Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites

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Ectoparasites are a ubiquitous environmental component of breeding birds, and it has repeatedly been shown that hematophagous ectoparasites such as fleas and mites reduce the quality and number of offspring of bird hosts, thereby lowering the value of a current brood. Selection acting on the hosts will favor physiological and behavioral responses that will reduce the parasites' impact. However, the results of the few bird studies that addressed the question of whether parasitism leads to a higher rate of food provisioning are equivocal, and the begging response to infestation has rarely been quantified. A change in begging activity and parental rate of food provisioning could be predicted in either direction: parents could reduce their investment in the brood in order to invest more in future broods, or they could increase their investment in order to compensate for the parasites' effect on the current brood. Since the nestlings are weakened by the ectoparasites they may beg less, but on the other hand they may beg more in order to obtain more food. In this study we show experimentally that (1) hen fleas (*Ceratophyllus gallinae*) reduce the body mass and size of great tit (*Parus major*) nestlings, (2) nestlings of parasitized broods more than double their begging rate, (3) the male parents increase the frequency of feeding trips by over 50%, (4) the females do not adjust feeding rate to the lowered nutritional state of nestlings, and (5) food competition among siblings of parasitized broods is increased. Ultimately the difference in the parental feeding response may be understood as the result of a sex-related difference in the trade-off of investing in current versus future broods. *Key words:* brood value, ectoparasites, food provisioning, great tit, investment trade-off, nestling begging, nestling competition, signaling. *[Behav Ecol 7:127–131 (1996)]*

Parasites can impose fitness costs by reducing the survival, fecundity, or mating success of their hosts or of their hosts' offspring (e.g., Milinski and Bakker, 1990; Møller, 1990, 1993; Møller et al., 1990; Richner et al., 1993; Schall and Dearing, 1987), and selection acting on the hosts will be expected to favor physiological and behavioral responses that will reduce the parasites' impact (e.g., Hart, 1992; Keymer and Read, 1991). For great tits (*Parus major*) it has been experimentally demonstrated that fleas reduce both offspring body mass and number (Richner et al., 1993), and it has been shown that fledging body mass correlates with the probability of survival of the offspring (Perrins, 1965; Smith et al., 1989; Tinbergen and Boerlijst, 1990). Ectoparasites may therefore lower the value of the current brood. A reduction in offspring quality and number could be the direct physiological consequence of the blood-sucking ectoparasites, or the consequence of a lowered begging and parental food provisioning response due to parasitism. The following, proximate behavioral responses to parasitism could be expected for nestlings and for their parents:

1. Parasitized nestlings may beg less because they are weakened by the blood-sucking parasite, and parents might then reduce the rate of food provisioning to the brood.
2. Since parasitized nestlings are of lower body condition they may be expected to beg more in order to obtain more food. If begging indicates honestly the nestlings' condition to the parents (Godfray, 1991; Hussel, 1988), parents should increase the rate of food provisioning.

Ultimately, however, the optimal response of the parents to parasitism is shaped by life-history trade-offs. In birds, parents are in control of food provisioning to the nestlings and, for iteroparous organisms such as the great tit, we expect them to maximize lifetime reproduction by optimally partitioning investment between current and future reproduction. If parasites lower the value of the current brood, as demonstrated for this host-parasite system (Richner et al., 1993), there may be the following parental responses:

1. If there is no trade-off between investment in current versus future reproduction, or if parasites lower the parents' likelihood of future reproduction independently of the level of investment in the current brood, we expect parents to increase their investment in the current brood in order to compensate for the parasites' effect on the offspring.
2. If there is a trade-off between investment in current versus future reproduction, that is, if an additional investment into the current parasitized brood lowers the parents' likelihood of future reproduction, we expect parents to modify their investment levels according to the ratio of the fitness benefits arising from an investment in current versus future reproduction.

In this study we investigate the begging response of nestlings and the investment response of adult great tits that were experimentally infested with a common ectoparasite, the hen flea (*Ceratophyllus gallinae*). We assess (1) the direction and magnitude of the modification of the begging response due to parasitism, (2) the rate of food provisioning to the nest by the male and female parent, and (3) whether ectoparasites increase food competition among nestlings.

METHODS

Great tits were studied around the campus of the University of Lausanne, Switzerland. Nest-boxes were placed in 1989. In our population the birds produce one brood per season. In

Table 1

Mean body mass (±1 SE), tarsus length (±1 SE), and nutritional condition (±1 SE) of nestlings in ectoparasite-free and infested broods of great tits

	Nestling mass (g) 14 days after hatching	Nestling mass (g) 17 days after hatching	Tarsus length (mm) 14 days after hatching	Nestling condition 14 days after hatching	Brood size
Parasite-free nests	15.9 ± 0.20 (17)	16.3 ± 0.41 (15)	22.4 ± 0.20 (17)	0.71 ± 0.01 (17)	5.82 ± 0.39 (17)
Infested nests	14.5 ± 0.32 (14)	14.6 ± 0.36 (13)	21.8 ± 0.16 (14)	0.67 ± 0.01 (14)	5.86 ± 0.51 (14)
_t_ test					
_t_ =	2.59	3.19	2.14	2.53	0.05
_p_ =	.007	.004	.041	.017	.96

Brood size (±1 SE) with and without ectoparasites 14 days after hatching. Sample sizes (in parentheses) are number of broods.

1991 and 1992 we manipulated flea load of nests during the laying period by infesting half of the nest-boxes three times with 20 fleas at each infestation. The other nests were heat-treated with a microwave appliance at intervals of from 4 to 8 days (for details see Richner et al., 1993). Thirteen days after hatching we monitored the rate of begging of nestlings and the rate of food provisioning of the male and the female parent by use of a video camera equipped with an infrared light source. For individual recognition, the nestlings were marked with minute spots of paint on their heads. Fourteen days after hatching we measured nestling body mass and size, and caught the parents by use of a trapdoor at the nest. Parents were measured and released within 15 minutes of being caught. Two nest-boxes were excluded from the analysis: one of them was located beside a beehive and parents fed the young exclusively with honey bees; at the other box a wood-pecker had enlarged the entrance hole and the parents spent most of their time defending the box. A further nest-box was used only for begging rates, brood size, and for the morpho-metric variables of nestlings and adults because we could not distinguish the male and female from the videotape. The sample size for the rate of nestling begging, brood size, and nest-ling morphometry then consists of 14 infested and 17 parasite-free broods, and for male and female rates of feeding visits of 13 infested and 17 parasite-free broods. One male and three females could not be trapped at the nest, and one female escaped before weighing. The sample size for adult morphom-etry is therefore 27 females for body mass, 28 females for tarsus length, and 30 males for both measures.

Brood size, time of day, and hatching date may affect food provisioning rates (e.g., Gibb, 1955; Royama, 1966; Smith et al., 1988). In our study, mean brood size 14 days after hatch-ing did not differ significantly between the parasite-free and infested nests (Table 1). Time of day was not correlated with rates of food provisioning ($r = -.11$, $p = .55$, $n = 31$), and the data did not show nonlinear trends. Mean hatching date of parasite-free nests was 21 May (±15 SD), and of infested nests 20 May (±13 SD) (_t_ test: $t = .28$, $p = .78$, $n = 31$).

"Begging" is a term that is frequently used to describe hun-ger signaling of chicks (Bengtsson and Rydén, 1983; Hussel, 1988; Rydén and Bengtsson, 1980; Stamps et al., 1985), which may be produced in the presence or absence of the parents from the nest. Although the begging vocalization is stronger during the presence of the parents, the chicks also beg loudly during the absence of the parents, and the begging noise is easily perceived by passing humans (or predators). Begging behavior was analyzed from videotapes where it can be rec-ognized by the characteristic gaping behavior of the nestlings. To quantify the begging rate of a chick we sampled ten 1 min clips from the video, one clip every 10 min, and measured the total length of time that each chick begged during each clip. If a parent entered the box during this time, we analyzed

the following minute. The mean begging rate per hour for each chick was then calculated from these measures. By sum-ming up the means of all chicks we obtained the total begging time per hour for each brood. Distribution of food items among the nestlings was also measured from the videotapes. We calculated the feeding rate of each nestling, and from this the variance in the feeding rate among the nestlings of each brood. For a statistical comparison of food distribution in par-asite-free versus infested nests, we compared the intrabrood variances of the two groups by means of a nonparametric test for two independent samples.

Statistical analysis was performed using the Systat Statistical Package (Wilkinson, 1989). Significance values are two-tailed.

RESULTS

Effects of ectoparasites on body mass and size of nestlings and adults

As shown in a previous study (Richner et al., 1993), the hen fleas affect the body mass and tarsus length of nestlings. In the present study, the nestlings in infested nests were, on av-erage, 1.5 g lighter than nestlings from parasite-free nests 14 days after hatching, and this difference increased further to-ward fledging (Table 1). Final tarsus length of nestlings, which is reached approximately 12 days after hatching, was also re-duced in parasitized nests (Table 1). The nutritional condi-tion of nestlings, expressed as the ratio of body mass to tarsus length, was significantly lower in infested nests.

There was no significant difference in body mass or tarsus length between adults of parasite-free and those of infested broods 14 days after hatching of their offspring (Table 2).

Begging rate

The total begging time per hour, expressed as the sum of all nestlings' begging time per hour, increased significantly (_t_ test: $t = 2.45$, $p = .021$) if broods were infested with hen fleas (Figure 1). Nestlings of infested broods begged on average 140% more than nestlings of parasite-free broods.

Rate of food provisioning to the nest

Male parents of infested broods increase the rate of food pro-visioning to the nest significantly (_t_ test: $t = 2.59$, $p = .015$). Males of infested broods return 24.4 times per hour with food, while the ones in parasite-free broods return 15.5 times, an increase of 57% (Figure 2). Ectoparasites do not significantly (_t_ test: $t = 0.47$, $p = .64$) affect the females' rate of food provisioning to the nest. The power of the latter test (Cohen, 1988) is below 10%, however, and the null hypothesis may not therefore be safely accepted.

Table 2

Body mass (±1 SE) and tarsus length (±1 SE) of male and female parents in ectoparasite-free and infested nests of great tits

	Female body mass (g)	Female tarsus length (mm)	Male body mass (g)	Male tarsus length (mm)
Parasite-free nests	16.9 ± 0.24 (14)	22.0 ± 0.20 (15)	17.9 ± 0.21 (16)	22.6 ± 0.17 (16)
Infested nests	16.7 ± 0.26 (13)	21.8 ± 0.17 (13)	17.7 ± 0.28 (14)	22.7 ± 0.21 (14)
t test				
t =	0.66	1.11	0.71	0.37
p =	.52	.28	.49	.71

Adults were caught 14 days after hatching of their offspring. Sample sizes (in parentheses) are number of males or females.

Food competition among nestlings

If ectoparasites increase the competition for food among nestlings within a brood, we predict an increase of the within-brood variance of the nestlings' feeding rate in parasitized nests. This variance is significantly larger in infested nests (Figure 3) than in parasite-free nests (Mann-Whitney U test, $U = 56$, $p = .023$). It shows that within broods, the nestlings in parasite-free broods are fed more equally than in infested broods where some of the nestlings are fed much more frequently than others. Sibling competition for the food brought by the parents is therefore higher in infested nests.

DISCUSSION

The study shows that nestlings of broods infested with hematophagous hen fleas are lighter and beg more than nestlings of parasite-free broods. Their lower body mass and size is not due to a parasite-mediated reduction of begging behavior. Begging behavior indicates to the parents the nutritional condition or "hunger level" of their chicks (e.g., Hussel, 1988) and is expected to be costly in order to be reliable (e.g., God-

fray, 1991; Redondo and Castro, 1992). Costs arise through the individual energetic costs or through the attraction of predators (Harper, 1986). The results of the few studies that addressed the question of whether parasitism also leads to a higher rate of food provisioning are equivocal. Rogers et al. (1991) have shown that parental rate of food provisioning of tree swallows (*Tachycineta bicolor*) is not affected by hematophagous blowflies (*Protocalliphora sialia*). Møller et al. (1994) showed that house martins (*Delichon urbica*) that were experimentally infested with the house martin bug (*Oeciacus hirundinis*) decreased the rate of food provisioning to the nest. Tropical fowl mites (*Ornythonyssus bursa*) infesting barn swallow nests (*Hirundo rustica*) have no effect on the rate of food provisioning to first broods of parents that raise two broods per season, but lower the rate of food provisioning of single-brooded parents (Møller, 1994). Our study shows that males of infested nests significantly increase the rate of food provisioning by more than 50%. Why should there be such interspecific differences in the response to parasitism?

A life-history view predicts that iteroparous organisms should make the level of investment in current offspring dependent on the consequences of this investment for success-
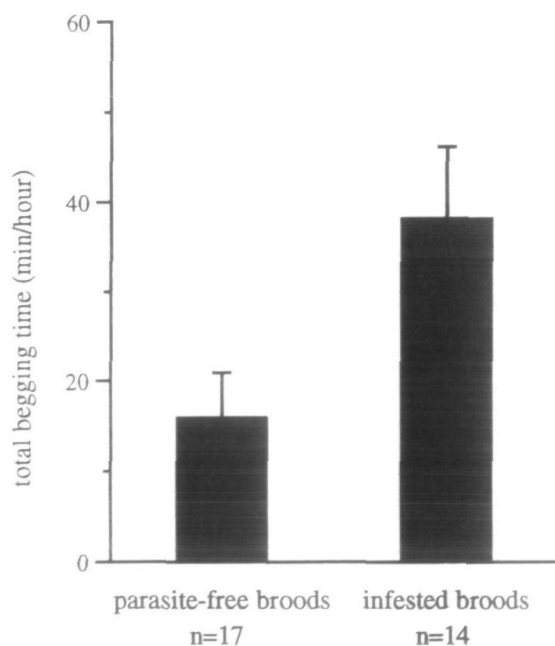

Figure 1
Summed begging time per brood and per hour (±1 SE) of nestlings in parasite-free and infested broods of great tits.
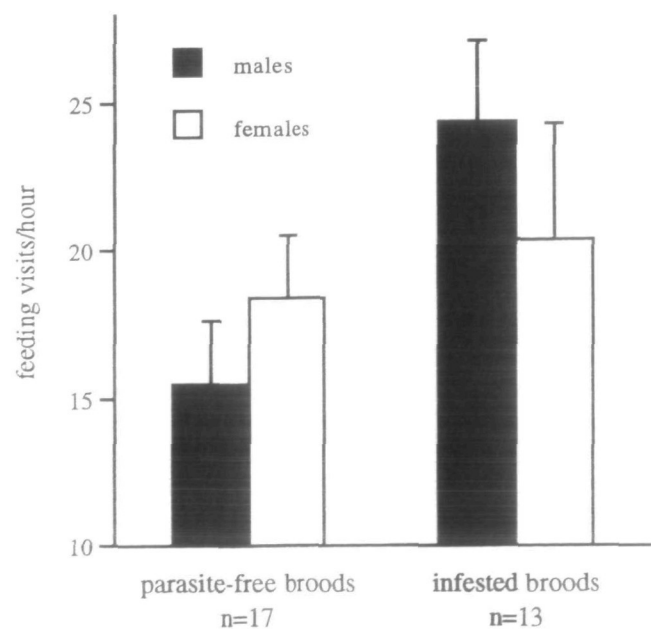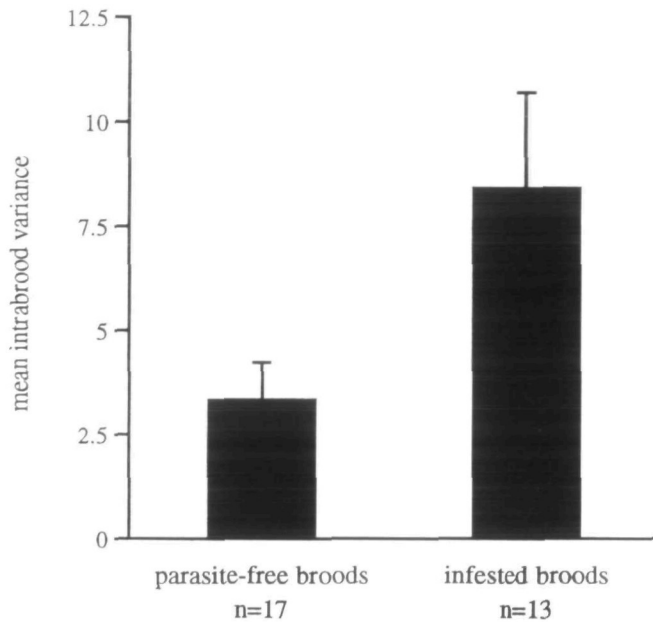

Figure 2
Mean number of feeding visits per hour (±1 SE) made by males and females of parasite-free and infested broods of great tits.

Figure 3
Mean intrabrood variance of feeding rates of nestlings (±1 SE) in parasite-free and infested broods of great tits.

fully raising offspring in the future. If parasites do not affect the value of the current brood, we do not expect a difference in the parental investment pattern between parasitized and unparasitized broods. This may be the case in the study by Rogers et al. (1991), where no effect of hematophagous blowflies on nestling tree swallows was found. In the three other studies (Møller, 1994; Møller et al., 1994; this study) parasites affected the nestlings, but parental investment varied. In house martins (Møller et al., 1994), parents of parasitized broods reduced their investment, and this could be due to a high cost of investment in the current brood for the survival or future fecundity of the parents. In the barn swallow (Møller, 1994), only the single-brooded parents reduce the investment, but not the double-brooded parents. As Møller suggests, parents may vary in phenotypic quality, and therefore the parents that are able to rear two broods may be better able to resist the effects of mites on the provisioning rate than the single-brooded parents. Thus, for the double-brooded parents an additional investment in an infested brood may have a much smaller effect on future reproduction than an additional investment would have for the single-brooded parents.

In our study the males, but not the females, of infested nests increased the rate of food provisioning. This finding agrees with that of a previous study where the energy demand of broods was increased experimentally by increasing brood size by two chicks, and where it was found that the males, but not the females, increase the rate of food provisioning by 50% (Richner et al., 1995). Why should only the males respond? For both studies, the life-history interpretation of a sex-related difference in the feeding effort is that, for females, the trade-off between investment in the current versus future broods is in favor of future broods, whereas for the male the trade-off is in favor of investing in the current brood. In great tits and blue tits the females readily divorce males after low breeding success or breeding failure (Dhondt and Adriansen, 1994; Lindén, 1991), and this may indicate that a female puts a relatively high premium on future broods. Males could then reduce the probability of a divorce by a heavier investment in the current brood. This also supports the interpretation of a

sex-related difference in the trade-off. For great tits, the cost of an investment in the current brood for future survival and reproduction of the parents has been assessed in several studies by brood manipulation experiments (for reviews see Lindén and Møller, 1988; Stearns, 1992). The results are equivocal and data are still insufficient to confirm a sex-related difference in this trade-off.

As shown here, the food brought by the parents of infested nests is less equally distributed among nestlings than the food brought to parasite-free nests. It is well established that ectoparasites can increase nestling mortality (e.g., Brown and Brown, 1986; Møller, 1990; Moss and Camin, 1970; Richner et al. 1993), and the finding of unequal food distribution among nestlings of infested broods shows that this mortality is not only a consequence of the energetic costs of parasites to individual nestlings, but may also be the consequence of both an increase in competition for food among siblings and a parasite-mediated change in food allocation among the nestlings that could lead to selective starvation. A change in the parental pattern of food allocation within broods may be adaptive under conditions of parasitism.

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