but not on time of day.

Aims To determine patterns of nestling provisioning, the effort made by the parents, and the factors which affect them.

Methods Mechanical counters to determine food provisioning patterns in 229 Great Tit *Parus major* nests over 4 years.

Results Feeding frequency per chick showed a linear increase with nestling age and total feeding frequency stabilized towards the end of the nestling period. The number of visits per nest increased linearly, while those per nestling decreased linearly with brood-size. Feeding rates per nest declined throughout the breeding season parallel to the seasonal brood-size decline; feeding frequencies per nestling did not vary seasonally. Adult effort was almost constant throughout the day, independently of variations in brood-size, ambient temperature and date.

Conclusion Previous studies of nestling provisioning patterns were either contradictory or poorly supported by low sample sizes. The present study involved a much larger sample and clarifies nestling provisioning patterns and the factors with which they are associated.

The rate of food provisioning to young is a basic aspect of the study of foraging behaviour in wild animals, which has been studied primarily in birds (e.g. Gibb & Betts 1963, Biermann & Sealy 1982, Blondel *et al.* 1991, Barba & Monrós 1999). The number of provisioning visits made by adults during the nestling period leads to a greater understanding of the foraging strategies (Tremblay *et al.* 2005, Kryštofková *et al.* 2006) and of the effort made to raise their young (e.g. Moreno *et al.* 1995, Stauss *et al.* 2005), as well as to a better identification of the environmental factors which might affect provisioning effort (e.g. Rytkönen *et al.* 1996, Naef-Daenzer & Keller 1999, Freitag *et al.* 2001).

In species where adults normally bring one prey item per visit (single-prey loaders; Orians & Pearson 1979), it is possible to estimate the number of prey items brought based on the number of visits made by the adults to the nest (e.g. Kluijver 1950, Stienen *et al.*

2000). Therefore, the study of feeding frequencies, and their patterns of variation should reveal important information on the effort that parents are making and the result of this effort from the nestlings' point of view, i.e. how many prey items they actually receive.

An important factor which might affect the rate of food provisioning is nestling age. Older nestlings are bigger and may therefore require more food. On the other hand growth rates are not constant, and nestlings may need more energy when growth rates are higher. A usual pattern is an increase in feeding rates with age during the first part of the nestling period, when nestlings are growing faster, and a levelling off when they are close to their final weight (Grundel 1987, Blondel *et al.* 1991). In some studies feeding rates have been shown to decrease in the days prior to fledging (Blondel *et al.* 1991, Rytkönen *et al.* 1996). A complicating factor could be the changes in either the size or type of prey brought by the parents as the nestlings grow, since parents might shift to more energy-rich and/or larger prey (e.g. Rytkönen *et al.* 1996, Stienen *et al.* 2000), or even

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change the degree of preparation of the prey brought (Barba *et al.* 1996, Ponz *et al.* 1999).

Furthermore, feeding frequencies could increase with the number of nestlings present in the nest, and this has been found in some studies (Gibb 1950, Rauter *et al.* 2000, Stauss *et al.* 2005). On the other hand, this increase in frequency is not always proportional to the increasing needs, so each nestling receives fewer visits as brood-size increases (Royama 1966, Rytkönen *et al.* 1996, Naef-Daenzer & Keller 1999, MacColl & Hatchwell 2003). Interacting with this, the energy requirements of the chicks change with brood-size, and greater heat loss in a small brood could be compensated for by the chicks being supplied with more food (Royama 1966).

Ambient temperatures might affect feeding rates (Rauter *et al.* 2000). Low temperatures might make the parents spend more time brooding at the nest, therefore decreasing the feeding frequency (e.g. Wiebe & Elchuk 2003). On the other hand, low temperatures increase thermoregulation costs of the nestlings, which might require more food, which in turn might result in increased feeding rates by the parents. Moreover, temperature might affect prey availability (Wiebe & Elchuk 2003). Therefore, the effect of temperature would very much depend on the actual ambient temperature, on the ability of nestlings to thermoregulate (i.e. their age), on the types of prey consumed and the effects of temperature on prey availability.

Most studies have found a decline in feeding frequencies during the breeding season (e.g. Naef-Daenzer *et al.* 2000), although both an increase (Smith *et al.* 1988) and a lack of seasonal variation have also been reported (Johnson & Best 1982, MacColl & Hatchwell 2003). A number of reasons could be behind these patterns, including variation in mean brood-size, the value of the current nestlings to the parents in terms of inclusive fitness (Winkler 1987), and the availability and size of prey items available (Royama 1966, Naef-Daenzer & Keller 1999).

Finally, parents might schedule their foraging activities considering those periods of the day when food demand by the nestlings is more intense (Freitag *et al.* 2001), food more easily available (Stienen *et al.* 2000) or foraging costs lower (Rastogi *et al.* 2006). Foraging should also be traded off against other activities, such as brooding small nestlings (Wiebe & Elchuk 2003). Therefore, feeding frequencies would be expected to vary throughout the day (see Knapton 1984), and this pattern of variation could change with factors such as nestling age, number of nestlings and ambient temperatures

(food demand, need of brooding), and throughout the season (food availability, temperature patterns, etc.).

Great Tits *Parus major* are a good model species to study patterns in feeding frequencies. Their tendency to occupy nestboxes allows detailed measurement of many breeding parameters (e.g. Gibb 1955, Royama 1966, Eguchi 1980, Smith *et al.* 1988, Tinbergen & Verhulst 2000). Great Tits typically behave as single-prey loaders (Gibb & Betts 1963, Naef-Daenzer *et al.* 2000), and most visits to the nest are for feeding young (Kluijver 1950, Eguchi 1980). Therefore, the number of visits made by the parents can be translated into the number of prey items received by the nestlings. Not suprisingly, several studies have been published either directly addressing the patterns of feeding rates of this species (Kluijver 1950, Gibb 1955, Gibb & Betts 1963, Royama 1966, Van Balen 1973, Eguchi 1979, Cowie & Hinsley 1988, Naef-Daenzer *et al.* 2000), or including feeding rates as a measure of parental effort in wider contexts (Smith *et al.* 1988, Verhulst & Tinbergen 1997, Naef-Daenzer & Keller 1999, Sanz & Tinbergen 1999, Tinbergen & Verhulst 2000).

In spite of this large number of reports, studies trying to describe feeding patterns in detail (e.g. Gibb & Betts 1963, Royama 1966, Eguchi 1980) have been done with relatively small sample sizes and lack statistical treatments. More recent studies, though including more adequate statistical treatments, have not included exhaustive analyses of the feeding patterns (see Cowie & Hinsley 1988 for an exception). Our main aim here was to describe the feeding patterns of Great Tits in detail. We explored the effect of nestling age, brood-size, time of season, time of day and temperature on this feeding behaviour.

METHODS

The study area was located in Sagunto (eastern Spain, 39°42′N, 0°15′W, 30 m asl) and was completely occupied by orange plantations (Andreu & Barba 2006). Nestboxes were distributed over the area, and checked periodically to determine the basic breeding parameters (laying date, clutch size, number of hatchlings and fledglings produced, etc.) of Great Tits occupying them (e.g. Barba *et al.* 1995). Most parents were trapped at the nest and individually ringed (e.g. Monrós *et al.* 2002). Data for this study were collected in 1996, 1998, 1999 and 2000 in 46, 7, 74 and 102 clutches respectively (198 first, 5 second and 26 replacement clutches). First clutches were defined as the first breeding attempt of the year; second clutches

were those laid after a successful first breeding attempt (i.e. at least one chick fledged) and replacement clutches were those laid after a breeding failure.

To estimate feeding rates, we used mechanical counters placed at the nestbox entrance. These consisted of a switch activated by a wire crossed at about two-thirds of the bottom of the entrance hole, so the bird pushed it down when entering or leaving the nestbox. These counters were not able to distinguish among the visits made by each member of the pair, so total number of visits is considered throughout. The counters were moved among available nests in our population, to maximize the sample size and distribute them among different nestling ages, brood-sizes and throughout the season.

We defined 'sample' as a continuous registration of feeding rates during at least 2 hours in a nest. Recording times varied between 2 hours and 1 day. In cases where a counter was operating overnight, we computed the number of hours of daylight using official sunset and sunrise times. When feeding nestlings parents usually start their visits by sunrise and finish close to sunset (e.g. Kluijver 1950; pers. obs.). The feeding rates recorded in these cases were assigned to the day in which the counter was operating most of the time.

Maximum, minimum and average ambient temperatures were gathered from a meteorological station placed close to the study area (c. 4 km) and were available for each of the sampling days. The three temperatures were closely related. We repeated the analyses with all of them, and relationships were always stronger with minimum temperatures, so we only present these results.

We could not analyze the data in full models, with all the independent factors considered and their interactions contributing to explain variations in feeding rates. The main reason was that, for some analyses (e.g. effects of nestling age or time of day), we needed repeated measurements of the same nests, so a limited set of nests fulfilled the requirements. These nests were randomly selected among available ones each year. Therefore, our approach was asking specific questions and using the best set of data available to answer them.

To analyze the effect of nestling age on feeding rates, we used four age-classes: 4–6, 7–9, 10–12 and 13–15 days. Data outside this range were too scarce and were removed from these analyses. We only used nests for which samples were available for each of the four age-classes. In cases where more than one sample per nest and age-class was available, we used the average frequency of the available samples. We ended up with data from 20, 20 and 12 successful first clutches collected in 1996, 1999 and 2000 respectively, and six replacement

clutches (one from 1996, five from 1999). No second clutches fulfilled the aforementioned criteria to be included in the analyses.

We tested how the number of nestlings present at the time of sampling affected the effort made by the adults using data from 229 clutches, including first, replacement and second clutches of all years. We performed both linear and quadratic regression analyses choosing the one which best fitted the data. When we had data for several days on a nest, we randomly selected one day.

To test for seasonal variation in feeding rates we used all the nests available in 1996, 1999 and 2000, including first, replacement and second clutches, and selected one sample per nest to remove the effect of nestling age. For each nest, we selected the sample closest to day 10, the day where food demand by the nestlings was more intense; 76% of the nests had samples between days 8 and 12, the rest between days 4 and 15. Then, we calculated the residuals of regressing feeding frequency against age of the nestlings, and explored the seasonal trend of these residuals. Data covered the period from 27 April to 26 June. To explore the effect of temperatures on seasonal variation, we also selected for each nest the minimum temperature when the nestlings were 10 days old.

Finally, data on diurnal variation were collected in 1996, 1998 and 1999. Each day was divided into six periods from sunrise to sunset. The first period from sunrise to 10:00 and the last one from 18:00 to sunset, all other periods were 2 hours long. We included in the analyses 40 nests (successful first clutches) for which we had data on feeding rates for each one of the six periods, as well as exact information on the age of the nestlings (mean 8.6 ± 0.5 days, range: 4–15) and brood-size (mean of 5.5 ± 0.29 chicks, range: 2–9) on the date of sampling. In nests where we had data for more than one day, one of the days was randomly selected for the analyses.

We next explored whether any of the potential factors considered affected diurnal variation in feeding rates. Each year, half of the nests were classified as 'early' and the other half as 'late', based on the date of laying of their first egg. Based on the minimum temperature, days were classified as either 'hot' ($T_{min} > 12$ °C) or 'cool' ($T_{min} \leq 12$ °C). Other factors included in the analyses were nestling age, brood-size and year.

Repeated measures anovas (RMANOVAS) were used when the feeding frequency (dependent variable) of the same nest was measured at different times, i.e. in testing for the effects of the age of the nestlings or time of day

(within-subject factors). In these cases, the assumption of sphericity was tested (Mauchly test), and Huynh–Feldt corrected degrees of freedom used if this assumption was not held. When between-subject factors were included in the models, we also tested for homogeneity of variances and covariances (M-Box test). Dunn–Sidak *post-hoc* tests were used to test for differences among categories in within-subject factors. The effect size was calculated through the strength of correlation (r_s) when both variables were continuous, and through the size of difference (d) when the response variable was continuous while the predictor was categorical (Nakagawa *et al.* 2007). In both cases, statistics are shown with their respective confidence intervals (CIs).

Values are presented as means ± 1 se. Statistical analyses were carried out using spss 15.0.

RESULTS

Nestling age

Considering all the available clutches ($n = 58$), feeding rates varied with the age of the nestlings (Huynh–Feldt test, $F_{2.5,140.4} = 4.2$, $P = 0.012$; Fig. 1). However, Dunn–Sidak *post-hoc* tests did not reveal any statistical differences among ages, though the increase from the first (4–6 days) to the third (10–12) age-class was close to statistical significance ($d = 0.25$ with 95% CI = −6.5 to 0.0, $P = 0.05$), levelling off later on.

A potential factor affecting this pattern might be the reduction of the number of nestlings throughout the nesting period by death of some nestlings. In fact, brood-size differed slightly between age-classes (Huynh–Feldt test, $F_{2.0,100.0} = 6.7$, $P = 0.002$), being highest (6.0 chicks ± 0.27) for the youngest and lowest (5.7 chicks ± 0.30) for the oldest age-class (Dunn–Sidak *post-hoc* tests, $P = 0.016$; no significant differences were detected among other age-classes). We therefore explored how the number of visits per nestling varied with their age, and significant differences among age-classes were found (Huynh–Feldt test, $F_{2.5,140.0} = 6.1$, $P = 0.001$; Fig. 1). The pattern of increase with age was almost linear until the oldest age-class, i.e. the final levelling was not observed. Significant differences (Dunn–Sidak *post-hoc* tests) were detected between the first and the fourth age-classes ($d = 0.28$ with 95% CI = −1.7 to –0.3, $P = 0.002$),
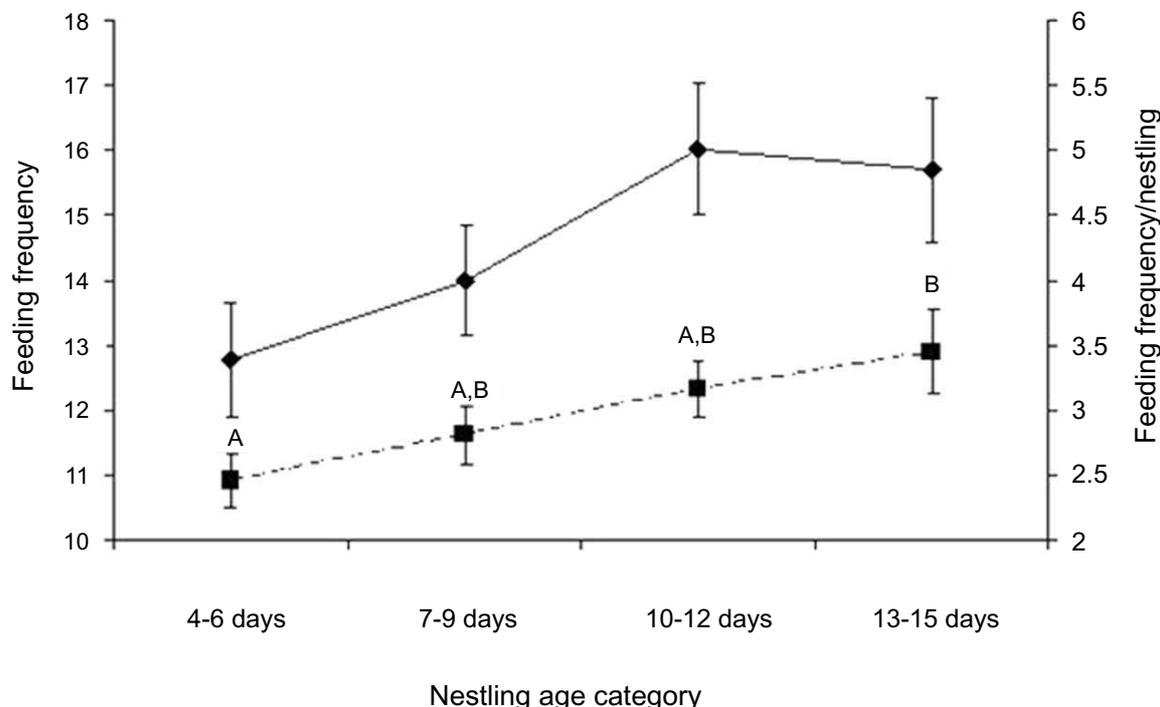

Figure 1. Variation of total feeding frequency (number of visits per hour, solid line) and feeding frequency per nestling (number of visits per nestling per hour, dashed line; $n = 58$ nests in both cases) throughout the nesting period. Nestling age-classes with the same letter were not significantly different. Means ± se are shown.

and marginally significant differences between the first and the third ($d = 0.20$ with 95% CI = -1.4 to 0.0, $P = 0.062$) and the second and the fourth age-classes ($d = 0.18$ with 95% CI = -1.3 to 0.0, $P = 0.054$). Therefore, the parents increased their effort per nestling as they grew older, at least within the range of ages explored, though the total number of visits they performed stabilized by the end of the nesting period when they had to feed fewer nestlings.

Another question addressed was whether the pattern of variation of feeding rates with age changed through the season. To check this possibility we used only first broods ($n = 52$), and divided them into 'early' and 'late', allocating half of the broods of each year into each category. The interaction term between nestling age and seasonal period was not significant whether considering feeding rates per nest (Huynh–Feldt test, $F_{2.4,121.7} = 1.4$, $P = 0.24$) or per nestling (Huynh–Feldt test, $F_{2.5,126.2} = 1.0$, $P = 0.40$). Therefore, the pattern of variation of feeding rates with age did not differ throughout the season among first clutches.

Brood-size

Considering all the clutches available ($n = 229$), the number of visits made by the parents increased linearly with brood-size ($r_s = 0.25$, with 95% CI = 0.5 to 1.5, $F_{1,227} = 14.7$, $P < 0.001$; Fig. 2). However, the number of feeding visits per nestling declined linearly as brood-size increased ($r_s = -0.41$, with 95% CI = -0.4 to -0.2, $F_{1,227} = 46.0$, $P < 0.001$; Fig. 2).
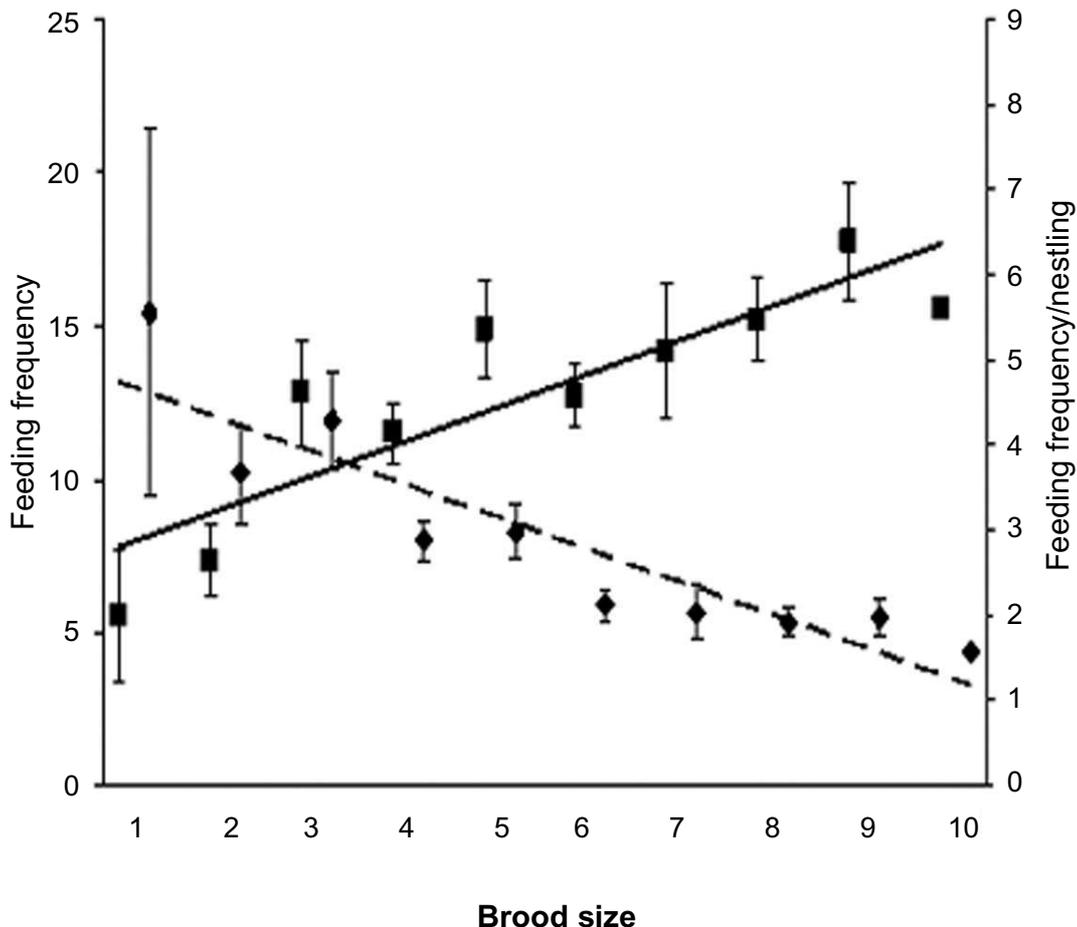

Figure 2. Brood-size effect on parental effort (solid line) for first ($n = 198$ nests), second ($n = 5$ nests) and replacement ($n = 26$ nests) clutches. Feeding frequency (number of visits per hour): $7.6 + 1.0 \times$ brood-size, $r^2 = 0.061$, $F_{1,222} = 14.3$, $P < 0.001$. Linear regression among brood-size and parental effort per nestling (dashed line) for the same sample size. Feeding frequency per nestling (number of visits per nestling per hour): $4.5 - 0.3 \times$ brood-size, $r^2 = 0.150$, $F_{1,222} = 39.1$, $P < 0.001$.

Quadratic terms did not significantly improve the fitting in any case. This means that parents with more nestlings made more effort, but that increase was not proportional to the increment in brood-size, and each particular nestling received fewer prey items in larger broods.

Seasonal variation

Seasonal variation was explored using one data point per nest and removing the effects of nestling age at the time of sampling (see Methods). The general pattern for the total feeding frequency was a decline during the breeding season (r_s = −0.13 with 95% CI = −3.4 to −0.01, $F_{2,221}$ = 4.0, P = 0.048). However, more detailed analysis showed that the seasonal pattern differed between years (ANCOVA, $F_{2,218}$ = 7.1, P = 0.001, with date as a covariate). Only in 1999 was the seasonal decline significant (Fig. 3).

Two of the studied factors might affect seasonal variation in feeding rates: brood-size and temperature. Brood-size decreased throughout the season in all three years (ANCOVA, date (covariate): $F_{1,218}$ = 47.7,

P < 0.001; year: $F_{2,218}$ = 6.0, P = 0.003), and ambient temperatures, when nestlings were 10 days old, varied during the season (ANCOVA, date (covariate): $F_{1,218}$ = 83.0, P < 0.001; year: $F_{2,218}$ = 12.0, P < 0.001) increasing in all of the three years. We therefore built a regression model for each year with date, brood-size and temperature as independent variables and feeding frequency as response variable, using a stepwise selection of variables. In all of the three years, brood-size was the only variable included in the regression model (1996: r^2 = 0.102, r_S = 0.33 with 95% CI = 0.2 to 3.0, $F_{1,45}$ = 5.0, P = 0.031; 1999: r^2 = 0.211, r_s = 0.46 with 95% CI = 1.1 to 3.0, $F_{1,73}$ = 19.2, P < 0.001; 2000: r^2 = 0.076, r_s = 0.27 with 95% CI = 0.4 to 2.0, $F_{2,101}$ = 8.2, P = 0.005). Therefore, the seasonal decrease in feeding rates was mostly explained by the seasonal decrease in brood-size. On the other hand, and agreeing with the above pattern, each nestling received the same number of visits during the season. Although the adult effort per nestling was different in different years, there was no seasonal variation in feeding rates per nestling within each year (ANCOVA, date (covariate): $F_{1,218}$ = 2.5, P = 0.115; year: $F_{2,218}$ = 12.7, P < 0.001).
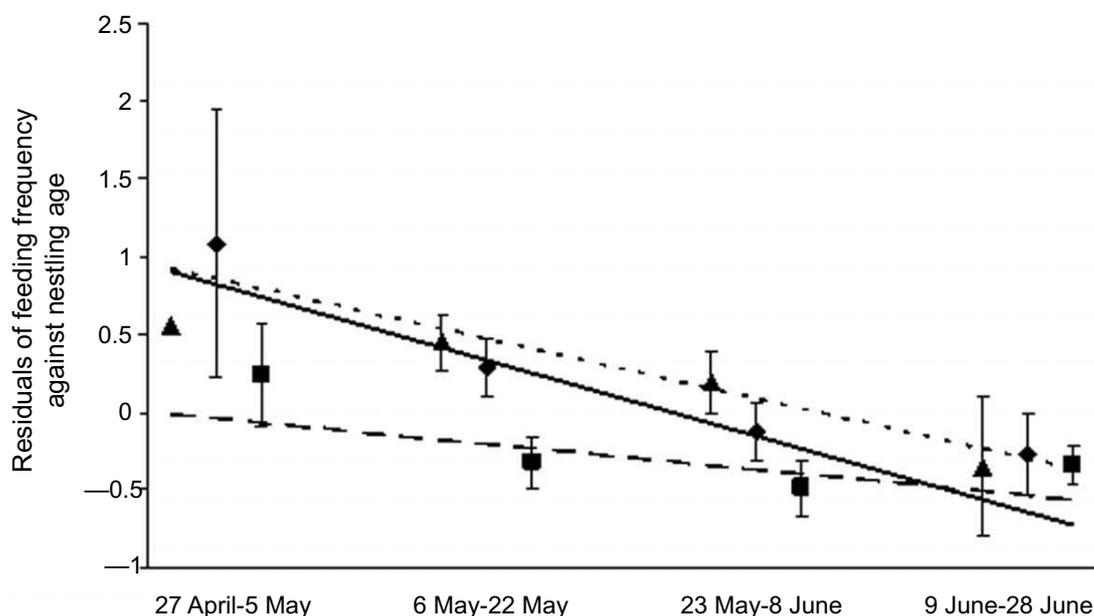

Figure 3. Seasonal variation in feeding rates for the three study years. Residual feeding rates, after removing the effect of nestling age, were used. To simplify the presentation, mean (± se) values are presented for arbitrary periods: 27 April–5 May, 6 May–22 May, 23 May–8 June and 9 June–26 June. However, regression analyses were performed using all data points: 1996 (solid line, triangles): 1.3 − 0.02 × date, r^2 = 0.050, r_s = −0.22 with 95% CI = −6.0 to 0.8, $F_{1,44}$ = 2.3, P = 0.068, data points from 46 nests; 1999 (dotted line, rhombi): 1.4 − 0.02 × date, r^2 = 0.069, r_s = −0.26 with 95% CI = −5.5 to −0.4, $F_{1,72}$ = 5.3, P = 0.012; data points from 74 nests; 2000 (dashed line, squares), r^2 = 0.013, r_s = −0.12, d = 41.33, $F_{1,100}$ = 1.4, P = 0.124; data points from 102 nests.

Diurnal variation

Over the 40 nests included in the sample, feeding rates did not vary significantly throughout the day ($F_{5,195} = 2.1$, $P = 0.062$). Mean values ranged between 12.1 and 14.7 visits per hour at the different periods considered (Fig. 4). Since differences among diurnal periods were, however, close to statistical significance, we also looked for the underlying factors associated with them (laying date, temperature, nestling age, brood-size and year). A full model, including all variables mentioned previously as between-subject factors, was not significant ($F_{5,110} = 0.3$, $P > 0.05$). However, when we only included the age of the nestlings as a between-subject factor, significant differences in feeding frequencies between age-classes were obtained ($F_{5,180} = 2.3$, $P = 0.045$). Dunn–Sidak *post-hoc* tests showed that feeding rates increased significantly from the first to the third age-class ($d = 0.40$ with 95% CI = −5.8 to −0.1, $P = 0.036$), while inspection of

Fig. 4 suggests that most of this difference was probably caused by the oldest nestlings. When other factors where individually included in the different models, no significant differences in feeding rates throughout the day were detected ($P > 0.05$ in all cases).

DISCUSSION

Nestling age

Total feeding rates usually increase linearly with the age of the nestlings, levelling off towards the end of the nestling period, and even decreasing before fledging (Johnson & Best 1982, Grundel 1987, Blondel *et al.* 1991, Karlsson 1994, MacColl & Hatchwell 2003). However, some studies failed to detect changes in feeding rates with nestling age, and changes in prey size and/or quality were suggested to compensate for this
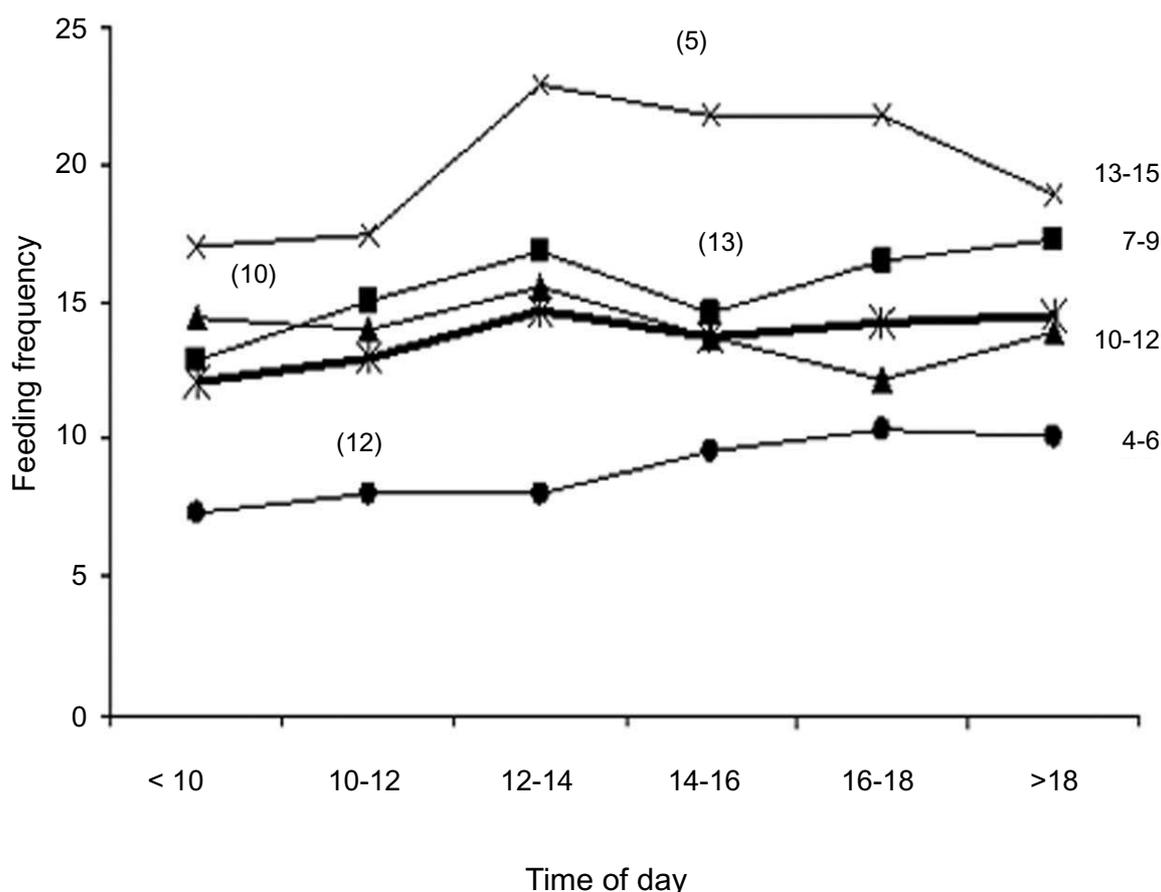

Figure 4. Effects of nestling age on diurnal patterns of variation in feeding frequencies. There is a thin line for each age-class; age ranges are shown at the end of the lines on the right; sample sizes for each line are in parentheses. Mean values are joined by the thickest line.

lack of increase (e.g. Knapton 1984, Laiolo *et al.* 1998, Stienen *et al.* 2000), though this is not always the case (e.g. Schadd & Ritchison 1998). Other authors argued that the lack of effect was because of the absence of samples from very young nestlings (Schadd & Ritchison 1998, Kryštofková *et al.* 2006).

Among the studies on Great Tits that have examined this pattern, Verhulst & Tinbergen (1997) found a linear increase of feeding rates with nestling age up to 14 days. Data presented by Gibb (1955) suggested a more-or-less linear increase up to 10–13 days of age (see also Eguchi 1980), levelling off afterwards, and even decreasing by the end of the nestling period in late broods. Some authors have suggested that this lack of increase of feeding rates at older ages was due to fatigue of the parents (e.g. Gibb 1955), or to changes in prey size with nestling age (Royama 1966, Knapton 1984), while the decrease was attributed by Kluijver (1950) to the fact that adults were preparing for a second brood.

Our results clearly showed that parents increased the number of feeding trips per nestling at least from 4 to 15 days. When considering the total number of visits, it seems to level off after day 12. These results strongly suggest that the lack of increase in parental effort towards the end of the nestling phase is mostly a consequence of a brood-size reduction due to nestling mortality throughout the nesting period, and not to fatigue of adults. On the other hand, while parents could bring smaller prey to very young nestlings (e.g. Slagsvold & Wiebe 2007, for Pied Flycatchers *Ficedula hypoleuca*), it is unlikely that changes in prey size occurred during the last part of the nestling period (e.g. Kabisch 1965). We have no data after day 15, so it is possible that feeding rates per nestling actually levelled off after this age, as suggested in previous studies (Gibb 1955, Grundel 1987, Blondel *et al.* 1991).

Brood-size

Probably the most commonly reported pattern is that parents feeding large broods make an effort to increase their feeding rate in order to fulfil the greater requirements of the brood (e.g. Gibb 1950, Nur 1984, Robinson & Hamer 2000). However, it is also usual that the increased feeding rates do not fully compensate for the increase in brood-size, resulting in fewer visits per nestling in larger broods (e.g. Royama 1966, Nur 1984). In a number of studies, however, feeding rates per nest were reported to be independent of brood-size (see e.g. Bengtsson & Rydén 1983, Knapton

1984, Schadd & Ritchison 1998 and references therein) while, at the other extreme, Naef-Daenzer *et al.* (2000) suggested that Great Tits could maintain a constant number of visits per nestling, therefore proportionally increasing the number of visits as brood-size increased. Agreeing with the general pattern, our results showed that adults worked harder when provisioning larger broods, but not enough to compensate for the increase in brood-size, so nestlings received fewer visits when they were more numerous.

Four different hypotheses could contribute to explain the patterns of feeding frequencies per nest and per nestling. First, larger broods would have thermal benefits, the chicks conserving their heat more efficiently than those in small broods (Royama 1966), and therefore needing less energy. For example, Schadd & Ritchison (1998) did not find differences in feeding rates between small (two chicks) and large (three to four chicks) broods of Yellow-breasted Chats *Icteria virens*, and they used the thermal benefits of larger broods to explain this. Royama (1966) restricted this effect to relatively small broods (up to five nestlings; see also O'Connor 1975), so that thermal benefits would not be significant for larger broods. This would predict that, above five chicks, per-nestling feeding rates would stay more or less constant (i.e. not decreasing any further with increasing brood-size). What we have observed in the present study is that feeding rates decreased linearly also among large brood-sizes, so the 'Royama effect' seemed to be unimportant to explain the patterns found in our population. Perhaps the hotter temperatures in our study area (see Greño *et al.* 2008) as compared with those in England, where Royama (1966) performed his study on Great Tits, could explain this, but this effect has not been found in colder environments either (see Rytkönen *et al.* 1996).

Second, the Gibb–Lack hypothesis (Nur 1984) suggests that there might be an upper limit to the effort that parents could make, so that broods above the modal size would receive fewer feeding trips per nestling. This predicts that total feeding rates would increase up to the modal brood-size and then level off, while rates per nestling should remain constant up to the modal brood-size and decline thereafter (see Nur 1984 for a graphical interpretation). This is clearly not occurring in our population.

Third, Pettifor *et al.* (1988) suggested that each particular pair optimizes its brood-size, so all the pairs are making the same relative effort independently of their actual brood-size. Taking this into account, the pattern that should be observed is an increase of feeding rates

proportional to the increase in brood-size, so that feeding rates per nestling would be kept constant. This did not occur in our studied Great Tit population.

Finally, parents might be optimizing costs and benefits of feeding nestlings in the long-term (Nur 1984). This implies that parents would not be prone to increase their investment in the current brood above a certain level, even though they potentially could. This trade-off model predicts a continuous increase in per-brood effort and a continuous decrease in per-nestling effort with increasing brood-size, perhaps levelling off at very large brood-sizes (see also Rytkönen *et al.* 1996). Thus, our data are consistent with Nur's (1984) hypothesis. We did not detect the levelling-off of the feeding frequency per nestling for large brood-sizes, but the results presented by Nur (1984) included experimentally enlarged broods, and perhaps this levelling-off is harder to find in unmanipulated clutches. Nevertheless, experimental studies (e.g. Smith *et al.* 1988, Moreno *et al.* 1995, Rytkönen *et al.* 1996, Tinbergen & Verhulst 2000) would be needed to determine whether particular individuals would be willing to increase parental effort in response to brood-size enlargement in our population.

Seasonal variation

Most studies to date have found a seasonal decline of feeding rates by Great Tits (Kluijver 1950, Gibb & Betts 1963, Royama 1966, Naef-Daenzer *et al.* 2000). We also found this general pattern, although the trend was only significant in one out of the three years studied.

We investigated potential causes of this seasonal pattern, and its variation between years, by considering whether other seasonally related variables could produce it (brood-size and temperature). It is obvious that changes in brood-size could affect total feeding rates (see earlier), while an increase in ambient temperature could reduce energy needs. When considering these two variables, we found that the seasonal pattern in feeding rates was mostly explained by seasonal changes in brood-size, i.e. total feeding rates decrease during the season because parents have fewer nestlings to feed as the season progresses. This is also consistent with our finding that feeding rates per nestling were constant throughout the season in our population.

Another potential cause of a seasonal decline in feeding rates is that, from the parental point of view, the fitness value of fledglings decreases during the season, and so parents would be less likely to invest in them (e.g. Winkler 1987). However, this would clearly predict a seasonal decrease in per-nestling feeding rate, something that does not occur in our population. It should be considered that Monrós *et al.* (2002) found that late fledglings had good survival prospects in some years in our study site, so parents could keep constant their investment per nestling due to the uncertainties of the outcome in this habitat.

Finally, seasonal changes in type, abundance and size of prey could affect feeding rates (Gibb 1950, Kluijver 1950). Gibb & Betts (1963) and Royama (1966) reported that the low feeding frequency in late broods resulted from an increase in the availability of large prey, mainly caterpillars (see Johnson & Best 1982). Naef-Daenzer & Keller (1999) made a more detailed analysis of how feeding rates in Great Tits varied seasonally with seasonal changes in caterpillar abundance and size. Nestling diet in our population was quite particular for Great Tits, since moths, and not caterpillars, form the bulk of the diet (Barba & Gil-Delgado 1990, Barba *et al.* 2004). These authors found that the size of the moth species found in the nestling diet was smaller late in the season. Therefore, if changes in prey size were determining the seasonal pattern in feeding rates, we should expect a seasonal increase in per-nestling feeding rates, which was not the case.

Diurnal variation

With 40 nests followed during a whole day, this is the most extensive study to date that has dealt with diurnal variation in feeding frequencies in Great Tits. The first attempts to describe diurnal variation in feeding frequencies in Great Tits produced very different results. Gibb (1955), for example, stated that 'When all stages of all broods were lumped together, no rhythm was apparent …' (p. 54). However, when the early and late phases of the nesting period were analyzed separately, he found that parents fed more often in the afternoon when nestlings were young, while the pattern later on was more variable, even feeding more frequently early in the morning in large broods. He thus identified two factors – nestling age and brood-size – that might affect the diurnal rhythm of feeding visits (see also Gibb 1950). Other diurnal patterns might be found in old studies (e.g. Kluijver 1950, Eguchi 1980), but they also based their conclusions on few nests and they did not apply statistical analyses to their data. More recent studies including proper statistical tests (Cowie & Hinsley 1988, Moreno *et al.* 1995, Verhulst & Tinbergen 1997) have failed to find significant diurnal variation in feeding

rates. The same lack of diurnal variation has been found in Blue Tits *Cyanistes caeruleus* (Parejo & Danchin 2006) as well as in other species (e.g. Black-throated Blue Warblers *Dendroica caerulescens*; Goodbred & Holmes 1996). This constancy contrasts with what would be theoretically expected since several factors could cause diurnal variation in feeding rates (e.g. Gibb 1955, Stienen *et al.* 2000, Freitag *et al.* 2001, Rastogi *et al.* 2006; see Introduction).

Our first analysis aimed at detecting diurnal variation in feeding rate approached significance, especially when nestling age was considered. Differences seem to be caused by the increase of feeding rates from the first hours of the morning to mid-day in nests with the oldest nestlings. This result does not fit with any of the theoretical patterns presented previously, and we have no explanation for it. We therefore conclude that in our study area Great Tits fed their nestlings at a constant rhythm throughout the day, independently, at least within the range of conditions explored, of variations in such factors as laying date, temperature, brood-size and year. The potential effect of nestling age on diurnal patterns of feeding rates should be explored further.

As a final note, results presented here have been collected in a southern European population, and the patterns obtained have been compared with those of central and north European populations. It is not conclusive whether the differences found are related to the small sample sizes and/or lack of statistical tests of previous studies, or to actual differences between populations. Both temperatures and nestling diet are different in Sagunto compared with northern Great Tit populations. If parents could adjust their feeding patterns to these local conditions, they might also differ with location. Clearly, to understand fully the provisioning patterns of Great Tits and other single-prey loaders, studies similar to those described here should be conducted in central and north European populations and appropriate comparisons made.

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