Feeding strategies in great tit *(Parus major)*:
Do parents adjust prey size to nestlings' size?

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Forord

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Abstract

The feeding behavior is favored by natural selection in the past and is based on getting a high fitness by maximizing net energy intake. Reproductive success among altricial birds is closely related to feeding strategies because nestlings are totally dependent on being fed by their parents from the day they hatch to the day they fledge. We have studied the patterns of feeding behavior in great tit parents and their ability to adapt to the current feeding situation by adjusting prey size to nestlings size. This has been an experimental study of parental care by great tits of 10-14 days old great tit and blue tit nestlings in their natural environment. We recorded the feeding behavior inside 30 nest boxes that were divided into three groups. Group great tit was an unmanipulated control consisting of the original great tit nestlings, Group blue tit consisted of only blue tit nestlings and Group mixed consisted of one original great tit nestling and the rest of the nestlings replaced with blue tit nestlings.

We found that the ability to adjust prey size would be an important skill in tits reproduction ecology because large prey increases the swallow time for all the nestlings which in time increases the feeding time for the parent. We assumed that the smaller body size of the blue tit nestlings would imply a more constrained capacity to swallow larger prey items so that prey size should have more critical consequences for blue tit than for great tit nestlings. However we did not find any indication of this since the blue tit nestlings were fed with prey of approximately same size as the great tit nestlings and that the proportion of long swallow times did not increase. We discuss possible reasons for the surprising result.

Introduction

The reproductive success of an individual is dependent on maximizing the total sum of reproduction through its entire life (Begon et al., 1996) for it self and its descendants. Many factors influence the reproduction decision such as seasonal timing, prey abundance, the parents' own physical quality, mate choice etc. The nestlings in most altricial birds are dependent on being fed by their parents in the early stage of their life so successful reproduction is highly dependent on the parents' ability to feed their young. Feeding ability is a combination of several behavioral factors; some are congenitally while others are learned (Krebs and Davies, 1993) and feeding behavior is supposed to be a matter of maximizing net benefit. Adults and nestlings differ to some degree in their diet because of constraints on development. Their morphological constrains limit the size and type of prey they can swallow (Marchetti and Price, 1989). The parents' feeding efficiency is a combination of their searching time, handling time and the nestlings swallow time. Bigger prey has a higher nutrition value but might increase searching, handling, and swallow time. The nestlings' swallow time does highly influence the parents feeding effiency because the parents wait for the nestlings to swallow the prey before leaving the nest in order to search for new food. This makes swallow time a more crucial factor of the feeding efficiency when feeding nestlings than in the bird's own foraging (Sherry and Mcdade, 1982). The success of the parents feeding behavior might not only be an issue of earlier learned or congenital behavior but also their ability to adapt to the current situation.

Great tit (*Parus major*) nestlings hatch at a quite early stage of development. When hatched the nestlings are small, blind and naked. The parents feed their nestlings for about 18-20 days before they leave the nest (Cramp, 1993). In this period the nestlings increase rapidly in size and they gain weight fast from a body mass around 1.5 g when they hatch up to 20 g when they leave the nest (Perrins, 1979). When the nestling are small the parents have to adjust the size of the food items to the size of the nestlings so that they are capable of swallowing the food (Moser, 1986). Right after the nestlings have hatched the parents brings small and easily digestible food items to the nestlings and then they gradually increase the size of the food items to a certain level (Balen, 1973). The nestlings grow rate is significantly influenced by the available mass of food which makes breeding timing very important for the great tit (Naef-Daenzer et al., 2000). The preferred food for nestling tits is known as the lepidopteran larvae (Balen, 1973; Perrins, 1979; Banbura et al., 1999) and the tits' success of reproduction is highly dependent on the right timing to the abundance of this larvae (Naef-Daenzer and Keller, 1999; Jones et al., 2003). A high proportion of the diet in nestling period consists of this larvae but it never reaches 100% (Royama, 1970; Balen, 1973) because of the need for different nutrition and because of the suitability of the larvae size related to nestling size. The ability of nestlings to swallow prey items is size-dependent and changes with age (Sherry and Mcdade, 1982; Marchetti and Price, 1989; Banbura et al., 1999). The time needed for prey preparation increases with prey size and decreases with nestling age (Royama, 1966; Barba et al., 1996). It seems like the size of the prey is of greatest importance the first 6 days after hatching where it follows the nestlings' growth curve. After day 6 is the prey size more constant (Royama, 1966, 1970; Balen, 1973). This might be a consequence of constraints on development of the nestlings in early age (Marchetti and Price, 1989) or simply reflecting the main prey size available in this period.

An issue is whether the great tit parents are capable of adjusting the prey size to the size of the nestlings after day 6 or is the feeding pattern only a matter of timing to abundance and size of the prey. If the parents are not capable of this adjustment then rapid increasing prey size or slowly growth of the nestlings might lead to reproductive failure (Naef-Daenzer and Keller, 1999). If the nestlings are fed with too big prey items then that might increase their swallow time and so increase the parents food handling time (Balen, 1973; Banbura et al., 1999). Minimizing food handling time is of great importance for reproductive success because the nestlings have a high nutrient requirement in order to grow and survive (Marchetti and Price, 1989) and for the parents it is a question of cost and benefit for their recent and future reproduction (Barba et al., 1996). If the parents can adjust the size of the prey item to the size of the nestling then a further question is whether there is a difference between the male and the female in this ability and in their food allocation among the nestlings. In some species the female provides more food to the youngest nestlings and the male to the oldest (Stamps et al., 1985; Sasvari, 1990; Slagsvold et al., 1994). The female might have a greater knowledge of the nestlings' needs since she often spend more time in the nest than the male, and she will therefore ensure that the youngest and often weakest nestling also get fed (Stamps et al., 1985;

Gottlander, 1987). Also the male may prefer the oldest nestlings more than the youngest because of the greater risk that the youngest offspring is a product of extra pair mating and therefore will be of no reproduction value to the male (Gottlander, 1987; Weatherhead and Yezerinac, 1998).

In order to address these questions we created three groups of great tit and blue tit nestlings all with great tit parents which we filmed when the nestlings were 10-14 days. Group great tit was an unmanipulated control group consisting of the original great tit nestlings. Group blue tit consisted of only blue tit nestlings. Group mixed consisted of one original great tit nestling and the rest of the nestlings replaced with blue tit nestlings. Experience from earlier experiments tells us that great tits have no problems of accepting blue tit nestlings (Hansen, 2003). By swopping great tit nestlings by blue tit nestlings we created a situation where the nestlings were generally smaller than normal. The blue tit is smaller (adult length 11.5cm) (Cramp, 1993) and lighter (adult mass ca.11g) (Haftorn, 1971) than the great tit (adult length 14 cm, adult mass ca.18g). We would expect the smaller body mass among the blue tit nestlings to imply a more constrained capacity to swallow large prey items.

We asked: 1. Do great tit parents adjust their prey choice to the size of their nestlings? and; 2. Do the male and female parents differ in prey choice and how they allocate the food among the nestlings? To address these questions we examined: if there were any significant differences (a) between the three treatment groups, (b) between the blue tit nestlings and the great tit nestling within the same brood and (c) between the sexes (parents). To make these comparisons we analysed: (1) The occurrence of long swallow time, (2) The size of the prey that was fed to the nestlings, (3) The correlation between swallow time and prey size, and (4) The food allocation to the youngest and the oldest nestling.

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Picture 1: Size differences between great tit nestling (left) and blue tit nestling (right) at day 13

Material and methods

The study site

The field work was carried out in the studying area Dæli near Oslo during the spring 2003. The study area included 400 nest boxes placed out in deciduous and mixed deciduous/coniferous forest. About 150 tits, blue tits and great tits nest in the boxes each year. 32 boxes were great tit nested were used in the experiment but after analyzing the videos, two boxes where removed from the dataset because only one of the parents was feeding. The boxes were checked every second or third day during the breeding period to record nest progress, clutch size, egg laying date, hatching date and number of young hatched. To estimate hatching date, a plot of body mass of birds with known age was used.

The experiments

The experiments were performed under licenses from the Directorate for Nature Management and the National Animal Research Authority in Norway.

We made one control group with unmanipulated broods and two groups with manipulated broods. The manipulation took place at hatching by changing eggs or nestlings between nests.

Group great tit consisted of 9 broods with a mean brood size of 5.6, Group blue tit of 12 broods with a mean brood size of 7.8 and Group mixed of 9 broods which consisted of one great tit and x blue tits, with a mean brood size of 6.2 (1 great tit and 5.2 blue tits). The minimum brood size was three and the maximum was ten.

On the day before filming (day 9-13) the nest was checked to record body mass of the nestlings and to estimate their age by looking at the development stage of their feathers on the wing and the tail. Four nestlings in each brood were then marked with a white spot on the head. The nestlings that were marked were the youngest (on the right side), the second youngest (on the left side), the second oldest (in the neck) and the oldest (in the front). On the day of filming, 10-14 days after hatching, we exchanged the original nest box by one constructed with a camera in one side to be able to film inside the nest. We then waited approximately one hour after this box change to be sure that the parents would accept the new box and start feeding. Each brood was then filmed for approximately 3 hours.

Each video was then analysed and 25 feeding visits of each parent described in detail starting from the end of the filming period to get the most undisturbed feeding. At each of the 50 feeding visits we registered: the time of visit, the sex of the adult, the size and type of the food items, the identity of the nestling that was given the food, feeding attempts of one or more nestlings before feeding, swallowing time if more than 5 sec and number of times the adult carried out a fecal sac. Prey items were measured in proportion to the length of the adult's beak. The remaining feeding visits were only registered with time and sex of the adult. The order in which the video analyses were performed was random to avoid systematic bias classification of prey size over time.

Statistical analyses

30 of the 32 nest boxes recorded were used for statistical analyses. All data were tested for normality before using parametric statistics. Proportions were arcsine square root transformed. The statistical analysis was carried out using S-Plus 6.1 statistical program. To test the factors affecting swallow time, prey size and which nestling was fed the Linear Mixed Effect model (LME) were used with "box" incorporated as a random variable. Fixed variables were swallow time, prey size, food providing to the youngest and the oldest nestling. The data from the LME-tests are presented as an ANOVA table. To compare swallow time between great tit and blue tit a paired t-test was performed. All statistic tests are two-tailed.

Picture 2: Left; installed video camera on the side of the temporary nest box. Right; the video construction seen from above with the nestlings placed inside.

Results

Body mass

The body mass of the nestlings in a brood was not correlated with date when all nests' were combined (r = 0.04 n = 30 p = 0.82; Fig. 1, Appendix 1). The blue tit nestlings in Group mixed and in Group blue tit had the lowest mean body mass as expected since the blue tit in general is smaller than the great tit. At this age (day 10-14) the body mass should be aproximately 10-12g for blue tit nestlings (O'Connor, 1984) and 14-16g for the great tit nestlings (Balen, 1973), which is consistent with our broods.

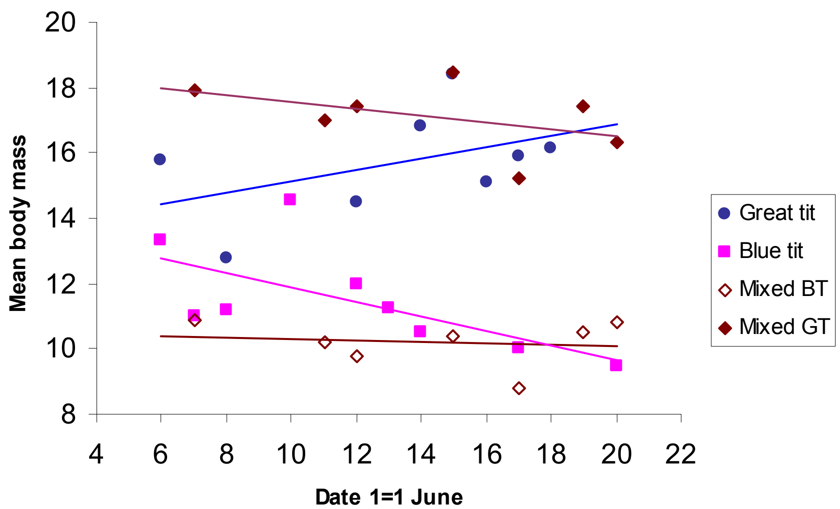

Figure 1. Nestlings mean body mass in each brood at the day of filming vs. date of filming. ● Great tit nestlings in Group great tit, ■ blue tit nestlings in Group blue tit, ◊ the blue tit nestlings in Group mixed and ♦ the great tit nestling in Group mixed. Regression lines are indicated.

Provisioning by great tits

The mean number of feeding visit per hour in each of the three treatment groups, great tit, blue tit and mixed did not differ significantly, ANOVA: (F =1.56, df = 2, P = 0.22) and there were no differences between the male and the female (F = 0.07, df = 1, P = 0.80; Table 1).

The mean number of feeding visits per nestling per hour in the three treatment groups differed significantly (F = 3.23, df = 2, P = 0.047; Table 1). The nestlings in the great tit broods had the largest number of feeds x ± SD: (3.38 ± 1.56) and the nestlings in the mixed broods had the lowest x ± SD: (2.50 ± 1.08). There was no significant differences between the feeding visits of the male and the female parent in any of the groups (F = 0.17, df = 1, P = 0.68; Table 1).

Larvae proportion

The proportion of larvae (of 25 visits) delivered to the nestlings in each group did not differ significantly, ANOVA ($F = 0.12$, $df = 2$, $P = 0.89$) and no difference was found between the male and female parent ($F = 0.08$, $df = 1$, $P = 0.77$; Table 1).

Proportion fecal sacs removed by adult after feeding

Proportion of times fecal sacs (of 25 visits) were removed by a parent after feeding did not differ significantly between groups but showed a weak tendency of a difference ($F = 2.32$, $df = 2$, $P = 0.11$; Table 1), the largest proportion removed by both parents was in mixed broods x ± SD (26.36 ± 9.34). There was no significant difference between the male and the female parents removing of fecal sacs in any group ($F = 1.69$, $df = 1$, $P = 0.45$; Table 1).

Table 1. Provisioning by great tit parents in three different treatment groups. Group great tit (great tit nestlings), Group blue tit (blue tit nestling), Group mixed (one great tit nestling and x blue tit nestlings). Mean ± SD.

Group	**Great tit** (n = 9)			**Blue tit** (n = 12)			**Mixed** (n = 9)		
Variable	Females	Males	total	Females	Males	total	Females	Males	total
Mean no. feeding visit pr. hour	20.13 ± 10.41	17.39 ± 6.12	18.76 ± 8.65	19.46 ± 7.32	20.37 ± 7.43	19.92 ± 7.39	15.56 ± 6.28	15.60 ± 7.08	15.58 ± 6.69
Mean no. feeding visit pr. hour pr. nestling	3.62 ± 1.87	3.13 ± 1.10	3.38 ± 1.56	2.51 ± 0.94	2.63 ± 0.96	2.57 ± 0.95	2.50 ± 1.01	2.51 ± 1.14	2.50 ± 1.08
% Larvae (of 25 visits)	70.67 ± 11.62	72.00 ± 11.78	71.33 ± 11.72	69.86 ± 20.69	67.67 ± 20.36	68.76 ± 20.55	64.75 ± 17.91	72.84 ± 11.20	68.80 ± 15.47
% fecal sacs removed by adult (of 25 visits)	16.89 ± 7.12	16.89 ± 7.95	16.89 ± 7.55	23.23 ± 6.25	25.00 ± 9.54	24.11 ± 8.11	25.34 ± 10.96	28.59 ± 7.00	26.97 ± 9.34
% where swallowing time is longer than 5sec. (of 25 visits)	3.11 ± 6.19	8.00 ± 12.22	5.56 ± 9.99	7.72 ± 6.63	5.00 ± 4.93	6.36 ± 6.00	5.67 ± 7.61	4.89 ± 4.12	5.28 ± 6.13
Mean prey size (of 25 visits)	1.44 ± 0.83	1.65 ± 0.90	1.55 ± 0.87	1.65 ± 0.88	1.65 ± 0.87	1.65 ± 0.88	1.48 ± 0.92	1.62 ± 0.93	1.57 ± 0.93
% feeding(of 25 visits) • youngest	20.00 ± 10.67	13.78 ± 6.56	16.89 ± 9.39	16.12 ± 7.49	13.67 ± 7.91	14.89 ± 7.80	20.31 ± 11.33	15.46 ± 10.61	17.88 ± 11.24
• oldest	20.00 ± 10.83	22.22 ± 4.26	21.11 ± 8.31	11.78 ± 6.30	14.67 ± 7.72	13.22 ± 7.19	22.26 ± 7.38	19.70 ± 10.07	20.98 ± 8.92

Swallow time

The factors affecting swallow time between nests were tested by Linear Mixed Effect Model (LME). Proportion of long swallow times (> 5 sec) showed no differences between groups or between the male and the female (Table 1 and Fig. 2). Only prey size had a significant effect on swallow time (Table 2 and Fig. 3). In addition, the interaction adult's sex and prey size, showed a tendency to significance (P = 0.07), but the adult's sex alone did not. No other variables or interactions were significant or had any tendency to be significant (Table 2).

Table 2. ANOVA showing factors affecting the proportion of feeding visits where the swallow time exceed 5 sec. The variables are the three treatment groups [great tit, blue tit and mixed (one great tit and x blue tit)], the sex of the adult, the prey size and the interactions between the variables.

Variable	df	F	P
Group	2	0.63	0.46
Sex	1	0.05	0.79
Prey size	1	11.28	0.002
Group:Sex	2	1.11	0.37
Group:Prey size	2	1.60	0.21
Prey size:Sex	1	3.52	0.07

Differences in the proportion of long swallow time between the Group great tit and Group blue tit showed no significance, unpaired t-test: (t = -0.32, df = 40, P = 0.75). In the Group mixed the differences in proportion of high swallow times between the great tit nestling and its blue tit nest mates were tested and no significant difference was found, paired t-test: (t = -0.22, df = 11, P = 0.83). The great tit nestling had swallow times over 5 sec in four of the nine mixed broods wereas its blue tit nest mates had swallow times over 5 sec in seven of the nine mixed broods (Fig. 3 and 4).

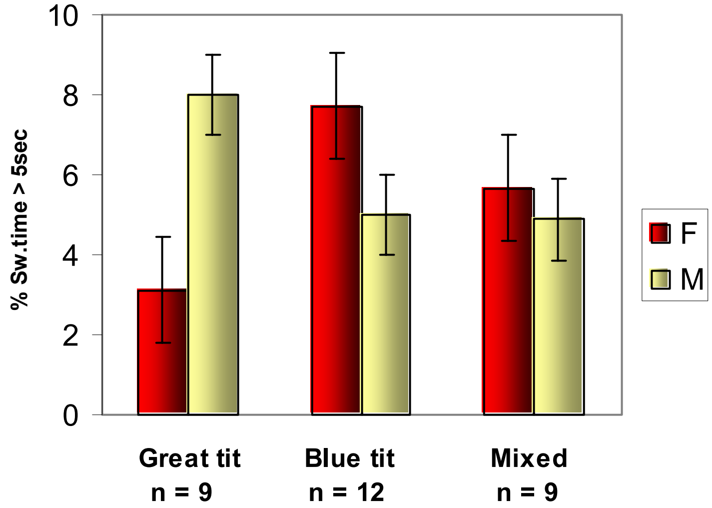

Figure 2. Observed distribution of swallow times over 5 sec. in the three treatment groups for the female (F) and the male (M). Sample size is indicated for each group. Mean + SE for each group and between the feeding adults

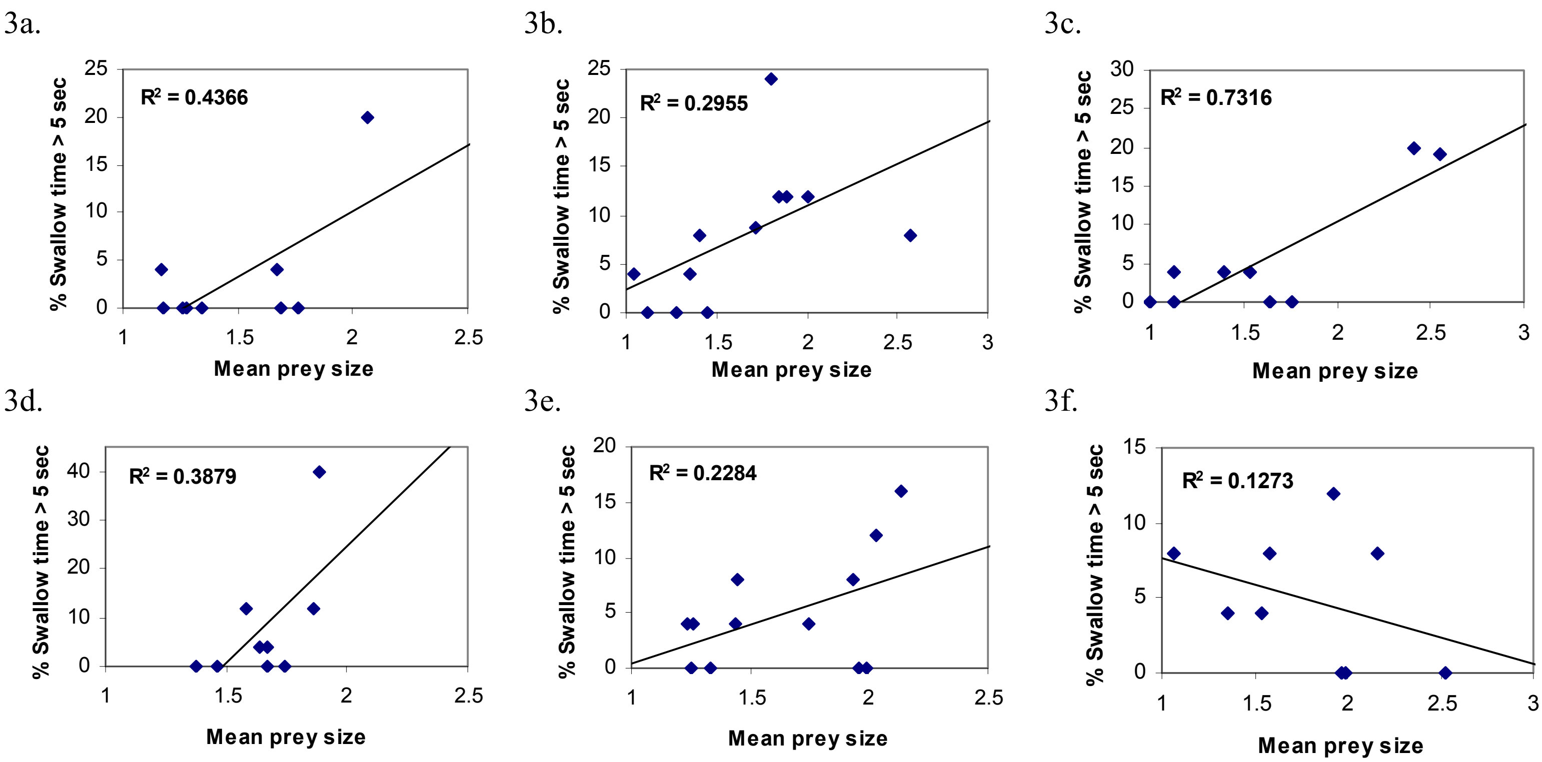

Figure 3. Proportion of swallow time over 5 sec. for each brood (y-axis) vs. mean prey size (y-axis) in each brood. Fig. 3a. - 3c. Show data for the female parent. Fig. 3d. - 3f. Show equivalent data for the male. Three treatment groups: 3a. & 3d. Great tit broods n = 9, 3b. & 3e. Blue tit broods n =12 and 3c. & 3f. Mixed broods (one great tit nestling and x blue tit nestlings) n = 9. Regression lines and the variance proportion (R^2) are indicated.

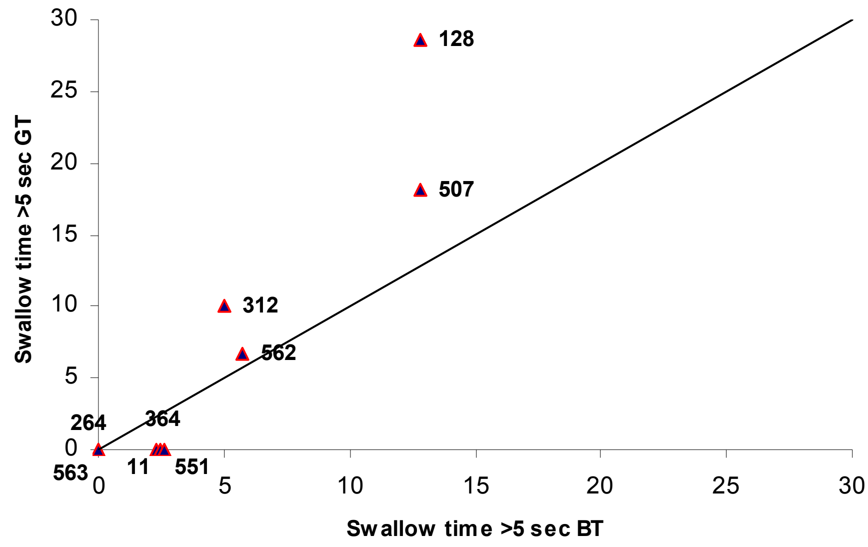

Figure 4. Proportion of swallow times over 5 sec for each brood (n = 9 broods) in Group mixed (one great tit and x-blue tit nestlings in each brood). The mean value for the blue tit nestlings plotted against the mean value for the great tit nestling for the same brood. Blue tit (x-axis) vs. great tit (y-axis). The line Y = X is added.

Prey size

The size of prey brought to the nestlings by the parents was not correlated with date of filming (r = 0.22, n = 30, p = 0.24; Fig. 5) and date is therefore not included in the tests as a variable. There were no signs of adaptation to differences in nestling size according to prey size, since there were no differences in prey size between groups (Table 1, Table 3). There were neither any signs of differences between the blue tit nestlings and the great tit nestling in Group mixed (Fig. 7). There were significant differences between the adults in prey size, the male was on average feeding with larger prey items x ± SD (1.7 ± 0.9) than the female x ± SD (1.6 ± 0.8) (Table 3 and Fig.6). In one (box 128) of the four boxes in mixed broods where the great tit nestling had swallow times over 5 sec it also was fed with relatively larger preys than it's blue tit nest mates (Fig. 4 and Fig. 7) whereas in the three other boxes (box; 507, 312 and 562), it was given prey of approximately same size as it's blue tit nest mates.

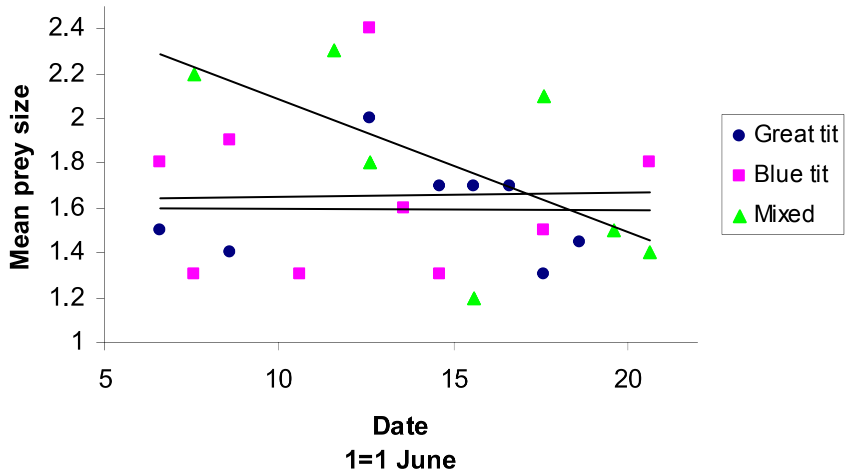

Figure 5. Mean prey size giving to nestlings in each brood vs. date of filming. ● Great tit brood (n = 9), ■ Blue tit brood (n = 12), ▲ Mixed brood (one great tit and x blue tits) (n = 9). Regression lines are indicated.

Table 3. ANOVA table showing factors affecting the prey size giving to nestlings. The variables are the three different treatment groups, Great tit (n = 9), Blue tit (n =12) and Mixed (n = 9), the sex of the adult and the interaction between the adults sex and group.

Variable	Df	F	P
Group	2	1.92	0.15
Sex	1	4.13	0.042
Group:Sex	2	2.15	0.12

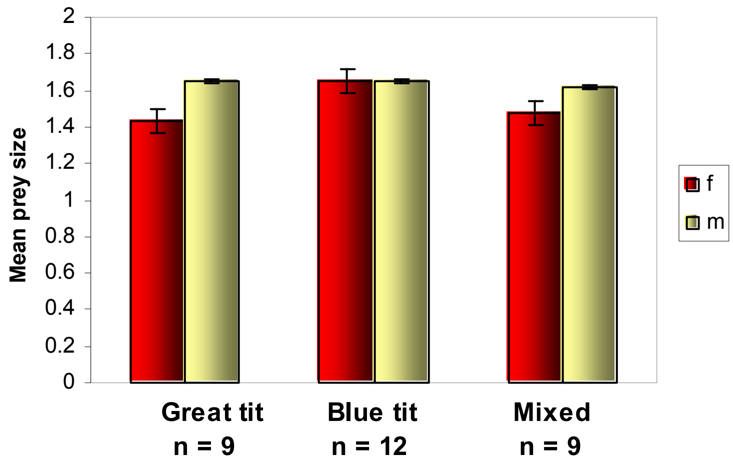

Figure 6. Mean prey size + SE for each of the three treatment groups. Sample size is indicated for each group.

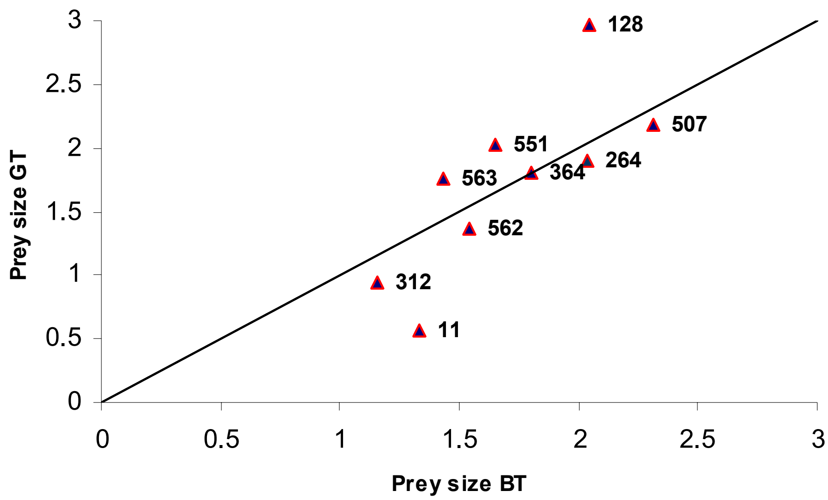

Figure 7. Mean prey size in each brood (n = 9 broods) in Group mixed (one great tit and x-blue tits nestling in each brood). The mean value for preys given to blue tit nestlings plotted against the mean value for the great tit nestling in the same nest. Blue tit (x-axis) vs. great tit (y-axis). The line Y = X is added.

Provisioning of the youngest and the oldest nestling

When testing factors affecting food providing to the youngest nestling by Linear Mixed Effect Model (LME), there was a tendency to significant difference between the male and female parent (P = 0.07). The female had a higher proportion of feeds to the youngest nestling than the male in all groups (Fig. 6, Table 1). The female was on average providing food to the youngest nestling 18.5% of her total feeds, the value for the male was 14.4%, all broods combined. Another factor that showed influence on the number of feeds to the youngest nestling was brood size, which by chance is expected to increase with decreased broodsize (Table 4).

Table 4. ANOVA analysis of factors affecting feeding of the youngest chick. ANOVA table. The variables are the three treatment groups, Great tit n = 9 broods, Blue tit n= 9 broods and Mixed n = 9 broods, the sex of the adult, brood size and the interaction between variables

Variable	df	F	P
Group	2	1.32	0.28
Sex	1	3.46	0.07
Brood size	1	10.98	0.002
Group:Sex	2	0.24	0.78
Group:Brood size	2	0.60	0.55
Sex:Brood size	1	0.22	0.64

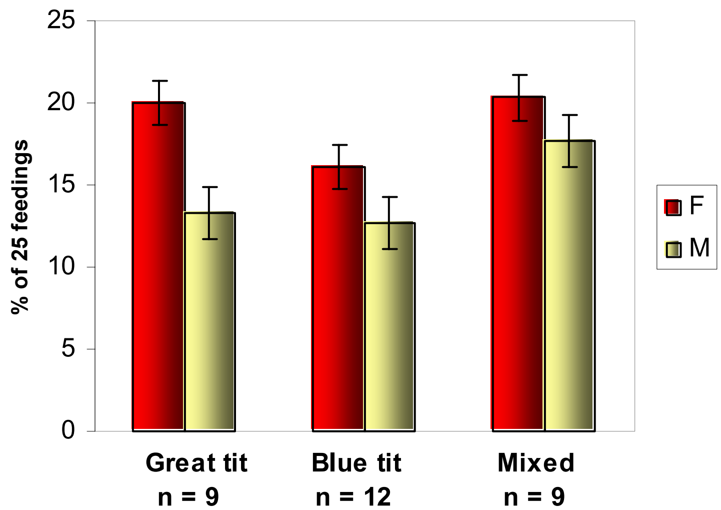

Figure 8. Proportions of 25 feeding attempts where the youngest nestling was provided food from each of the parents in the three treatment groups. Sample size is indicated for each group. Mean + SE for each group and between the feeding parents.

When testing the factors affecting food providing to the oldest nestling there was a significant effect of treatment (P = 0.006) and brood size (P = 0.013; Table 5). The number of feeds to the oldest nestling would by chance be expected to increase with decreased broodsize. The differences between groups showed that the oldest nestling was fed most often in Group great tit and in Group mixed and less often in Group blue tit (Fig.7, Table 1).

There was no significant difference between the male and the female parent in food providing to the oldest nestling neither in any group nor between the three treatment groups.

Table 5. ANOVA analysis of factors affecting feeding of the oldest chick. ANOVA table. The variables are the three treatment groups, Great tit n = 9 broods, Blue tit n= 9 broods and Mixed n = 9 broods, the sex of the adult, brood size and the interaction between variables..

Variable	df	F	P
Group	2	5.681	0.006
Sex	1	0.04	0.83
Brood size	1	6.608	0.013
Group:Sex	2	0.84	0.44
Group:Brood size	2	0.58	0.56

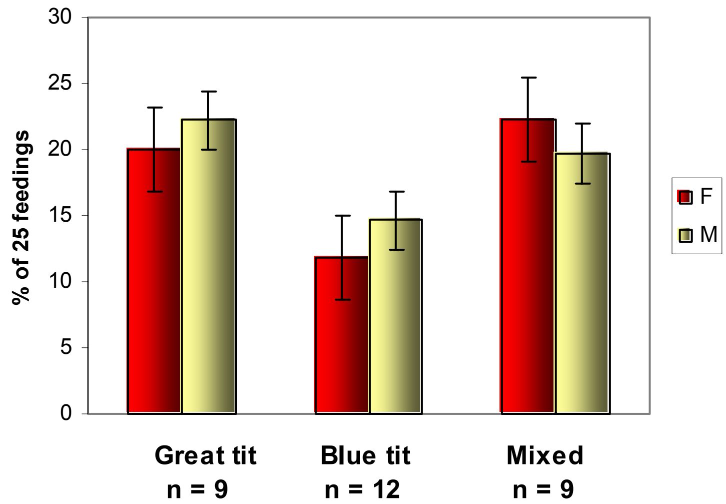

Figure 9. Proportions of 25 feeding attempts where the oldest nestling was provided food from each of the parents in the three treatment groups. Sample size is indicated for each group. Mean + SE for each group and between the feeding parents.

Discussion

Because the great tit is a single prey loader (Orians & Pearson, 1979), the prey selection when feeding nestlings is a trade off between searching for large prey with relatively high nutrient content and taking smaller and more common prey with lower nutrient value (Kluyver, 1950; Royama, 1966; Houston et al., 1980;). When feeding with small prey the parents must increase their feeding frequency to sustain the nestlings' nutrient requirements (Kluyver, 1950). The parents' prey choice is dependent on prey availability (type and size) and the nestlings' stage (age and size) (Cowie and Hinsley, 1988).
We tested the parents' ability to adjust prey choice to the nestlings' size by swopping the original great tit nestlings by smaller blue tit nestlings. If the smaller body size of the blue tit nestlings implies a more constrained capacity to swallow larger prey items then the prey size should have more critical consequences for blue tit than for great tit nestlings.

This study shows that the nestlings at day 10-14 had difficulties swallowing large prey because we found that the proportion of swallow times over 5 sec increased with prey size. However we did not find any statistical evidence that the blue tit nestlings had greater problems swallowing large prey items than the great tit nestlings since neither prey size nor the proportion of long swallow times did differ significantly between the two species. But in the mixed broods (one great tit nestling and x blue tit nestlings) there were fewer boxes (n = 4) where the great tit nestling had swallow times over 5 sec than what was the case for the blue tit nestlings (n = 7). Although in the boxes where the great tit nestling had swallow time above 5 sec the proportion was higher than for the blue tit nestlings. This may have been due to chance because of sample size or way of analysing. Since there was only one great tit nestling in each mixed brood it may indicate that the swallow constraint was related to few individuals rather than to all the great tit nestlings in this group. In one of the broods (box 128) the larger proportions of swallow time was probably a consequence of the great tit nestling being fed with larger preys than it's blue tit nest mates. The higher proportion of long swallow time in the three other broods among the mixed broods was not related to any differences in prey size and might have been caused by other factors or by chance. We used swallow times over 5 sec as a measurement for a relatively long swallow time which might not be an optimal measure to considerate the ecologic perspective in feeding time. Perhaps a difference between the two species had appeared if we had measurements of the duration of each feeding.

Development constraints in birds is known to cause differences in foraging of nestlings, juveniles and adults (Carey, 1996; Ricklefs, 1973; Marchetti and Price, 1989). Body size is related to gape size and digestive capacity which often can limit the prey size because birds usually swallow prey hole (Kaspari, 1990; Gille et al., 1999).
Surprisingly the differences in body size between the two chosen species (great tit and blue tit) in this study did not seem to reflect such differences in development constraint. It is therefore difficult to estimate whether the parents are capable of adjusting prey size to the size of the young. We can though not reject the parents' adaptive ability on the statistical basis in this study because our data amount is limited. And since all data have been collected in the same season and in a restricted area, it provides no information of possible seasonal and location variations. It is a possibility that the prey this year was smaller than average due to seasonal variations and the nestlings' swallowing problems, therefore not was as noticeable as usual, at least for the blue tit nestlings. It may also be possible that the parents already had adjusted prey size to the size of the nestlings at this age since the manipulation took place at hatching. But if that was the case then there should be a significant difference in prey size between the control group, Group great tit and the treatment group, Group blue tit, which there wasn't.

Previous studies show that the prey size constraints are most important in the early stage (first week) of the nestlings life (Balen, 1973) while others show that it may still be important until day 15 (Royama, 1966, 1970). This study has no data on swallow time from early nestling ages so we cannot describe any age-dependent tendency in swallow capacity. But since the proportion of long swallow time increases with increased prey size, it supports that prey size still is an important factor according to feeding efficiency on day 10-14. At this age stage there is a peak in the nestlings' nutrient requirements in order to grow and survive until fledging at day 18 (Bengtsson and Ryden, 1981; Cramp, 1993). The nestlings fledging weight is closely related to their future survival and own reproductive success (Perrins, 1965; Perrins and Mccleery, 1989; Smith et al., 1989; Tinbergen and Boerlijst, 1990; Verhulst and Tinbergen, 1991; Barba et al., 1995;), so the amount and quality of food is therefore of great importance. Since the nestlings still are totally dependent of being fed at this stage, their survival will depend on their parents' feeding skills. The nestlings' swallow time do influence food handling time because the parents wait for the nestlings to swallow the prey before leaving the nest in order to search for new food. This makes swallow time a more crucial factor of the feeding efficiency when feeding nestlings than in the bird's own foraging.

If the prey fed to the nestlings is too large to swallow whole, it must to be prepared by the parents (Kaspari, 1990; Barba et al., 1996; Banbura et al., 1999). Modifying prey instead of ingesting it as captured is an investment of time and energy. The increased food handling time in relation to prey size should count for an important component and affect the parents' food choice when feeding their nestlings. The nutrient value of prey is positively correlated to their size (Naef-Daenzer et al., 2000) and since the great tit usually is a single loader it is a matter of trade off between searching time for proper prey sizes and prey preparation time if prey is too large (Houston et al., 1980). But since the nestlings' nutrient requirement in this period is relatively high it might be that the parents do not have opportunity to be selective in their prey choice.

The reproduction success in tits is highly dependent of timing of the brood to food abundance and the size of the prey (O'Connor, 1984; Van Noordvwijk A.J., 1995; Monros et al., 2002;). As we found in this study the main prey choice in the nestling diet of great tits and blue tits is larvae because of its availability and suitability as nestlings' food (Balen, 1973; Perrins, 1979; Banbura et al., 1999). We did not find any tendency to mistiming in any brood since neither prey size nor the nestlings' body mass was correlated with date. It is however reasonable to believe that there is a close relation between prey size and abundance to nestling survival. Recent studies suggest that it is important that the available larvae have reached their maximum size in the late nestling period (Naef-Daenzer and Keller, 1999), but since we found that large prey causes difficulties for 10-14 days old nestlings, it may be of consideration that timing to maximum prey size not always creates the most effective feeding situation. If only large prey is available in the nestling period or small prey are rare, the parents' food handling time may increase because of the need for preparation but also due to increased searching time. An increase in handling cost may reduce the net energy value of a prey (Lifjeld and Slagsvold, 1988). We found no effect of date on the size of the prey items the parents brought to the nest, but this is not necessarily reflecting prey types and sizes available. Earlier studies show that the parents are highly selective in their prey choice (Naef-Daenzer et al., 2000) and the larvae delivered to the brood were well above the mean larvae size available.

Several hypotheses have been suggested to explain sex differences in care allocation in relation to offspring size (Slagsvold, 1997). We did find that females provisioned significantly smaller prey than males and also that females fed the youngest nestling more than the males did. This is consistent with data found in other studies of tits feeding behavior showing that the female often invests more in the youngest nestling than the male does (Stamps et al., 1985; Sasvari, 1990; Slagsvold et al., 1994). The youngest offspring might be a product of extra pair mating and will therefore be of no reproduction value to the male (Gottlander, 1987; Weatherhead and Yezerinac, 1998) but the differences could also be a result of various begging behavior between the nestlings which triggers off different feeding response from the parents (Gottlander, 1987; Krebs and Magrath, 2000; Clark, 2002; Lessells, 2002). Food-deprived nestlings may get a higher proportion of the female's feeds than of the males, but they may also beg at higher intensity towards the female than the male (Kölliker et al., 1998). Because males wait longer before feeding, the nestlings begging effort may be costlier and especially food-deprived nestlings should try to minimize the cost of obtaining food. One hypothese from previous studies suggest that in species where the female spends the most time in the nest she has more time and knowledge to seek out and feed the nestling which need most care which often is the smallest nestling (Stamps et al., 1985; Gottlander, 1987). Differences between the males' and females' feeding locations in the nest in relation to the nestlings' positions might also give a skew provisioning among nestlings (Kölliker, 2004).

We can conclude that the ability to adjust prey size is an important skill in tits' reproduction ecology because large prey increases the swallow time for the nestlings which in time increases the feeding time for the parent. Because of limitation of the data in this study, it was not possible to distinguish development constrains between the great tit and the blue tit nestlings in order to evaluate the parents' adjustment skills.

Further studies on adaptable behavior in feeding ecology of great tit and blue tit should include measurements of the development constraints in relation to the swallow capacity at different age stages in each of the species. Also larger and broader data samples and accurate measurements of prey size and swallow time should provide further information of possible adaptive feeding ability and distinguish potential differences between males and females. Furthermore data from several seasons and locations should be included to detect and analyze variations in prey size in relation to swallow time.

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Appendix 1

	Variable / Box No.	Date 1.egg	No. Nestlings at hatching		Hatching Date	Filming date	Age at filming	No. Nestlings at filming		No. feeding visits		Mean weight at filming	
			BT	GT				BT	GT	Male	Female	BT	GT
Group great tit	71	17.05.03	0	6	06.06.03	18.06.03	12	0	6	41	54	-	18.0
	77	12.05.03	0	4	03.06.03	15.06.03	12	0	4	31	58	-	18.4
	120	16.05.03	0	7	07.06.03	18.06.03	11	0	7	56	88	-	14.3
	168	16.05.03	0	7	05.06.03	16.06.03	11	0	7	69	124	-	15.1
	287	11.05.03	0	6	03.06.03	14.06.03	11	0	6	58	49	-	16.8
	456	04.05.03	0	6	23.05.03	06.06.03	14	0	5	41	47	-	15.8
	486	05.05.03	0	5	27.05.03	08.06.03	12	0	5	60	57	-	12.8
	519	16.05.03	0	7	06.06.03	17.06.03	11	0	7	103	64	-	15.9
	606	15.05.03	0	3	01.06.03	12.06.03	11	0	3	37	5	-	14.5
Group blue tit	H1	15.05.03	6	0	06.06.03	17.06.03	11	6	0	25	27	10.0	-
	3	10.05.03	7	0	01.06.03	12.06.03	11	7	0	50	26	12.0	-
	30	12.05.03	9	0	02.06.03	13.06.03	11	9	0	36	23	10.7	-
	222	13.05.03	7	0	01.06.03	13.06.03	12	7	0	43	65	11.8	-
	281	07.05.03	8	0	31.05.03	14.06.03	14	8	0	57	59	10.5	-
	305	10.05.03	9	0	30.05.03	10.06.03	11	9	0	86	83	9.6	-
	343	24.05.03	7	0	23.05.03	06.06.03	14	7	0	76	52	13.8	-
	418	27.05.03	10	0	25.05.03	06.06.03	12	10	0	77	76	12.8	-
	453	03.05.03	8	0	30.05.03	10.06.03	11	8	0	54	85	19.5	-
	476	05.05.03	7	0	25.05.03	07.06.03	13	7	0	61	74	11.0	-
	479	14.05.03	7	0	29.05.03	08.06.03	10	7	0	107	46	11.2	-
	552	16.05.03	8	0	09.06.03	20.06.03	11	8	0	46	22	9.5	-
Group mixed	11	13.05.03	9	1	03.06.03	15.06.03	12	9	1	81	58	10.4	18.5
	128	03.05.03	5	1	26.05.03	07.06.03	12	5	1	49	21	10.9	17.9
	264	13.05.03	4	1	06.06.03	17.06.03	11	4	1	9	14	8.8	15.2
	312	31.05.03	4	1	10.06.03	20.06.03	10	4	1	54	43	7.6	13.5
	364	09.05.03	7	1	31.05.03	12.06.03	12	7	1	51	63	9.8	17.4
	507	14.05.03	6	1	31.05.03	11.06.03	11	6	1	68	37	10.2	17.0
	551	10.05.03	3	1	08.06.03	20.06.03	12	3	1	29	53	14.0	19.1
	562	04.06.03	4	1	07.06.03	19.06.03	12	4	1	38	40	11.3	18.5
	563	21.05.03	5	1	08.06.03	19.06.03	11	5	1	39	72	9.7	16.3