

Host responses to ectoparasites: food compensation by parent blue tits

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Parental food compensation has been proposed to account for the absence or small negative effects of parasites on offspring in various bird-parasite systems. An increase in the quantity of energy and nutrients provided by the adults would therefore compensate for the offspring's loss of blood to blood-sucking ectoparasites. We studied parental food compensation in a blue tit *Parus caeruleus* population with experimentally controlled infestations by the bird flea *Ceratophyllus gallinae*. Parental feeding effort, offspring quality, and parasite reproduction were measured in randomly assigned parasite-free and infested broods. Although the ectoparasites reproduced at a high rate in infested nests, the nestlings did not suffer higher mortality or reduced body size and body condition than nestlings in parasite-free nests. Fleas had a small negative effect on feather development of nestlings. Parent blue tits of infested nests increased rate of food provisioning by 29%. The results support the parental food compensation hypothesis. No short-term costs (i.e. lowered body condition) of parasites on the parents could be detected. Although the long-term costs of parasites on parents were not measured in this study, the results lend support to previous suggestions that the absence of an effect of ectoparasites on the offspring may be due to the fact that parents bear the cost of parasitism.

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Parasites are defined as organisms deriving their resources from the bodies of other species on which they spend part or all of their lives (Price 1980). Damage caused to the host can include loss of blood, tissue or nutrients. Host responses include energetically costly immune defence, or energy and time-consuming behavioural responses which serve to reduce the parasites' impact. Parasites affect host fitness through increased mortality, reduced growth or decreased reproductive success. Parasite susceptibility or resistance of hosts is influenced by their health (Marshall 1981, Noble et al. 1989, Lehane 1991) and nutritional status (Wakelin 1978, Solomons and Keusch 1981, Crompton 1991). This suggests that a host's ability to limit parasite costs, whether direct costs or costs arising from costly responses, could depend on environmental factors affect-

ing its energy balance such as resource availability (De Lope et al. 1993, Dufva 1995).

Bird nests harbour a variety of haematophagous ectoparasites whose costs can be measured directly in terms of bird reproductive success (review in Møller 1996). Nestlings of passerine birds rely entirely on their parents to increase their food intake in order to compensate for the loss of blood to ectoparasites. An increase in parental feeding effort could therefore account for the absence or the small effect of parasites on number of nestlings as observed in other studies (e.g. review in Møller et al. 1990, Johnson and Albrecht 1993, Møller 1994).

We investigated the hypothesis of parental food compensation in a blue tit population inhabiting an oak forest in Northern Switzerland. Previous work on this

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population found high natural infestation rates by *Ceratophyllus gallinae* (Schrank) (H. Zandt pers. comm.), a flea reaching a prevalence of 40 to 100% in nests of blue tits and great tits (*Parus major*) (Nordberg 1936, Ash 1952, Kime 1962, Jurik 1974, Harper et al. 1992). Adult fleas bite and consume blood from the adults and nestlings throughout the nesting period, while the larvae feed on detritus and adult flea faeces (Rothschild and Clay 1952). In a preliminary study in the same habitat, blue tit and great tit broods experimentally infested with *C. gallinae* all fledged young in good condition (Tripet pers. obs.). This apparent lack of costs contrasts with the mortality sometimes observed in blue tit nests in the presence of fleas (Winkel 1975); and the severe effects on survival and growth found in great tits in Southern Switzerland (Richner et al. 1993). A likely explanation for this absence of flea effects on offspring quality was that parents compensated for parasite effects by increasing their feeding effort. We therefore compared offspring quality and parental feeding effort in experimentally infested versus non-infested blue tit nests. The parental food compensation hypothesis predicts higher feeding rates in infested broods, and little or no detectable effects of parasites on nestlings.

Methods

The study was conducted in the spring 1995 in the Allschwilerwald, a 60-ha forest 8 km south-west of Basel, Switzerland (47°32'N, 7°32'E). This 120-yr old forest is part of a nature reserve with little tree-management only by the forest authorities. The vegetation is dominated by oak, mixed with hornbeam and beech. Food availability is high. Nest boxes have been provided for hole nesting birds for many years in this area and are commonly used by blue and great tits as well as a few pied flycatchers *Ficedula hypoleuca* and nuthatches *Sitta europaea*.

At the beginning of the blue tits' breeding period we visited the nest boxes regularly and recorded the onset of laying, number of eggs laid, start of incubation, and the first day of hatching referred to as day 0 of the nestling period. At hatching time we temporarily swapped the birds' nest for a dummy nest made out of moss, cotton wool, and feathers. The birds readily accepted the dummy nests in all 43 cases. This stratagem enabled us to clean their nest from wild fleas susceptible to interfere with our experiment. The bottom part of the nests and the nest cup material were dismantled separately and the larvae and adult fleas from both layers were collected with tweezers. The nests were then rebuilt and sterilised using a microwave oven in order to kill any remaining parasites. When this was done (after 4 h on average), we exchanged the dummy nest against the original one. Two d later, we infested half the nests with 90 adult fleas. Five pairs deserted

during the nestling period; two were of the parasite-free group and three of the infested one. For the analysis we also excluded three pairs with known polygamous males. The resulting sample size is 19 parasite-free nests and 16 infested nests. The mean hatching date was May 4.9 (± 1.8 SD) for parasite-free nests and May 5.3 (± 1.9 SD) for infested nests. Brood size at hatching was 10.8 (± 1.4 SD) for parasite-free and 10.2 (± 2.5 SD) for infested nests.

On day 7 after hatching we captured both parents by means of a spring-loaded trap shutting the entrance hole as the bird enters the nest. We sexed the birds according to the presence or absence of a brood patch, weighed them to the nearest 0.1 g using a Sartorius portable 1200 electronic balance, and measured their tarsus and length of the 4th primary feather to the nearest 0.1 mm using a calliper. The same measurements were taken on the nestlings on day 14 after hatching. There was no statistical difference between the two experimental groups in length of male and female tarsus. Mean tarsus length was 19.3 mm (± 0.1 SE) for females of parasite-free and 19.1 mm (± 0.1 SE) for females of infested nests (*t*-test: *t* = 0.950, *n* = 35, *p* = 0.349). Mean tarsus length of males was 19.7 mm (± 0.1 SE) in the parasite-free group and 19.8 mm (± 0.1 SE) in the infested group (*t*-test: *t* = 0.652, *n* = 35, *p* = 0.519). For the comparison of body condition of adults and nestlings of the two treatment groups we calculated the residuals of the regression of body mass on tarsus length.

On the morning of day 13 we observed the nest boxes from a distance and recorded all parental visits to the nest during 30 min of undisturbed feeding behaviour. We took special care not to be detected by the parents. When the birds were disrupted by pedestrians or predators (e.g. crows, woodpeckers, sparrowhawks), we stopped the observations and re-initiated them once the pair re-started feeding the young. We recorded feeding frequencies for 30 out of the 35 bird pairs. The two experimental groups did not differ in time of day of observations (*t*-test: *t* = 0.833, *n* = 30, *p* = 0.412).

On day 14 we collected the nest material from all nests and immediately sterilised it with a microwave appliance for later parasite counts. We provided all birds with a dummy parasite-free nest for the remaining days before fledging. The nests collected on day 14 of the nestling period were stored in open plastic bags in an aerated room to avoid moulds. Two month later we entirely dismantled the nests and inspected all the material for flea larvae. Parasite reproduction was measured as the number of larvae produced during the 12 d of experimental infestation in both parasite-free and infested nests.

Statistical analysis were performed using the Systat statistical package (Wilkinson 1992). Significance levels are two-tailed. Power analysis calculations were made following Cohen (1988).

Table 1. Number of flea larvae recovered from 'parasite-free nests' and infested nests.

	Parasite-free nests	Infested nests
Mean per nest	2.4	756.8
SD	8.0	454.1
Median	0	671
Range	0-35	205-1967
Number of nests	19	16

Results

Parasite reproduction

Adult fleas used nestlings as a food source between day 2 and day 14 of the nestling period as evidenced by the production of numerous larvae (Table 1). A few larvae were also found in parasite-free sterilised nests (Table 1). These result either from the reproduction of immigrant wild fleas or they are larvae that escaped collection prior to sterilisation of the nests at hatching time (see Methods).

Effect of parasites on nestling survival and quality

The survival of the nestlings from hatching to day 14 was 100% for infested nests and 99.5% for parasite-free nests. There was therefore no nestling mortality attributable to fleas. Brood size 14 d after hatching did not significantly differ between infested and parasite-free nests (Table 2). Feather length was negatively affected by ectoparasites (Table 2). The fleas had no significant effect on body mass, tarsus length, and body condition of the nestlings at day 14 (Table 2). The power of these last comparisons ranges from 13 to 20% and the effects are all in the expected direction; therefore we cannot reject the possibility that fleas had minor effects on those variables.

Effect of parasites on feeding frequencies

Blue tit pairs of infested nests provisioned their young at a higher rate with food (61 feeding trips $h^{-1} \pm 4$ SE) than pairs of parasite-free nests (47 trips $h^{-1} \pm 3.4$ SE) (t -test: $t = 2.688$, $n = 30$, $p = 0.01$). The summed increase in feeding effort of both parents is 29% (Fig. 1).

Table 2. Mean body mass, tarsus length, body condition (residuals), feather length and brood size of nestlings in ectoparasite-free and infested broods of blue tits 14 d after hatching. All measures are shown ± 1 SE and with sample sizes (number of broods) in parentheses.

	Parasite-free nests	Infested nests	t	p
Nestling mass (g)	11.7 \pm 0.1 (19)	11.4 \pm 0.2 (16)	1.093	0.282
Tarsus length (mm)	19.4 \pm 0.1 (19)	19.2 \pm 0.1 (16)	1.072	0.291
Body condition (res.)	0.03 \pm 0.10 (19)	-0.04 \pm 0.12 (16)	0.417	0.680
Feather length (mm)	29.6 \pm 0.4 (19)	27.6 \pm 0.7 (16)	2.53	0.016
Brood size	10.7 \pm 0.3 (19)	10.1 \pm 0.6 (16)	0.91	0.369

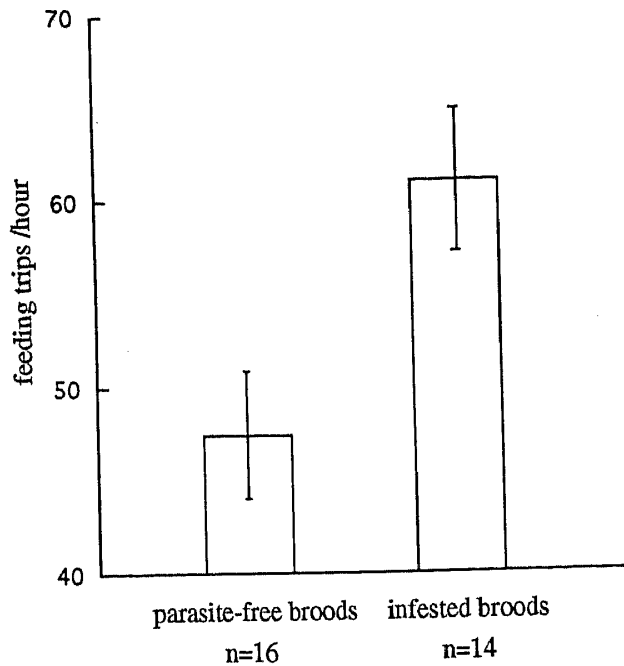


Fig. 1. Number of parent feeding trips to the nest box per hour (\pm SE) in ectoparasite-free and infested broods.

Parental feeding behaviour did not vary with time of day (Ancova: fleas $F_{1,27} = 6.876$, $p = 0.01$; time $F_{1,27} = 0.001$, $p = 0.976$).

Adult body measurements

Due to the increased work load, a lowered body condition of parents in infested broods might be expected. Body condition of both males and females was not significantly different between the two experimental groups, i.e. the mean value of the residuals of the regression of body mass on tarsus length is 0.06 (± 0.11 SE) for females in parasite-free nests and -0.07 (± 0.10 SE) in infested nests (t -test: $t = 0.82$, $n = 34$, $p = 0.421$). For males the mean is -0.11 (± 0.10 SE) in parasite-free and 0.13 (± 0.16 SE) in infested nests (t -test: $t = 1.31$, $n = 33$, $p = 0.199$).

Discussion

We found a mean 29% increase in combined male and female food provisioning rate from parasite-free to flea

infested nests, but very little effect of the fleas on body measurements of the young. This suggests that parents can compensate for the effect of the parasite by the provisioning of additional food. The small reduction in feather growth has probably no carry-over effect on post-fledging survival and later reproductive success of the fledglings. For great tit (*Parus major*) nestlings it has been shown, however, that age at fledging decreases with increasing wing length (Verhulst 1995). This suggests that fleas could retard fledging and increase the probability of nestlings being killed within the nest by predators (Perrins 1979, Nilsson 1986). In a study of flea-infested great tits inhabiting a beech-dominated forest in southern Switzerland (Christe et al. 1996), severe effects on nestling body mass and size have been found despite a 24% increase in combined rate of food provisioning. Flea-induced reductions in offspring quality vary among different great tit populations, and also among different breeding seasons within populations (Richner et al. 1993, Dufva 1995). The extent to which parasite damage can be compensated by increased parental food provisioning is likely to depend on factors such as parasite load, temperature affecting the energetic requirements of the young, and food availability. Severe flea effects on nestling body condition or growth potentially lower post-fledging survival and later reproductive success of nestlings of infested broods (Garnet 1981, Nur 1984, Tinbergen and Boerlijst 1990, Richner et al. 1993). In this case both parents and offspring may pay for the cost of parasitism.

Neither in our blue tit population inhabiting an oak forest with abundant food resources nor in the great tit population inhabiting a poorer beech-dominated forest in southern Switzerland (Christe et al. 1996) did the increase in parental food provisioning result in short-term parasite costs (i.e. lowered body condition) for the parents. Within the range of additional work that the adults are willing to accept, parents may give a high priority to the maintenance of their body mass and condition, and the cost of parasitism may then be expressed in a correlate which is important over a longer time-scale only (see also Richner et al. 1995).

Life history models assume a trade-off between current reproductive effort and future reproduction (Williams 1966, Stearns 1992). Food compensation, as observed in the present study, implies that parents rather than their offspring pay the cost of ectoparasitism, and therefore predicts a lowered future reproductive success of parents. Given that for parents food compensation carries costs for their future reproduction, what are the critical conditions favouring food compensation? Why do parents not rather reduce investment in the current brood of parasite-induced low value in order to have an increased potential to invest in future broods? Offspring condition is most plausibly a decelerating function of food intake. Parents will therefore lose less in terms of lifetime reproductive success by

increasing their food provisioning than by reducing current effort (Perrin et al. 1996). Fleas probably have a stronger negative effect on nestlings which are already in bad condition. In other words, nestlings may well be able to cope with fleas when well-fed, but suffer growth reduction or even death if undernourished. A decrease in current reproductive effort may therefore drastically reduce current reproductive success, while an increase in current reproductive effort minimises parasite effects and maximises life time reproductive success (for details see Perrin et al. 1996). Inter-population differences in flea effects due to differences in parental food compensation are expected if the cost function between current effort and future reproduction changes for populations living in poor and rich habitats. For the same reason, variation in food compensation and flea costs is expected from one reproductive season to another. We would therefore predict that the extent to which birds compensate for parasite effects depends on the local food availability in the current reproductive event. The results found by Dufva (1995) in a great tit population in Sweden support this hypothesis. Flea costs occurred in years with cold springs and it was suggested that birds suffered costs due to flea infestation only when simultaneously experiencing food shortages.

Similar patterns might be expected in other bird-parasite systems showing comparable parasite effects. Depending on the availability of resources, parasite costs are predicted to be borne by the offspring, by the parents, or shared between the two. This study therefore stresses the need to measure food provisioning in bird-parasite systems and more generally host food intake in studies aimed at showing parasite-related fitness costs. The causal relationships between parasitism, offspring quality, parental food compensation and food availability remains to be experimentally demonstrated by randomised and simultaneous manipulations of parasite levels and food availability within the same population.

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