

Behavioural responses to ectoparasites: time-budget adjustments and what matters to Blue Tits *Parus caeruleus* infested by fleas

FRÉDÉRIC TRIPET,* MARKUS GLASER & HEINZ RICHNER

Zoology Department, University of Bern, CH-3032 Hinterkappelen, Switzerland

Blue Tit nests are often heavily infested by fleas, which feed on the incubating female and the nestlings. Depending on habitat quality, the drawing of blood by fleas reduces offspring quality, or it is compensated by an increase in food provisioning by the adults and may reduce their future reproduction. Given these fitness costs, tits are expected to have evolved behavioural responses enabling them to remove, destroy or minimize the contact with fleas. To identify these traits, we video-recorded the changes in frequency and duration of the hosts' potential anti-flea behavioural defences in nests experimentally infested with low and high flea densities. We also investigated whether flea load affected the number of male feeds delivered to incubating females, and whether the parents increased their rate of food provisioning to the nestlings equally at high flea density. Flea density significantly affected the nest sanitation and sleeping behaviour of Blue Tit females but had no significant effect on grooming. Female Blue Tits increased the frequency but decreased the duration of bouts of these behavioural traits, and hence their time-budgets, based on per hour duration of behaviour, were not significantly affected by flea density. High flea density reduced nestling weight at the early nestling stage but these costs were fully compensated by an increase in female feeding effort. Males did not increase their frequency of food provisioning to incubating females nor to nestlings in heavily infested nests. The results are discussed in the light of parasite-mediated selection on host behaviour and the reciprocal host selection on flea life-history and behavioural traits.

The majority of living organisms have to cope with a variety of parasites in their environment and have evolved defence mechanisms allowing them to avoid or minimize the costs of parasitism. Behavioural responses can be viewed as a first line of defence (Nelson *et al.* 1975) that are complementary to the immune system of the host (Hart 1992, 1997). In contrast to endoparasites, ectoparasites are not always in close contact with their host immune system and behavioural responses that enable hosts to remove, destroy or minimize contact with ectoparasites may be the hosts' main way to control ectoparasite infestations.

Bird nests are often teeming with bugs, fleas and mites that take advantage of the presence of breed-

ing hosts and their offspring to feed and reproduce (Rothschild & Clay 1952, Marshall 1981, Lehane 1991). A particularly extensively studied host-parasite system involves the bird flea *Ceratophyllus gallinae* and its major hosts the hole-nesting Blue Tit *Parus caeruleus* and Great Tit *P. major*. Experiments have shown that tits avoid nesting in heavily infested nests (Oppliger *et al.* 1994, Christe *et al.* 1994, Merilä & Allander 1995). In habitats with low food availability, the drawing of blood by fleas impairs the growth and survival of nestlings, and sometimes causes nest desertion (Richner *et al.* 1993). In food-rich habitats the negative effects of fleas on offspring may be compensated by an increase in food provisioning by the adults (Perrin *et al.* 1996, Tripet & Richner 1997a) and this increase in current reproductive effort may in turn affect their future reproduction (Richner & Tripet 1999).

Given the fitness costs associated with flea infestation, one might expect tits to have evolved behavioural

*Corresponding author. Present address: Vector Genetics Laboratory, W.H.O. Collaborating Center for Tropical Diseases, University of Texas Medical Branch, Galveston, TX 77555-0609, USA.

Email: frtripet@utmb.edu

defences aimed at minimizing the amount of blood drawn by adult fleas and controlling the growth of the flea population within their nests. During the incubation period, fleas climb onto the female bird in order to feed, and could be killed or damaged by her preening or scratching. Adult fleas and larvae could also be nipped at, or driven away from the upper region of the nest-cup. Such behavioural defences would make feeding on hosts a risky task and could explain why fleas survive only about 10 days when feeding on hosts and producing eggs (Tripet & Richner 1999b), while they can survive for months without food when waiting for a suitable host (Tripet & Richner 1999a).

We manipulated the density of fleas in nests of a Blue Tit population in northern Switzerland. We then video-recorded host behaviour within the nests during the incubation and nestling periods. These data were intended to give insights on two major aspects of bird–flea interactions. (1) Changes in frequency or duration of behaviour such as grooming and nest sanitation should allow us to identify behavioural traits that have evolved in response to fleas. Although fleas are predicted to coevolve chiefly with their main tit hosts (Tripet & Richner 1997b), until recently few flea behavioural traits could be interpreted clearly as specific adaptations to living in Blue and Great Tit nests. Such data are therefore crucial both for our understanding of the parasite selection on their hosts' life-history and behaviour, and for evaluating the reciprocal host selection on fleas. (2) Fleas increase the energy demand of nestlings which, in turn, beg more and receive more food from the adults (Christe *et al.* 1996a; Tripet & Richner 1997a). Adult Blue Tits in our study population are able to increase their rate of food provisioning thereby compensating for the negative effects of fleas on offspring growth (Tripet & Richner 1997a). However, we still do not know whether both sexes share equally in this increase in reproductive effort linked to food compensation. Because fleas feed essentially on the female during incubation, females may be forced to allocate more time for foraging at the expense of egg attendance, in order to compensate for the loss of blood to fleas. We would therefore expect that, as the costs of incubation increase with parasite density, females would provide a smaller proportion of compensatory feeds to the young during the nestling period. Fleas, by differentially affecting female and male trade-offs within the nesting period, could therefore create an apparent asymmetry in the birds' parental care.

METHODS

Study area

The study was conducted in spring 1996 in the Allschwilerwald, a 60-ha forest 8 km south-west of Basel, Switzerland (47°32'N, 7°32'E). This 120-year-old forest is part of a nature reserve with little tree-management. The vegetation is dominated by oak *Quercus* spp., mixed with Hornbeam *Carpinus betulus* and Beech *Fagus sylvatica*. Food availability is high. Nestboxes have been provided for hole-nesting birds for many years in this area and are commonly used by Blue Tits. Previous researchers working on this population on other topics reported high natural infestation rates by *Ceratophyllus gallinae* (H. Zandt pers. comm.). In February 1996, before the birds started nest building, we removed the old nest material from the nestboxes in the study area and stored it in plastic bags.

Parasite life-cycle

C. gallinae usually completes one or two flea generations within the nesting period of the host (Tripet & Richner 1999b). The eggs are laid within the nest material and develop into larvae which feed on organic material from the nest and blood faeces produced by adult fleas (Rothschild & Clay 1952, Lehane 1991). Some first-generation larvae spin cocoons under the nestcup at the end of the bird incubation period. They pupate, hatch around the hatching time of the nestlings and start laying second-generation eggs. When the nestlings fledge, the larvae spin cocoons and remain dormant for several months before searching for a new host (Tripet & Richner unpubl. obs., Humphries 1968).

Experimental infestations

We visited the boxes daily around the end of the egg-laying period and around the end of incubation in order to detect the start of incubation, referred to as 'day 0' of the incubation period, and the first day of hatching, or 'day 0' of the nestling period. On the first day of incubation, Blue Tit nests were temporarily collected, put into a plastic bag to prevent desiccation, and heat-treated using a microwave oven to kill all ectoparasites. To compensate for the loss of water during the heat-treatment, the nests were then sprayed with 4 mL of water and put back in the nestbox.

The following day, the nests were all infested with 12 adult fleas. The fleas were randomly picked from a mixture of old nest material collected from the nestboxes in the study area. In total, 58 nests were infested using this method, which has been used successfully in all previous experiments (e.g. Richner *et al.* 1993, Christie *et al.* 1996a, 1996b) and in the same habitat (Tripet & Richner 1997a, 1999a, 1999b).

We then assigned the 58 nests randomly to two groups. The first was left unmanipulated and we video-recorded the bird behaviour within the nest at day 6 of the incubation period and on day 10 of the nestling period. In the second experimental group, we increased the number of adult fleas one day before video-recording the bird behaviour. We added 30 adult fleas on day 5 of the incubation period and 60 on day 9 of the nestling period.

The flea life-cycle and population dynamics within Blue Tit nests have been studied in detail by Tripet and Richner (1999a, 1999b). In the low flea density group, the 12 founders will give rise to a new flea generation during the nestling period. The resulting number of adults expected in the nest ranges from 30 to 50 (Tripet & Richner 1999a). It is important to note that in the high density group, the offspring of fleas added at day 5 of incubation will not be able to pupate early enough to affect the number of first generation adult fleas during the nestling period. Not considering adult flea mortality, our manipulation therefore increased the expected number of adult fleas during the incubation period by roughly 300% (from 12 to 42 individuals) and during the nestling period by ~200% (from ~40 to 130 individuals). These intensities are within the range of natural infestations (e.g. Heeb *et al.* 1996).

Video recordings

For video recordings, an infra-red light and a camera were mounted inside the nestbox. The birds were habituated to the camera and infra-red light by replacing the usual top of their box with one with a dummy camera and infra-red light one day before recording. We swapped the sham material for the real recording devices immediately before recording. We recorded a 3-h tape of bird behaviour on day 6 of the incubation period, and a 1.5-h tape on day 10 of the nestling period. All recordings were made between 08:00 h and 18:00 h. Preliminary viewing of recordings showed that during the incubation period females returned to their nest shortly after we started the recording,

while during the nestling period, the adults sometimes took more than 15 min before returning to their nest. We therefore excluded the first 30 min of all recordings made during the nestling period from all analysis in order to minimize biases in our measures of behavioural traits.

Behavioural data analysis

We monitored three types of female behaviour from the video recordings made during the incubation period: 'sleeping', 'nest sanitation' and 'grooming'. 'Sleeping' is defined as in Amlaner and Ball (1983), as the time when the beak is pointed backwards and tucked under the scapulars (classical sleeping posture). 'Nest sanitation' is a period of active search with the head dug into the nest material and 'grooming' is the combined time the female spends preening or scratching (Clayton & Cotgreave 1994). We also calculated the total amount of time the female spent inside the box on the eggs, or 'egg attendance' which includes the time allocated to incubating awake and turning the eggs plus the three activities defined above. In addition to these female activities, we also counted the number of male feeds delivered to the female when she was in the nestbox.

From the recordings made during the nestling period we monitored the number of parental feeds to the young and the amount of time spent by females on 'nest sanitation'. The rest of the time was spent on distributing the food to the young and activities outside the nest such as foraging and territory defence. Females did not exhibit 'incubating', 'grooming' or 'sleeping' behaviours during our recordings of the nestling period.

Because of technical problems, we failed to record the behaviour of one Blue Tit pair. Sample sizes for the behavioural data are therefore 29 nests with low flea density and 28 nests with high flea density. From the analysis of feeding behaviour, we also excluded the data from two nestboxes where the males were missing and one with a known polygamous male. The resulting samples had 27 nests in each group.

Bird measurements

At hatching time, we weighed newly hatched nestlings to the nearest 0.1 g using a Sartorius 1200 portable electronic balance. To reduce the variance in our measure of nestling weight at hatching, only freshly hatched nestlings, as indicated by their wet down, were included in our analysis.

On day 14 of the nestling period we captured both parents by means of a spring-loaded trap shutting the entrance hole as the bird entered the nest. We sexed the birds according to the presence or absence of a brood patch, weighed them, and measured their tarsus and length of the 4th (ascendent) primary feather to the nearest 0.1 mm using a caliper. The same measurements were taken on the nestlings. There was no statistical difference between the two experimental groups in length of male and female tarsus. Mean tarsus length was 18.93 ± 0.65 mm for females of low infested nests and 18.86 ± 0.58 mm for females of highly infested nests (*t*-test: $t = 0.386$, $n = 57$, $P = 0.701$). Mean tarsus length of males was 19.4 ± 0.2 mm in the low infestation group and 19.6 ± 0.1 mm in the highly infested group (*t*-test: $t = 1.6$, $n = 56$, $P = 0.106$). The two groups did not differ significantly in terms of clutch size (*t*-test: $t = 0.331$, $n = 58$, $P = 0.742$). The variable 'body condition' was calculated as the residual of the regression of body mass on tarsus length. It is a measure that expresses how much a bird deviates from the mean relationship between body mass and body size. Two males went missing during the nestling period and one female could not be captured. The resulting sample sizes for adult bird measurements were

therefore 29 females and 27 males in the low flea density group and 28 and 29 in the high flea density one.

Statistical analyses were performed using the Systat Statistical Package (Wilkinson *et al.* 1992). Values reported throughout are means \pm se.

RESULTS

Incubation period

Effect of flea density on female nest sanitation, grooming, and sleep

Female Blue Tits with higher flea densities showed an increase in nest sanitation bouts, as well as grooming and sleeping bouts. The effect was significant for nest sanitation and sleeping but not for grooming (Table 1). The mean duration of female nest sanitation, grooming and sleeping bouts was lower in the high infestation group but not significantly so (Table 2).

The combined effects of the increase in the number of female nest sanitation and grooming bouts, and the decrease in their duration in response to high flea numbers, resulted in no significant difference between the two experimental groups in the duration of those behaviours per hour (Fig. 1, Table 3). Females tended

Table 1. Number of bouts (bouts/h \pm se) of nest sanitation, grooming and sleeping behaviour in incubating female Blue Tits infested with low and high flea density (see text)

Behaviour (bouts/h)	Low flea density	High flea density	Statistics	<i>P</i>
Nest sanitation	12.8 ± 0.8 (29)	15.4 ± 0.8 (29)	$T = 2.2$	0.03
Grooming	12.3 ± 1.3 (29)	14.4 ± 1.2 (29)	$T = 1.2$	0.249
Sleeping	6.9 ± 1.0 (29)	11.7 ± 1.4 (29)	$U = 272$	0.021

Table 2. Duration of bouts (s/bouts/ \pm se) of nest sanitation, grooming and sleeping behaviour in incubating female Blue Tits infested with low and high flea density

Behaviour	Low flea density	High flea density	Statistics	<i>P</i>
Nest sanitation	19.01 ± 2.09 (29)	14.95 ± 0.77 (29)	$U = 511$	0.159
Grooming	13.46 ± 1.81 (29)	9.91 ± 0.84 (29)	$U = 484$	0.323
Sleeping	78.70 ± 7.35 (29)	69.95 ± 5.59 (29)	$T = 0.95$	0.247

Table 3. Per hour duration (min/h \pm se) of nest sanitation, grooming and sleeping behaviour in incubating female Blue Tits infested with low and high flea density

Behaviour	Low flea density	High flea density	Statistics	<i>P</i>
Nest sanitation	3.8 ± 0.3 (29)	3.8 ± 0.3 (29)	$T = 0.2$	0.845
Grooming	2.5 ± 0.3 (29)	2.4 ± 0.3 (29)	$U = 426$	0.932
Sleeping	9.1 ± 1.8 (29)	12.5 ± 1.4 (29)	$T = 1.8$	0.073

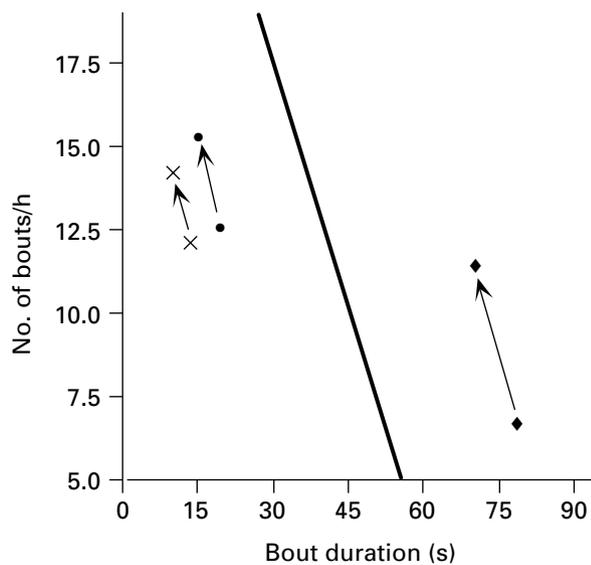


Figure 1. The difference in the relationship between the mean number of bouts and their mean duration for nest sanitation (●), grooming (×) and sleeping (◆) in incubating female Blue Tits with low and high flea densities. Arrows point from the low flea density group to the high density one. The thick line indicates the slope at which the product of the number and duration of bouts of a given behaviour, equal to its per hour duration, is constant.

to sleep more per hour in nests with high infestations (Table 3).

The total amount of time the female spent attending the eggs was not significantly affected by flea density. Females with few fleas spent on average 50.8 ± 0.6 min/h on the nestcup and females with higher flea loads 50.6 ± 0.7 min/h (t -test: $t = 0.184$, $n = 58$, $P = 0.855$).

Effect of flea density on male food provisioning to females

Males did not feed at the box significantly more often when their partner incubated in a nest with high flea numbers. On average, males made 1.5 ± 0.4 feeds/h in low and 1.3 ± 0.3 feeds/h in high flea density nests (t -test: $t = 0.445$, $n = 58$, $P = 0.658$).

Effect of flea density on female egg attendance

Clutch size is known to be an important determinant of the energy expenditure of incubating females (Haftorn & Reinertsen 1985) and, similarly, the male's feeds to the female may affect her energy balance and her need to forage. We therefore included these two variables in a general linear model examining the effect of flea density on egg attendance. The model explains 31% of the variance in female attendance (Table 4). Flea density (see also t -test in first section)

Table 4. General linear model of the effects of flea density and the correlates: number of male feedings and clutch size on female egg attendance. Interaction terms were not significant

Variable	Sum-of-squares	df	F-ratio	R ²	P
Male feeding	117.43	1	12.51	0.248	0.001
Clutch size	45.35	1	4.83	0.062	0.032
Flea density	0.10	1	0.01	0.000	0.917
Error	507.05	54			

had no significant effect on female attendance, neither was there an interaction between flea density and the amount of male feeding. The total variance explained was accounted for by the main effects of the number of male feeds to the female, and the size of her clutch. Female attendance decreased significantly with the number of male feeds and increased with clutch size (Table 4).

Nestling period

Effect of flea density on female behaviour

Female Blue Tits with higher flea densities cleaned their nests significantly more frequently (Mann–Whitney: $U = 250$, $P = 0.013$) but for shorter periods than females with low flea infestations (Mann–Whitney: $U = 556$, $P = 0.017$, Fig. 2). The two experimental groups did not differ significantly in the amount of time that females spent performing nest sanitation per hour (t -test: $t = 0.266$, $n = 58$, $P = 0.791$). On average, females with few fleas spent 8.3 ± 0.8 min/h cleaning the nest and females with higher flea loads 8.6 ± 0.8 min/h.

Females tended to clean their nests less often during the nestling period than during incubation (Paired t -test: $t = 1.82$, $n = 57$, $P = 0.074$) but for longer periods (Wilcoxon signed-rank: $Z = 6.26$, $n = 57$, $P < 0.0001$; Tables 1, 2 and Fig. 2). The amount of time allocated to nest sanitation was much higher during the nestling period, but this increase was independent of the presence of fleas (repeated ANOVA: flea density, $F_{1,52} = 0.098$, $P = 0.755$; time (repeat): $F_{1,52} = 72.3$, $P < 0.0001$; interaction: $F_{1,52} = 0.03$, $P = 0.864$) (Table 3 and Fig. 2).

Effect of flea density on nestling number and quality

A total of $92.4 \pm 1.6\%$ of the eggs hatched in low flea density nests and $95.7 \pm 1.2\%$ in high flea density nests. There is no statistical difference between the two groups (Mann–Whitney: $U = 0.215$, $n = 58$, $P = 0.215$). Recently hatched nestlings (see Methods)

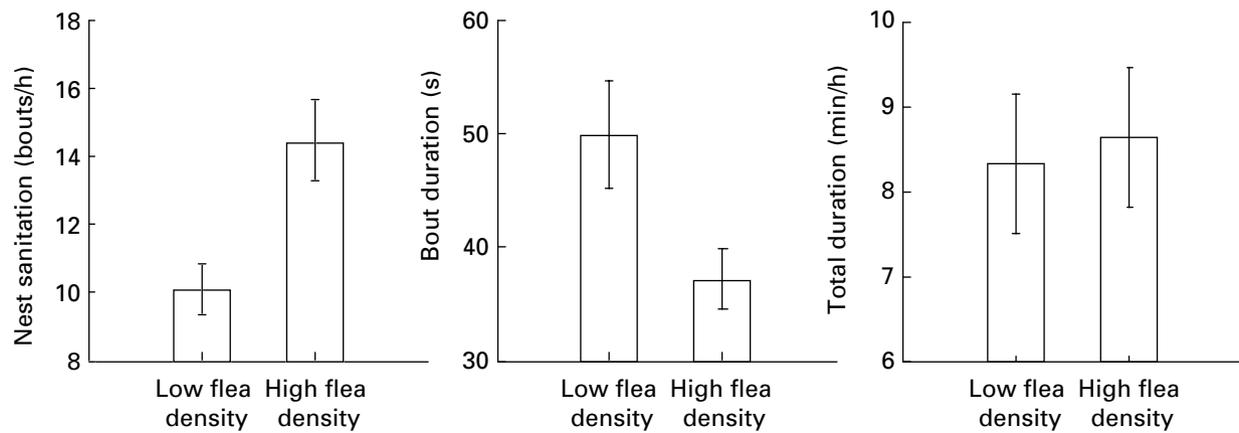


Figure 2. Number (left) and duration (middle) of bouts and per hour duration (right) of female nest sanitation during the nestling period. Values are shown with standard error bars.

Table 5. Nestling weight at hatching time and 14 days later, tarsus length and brood size in Blue Tit nests with low and high flea densities

Trait	Low flea density	High flea density	Statistics	<i>P</i>
Weight at day 0 (g)	0.91 ± 0.02 (29)	0.86 ± 0.02 (29)	<i>T</i> = 2.1	0.047
Weight at day 14 (g)	11.4 ± 0.1 (29)	11.4 ± 0.1 (29)	<i>T</i> = 0.06	0.952
Tarsus length (mm)	19.2 ± 0.1 (29)	19.2 ± 0.1 (29)	<i>T</i> = 0.09	0.928
Brood size	9.8 ± 0.3 (29)	10.0 ± 0.3 (29)	<i>T</i> = 0.58	0.568

were significantly lighter in nests with higher flea densities (Table 5). However, 14 days later, there was no significant difference in either the body weight or the tarsus length between nestlings from low and high flea density nests (Table 5).

Effect of flea density on female and male feeding effort

Male Blue Tits provisioned the nestlings significantly more often than did females in low infested nests but not in highly infested ones. Thus there was a significant interaction between female feeding effort and the level of flea infestation (ANOVA: flea density, $F_{1,104} = 3.4$, $P = 0.067$; sex: $F_{1,104} = 10.5$, $P = 0.006$; interaction: $F_{1,104} = 7.2$, $P = 0.008$) (Fig. 3).

There was no statistical difference between the two experimental groups in the body condition of adult birds. Mean body condition was 0.037 ± 0.102 (res. g/mm) for females of low infested nests and -0.039 ± 0.073 (res. g/mm) for females of highly infested nests while body condition of males was 0.023 ± 0.081 (res. g/mm) in the low infestation group and -0.021 ± 0.082 (res. g/mm) in the highly infested group. Males and females did not differ significantly in terms of body condition (ANOVA: flea density,

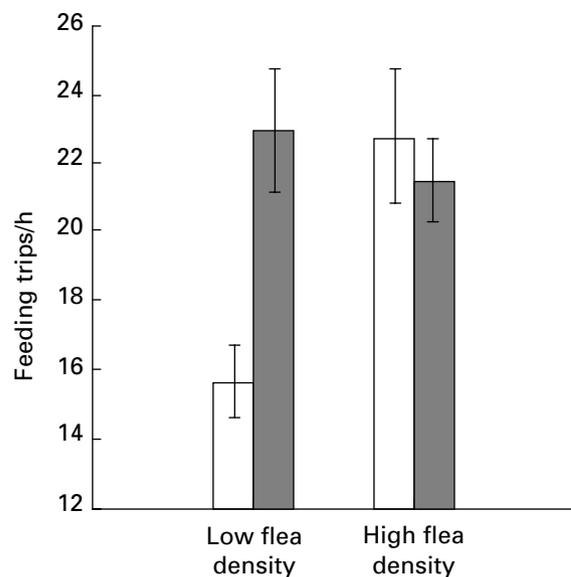


Figure 3. Mean (\pm se) number of female (□) and male (■) feedings per hour to the nestlings in nests with low and high flea densities.

$F_{1,109} = 0.9$, $P = 0.336$; sex: $F_{1,109} = 1.8$, $P = 0.219$; interaction: $F_{1,109} = 0.176$, $P = 0.676$).

DISCUSSION

Host responses and time-budget adjustments

This study shows that flea density significantly affects the frequency of female nest sanitation bouts during the incubation and nestling periods. The number of grooming bouts also increased but not significantly so. This suggests that these behavioural traits may have evolved in response to ectoparasites and that hosts, by preventing fleas from feeding or by killing them, could minimize the fitness costs associated with flea infestation (e.g. Richner *et al.* 1993). To test this assumption directly would require manipulation of those host behavioural responses and measurement of the impact of the manipulation on nestling growth components, adult body condition and flea fitness. Such experiments have been carried out on louse-infested pigeons by fitting steel rings around their upper beak to prevent preening (Clayton 1990, 1991). In the case of our wild tit and flea populations, the validity of such an approach was questionable since the manipulation would interfere with the hosts' feeding rates, and hence also with the food compensation behaviour. There is, however, substantial evidence that grooming and, to a lesser extent, nest sanitation may have a direct impact on fleas. Fleas that have been distinctively nipped at or nibbled on, or even cut in two, are regularly found dead in nest material (pers. obs.). Fleas have also been found in the stomach of tits (Rothschild & Clay 1952), which suggests that fleas are often swallowed after being killed, a behaviour also observed on video-recordings of infested tits (P. Christe, M. Kölliker pers. comm.). It is unknown whether, while performing nest sanitation, tits catch fleas or whether fleas are killed while the host is grooming. Nest sanitation could simply be used to chase adult fleas away, thereby preventing them from biting the incubating female or the nestlings. On our video-recordings we have also observed that, while cleaning the nest, females catch and destroy flea cocoons. Female Blue Tits may therefore reduce flea reproduction by chasing the adults from their source of food and by preventing larvae from feeding and building cocoons within the lining of the nestcup. This might force flea larvae to pupate in cooler parts of the nest where their development will be slowed down (Tripet & Richner 1999a).

The absence of a difference in the total time invested in behavioural defences indicates that females may not be able to choose to increase the amount of time allocated to anti-flea defence. During incubation, females seem to be constrained by energy intake and expenditure as indicated by the high proportion of variance in egg attendance explained by the amount of male mate feeding, and by clutch size (Haftorn & Reinertsen 1985). Female tits may also be constrained in their nest-cleaning behaviour by the amount of disturbance that eggs can sustain. During the nestling period, the time that birds allocate to anti-parasite behaviour may compete with that devoted to foraging and feeding the nestlings (see Christe *et al.* 1996b). Tits in food-rich habitats may not increase the time allocated to nest sanitation if food compensation is the only effective way of avoiding fitness costs in terms of offspring number and quality (Tripet & Richner 1997a). In other species, and tits in poor habitats, however, an increase in anti-parasite defences may reduce the costs of parasitism more efficiently (e.g. Cotgreave & Clayton 1995, Christe *et al.* 1996b).

The fact that birds did not allocate more time to anti-parasite behaviour does not necessarily imply that fleas are more likely to survive at high densities. In a previous experiment conducted in the same bird population we found the survival of adult fleas during the bird nesting period to be independent of flea density within the nests (Tripet & Richner 1999a). The exact relationship between the duration of nest sanitation or grooming bouts and ectoparasite fitness at different levels of infestation remains to be investigated.

Changes in the frequency of nest sanitation or grooming may be interpreted as responses to ectoparasites. The change in the frequency of sleeping bouts, however, was probably the result of the birds' sleep being interrupted by grooming and nest sanitation bouts. The number of sleeping bouts significantly correlated with the number of grooming bouts ($r = 0.312$, $n = 58$, $P = 0.017$) but not with nest sanitation ones ($r = 0.035$, $n = 58$, $P = 0.794$). Thus highly infested incubating females probably interrupt their sleep to groom. They also tend to spend more time sleeping. The function of sleep in birds is poorly understood (Toates 1980, Christe *et al.* 1996b). If we assume that sleep has a restorative function (Amlaner & Ball 1983), the duration of sleeping bouts may correlate systematically with its effect on host physiology. Infested females may therefore need to compensate for the numerous sleep interruptions by increasing their total sleep duration. Christe *et al.* (1996b)

found that infested female Great Tits slept less at night because of an increase in nest sanitation. It may therefore also be that incubating female Blue Tits sleep more during daylight because of an increase in nest cleaning behaviour at night.

Food compensation

Our manipulation of flea burden did not affect the amount of energy lost to fleas by incubating females to the point that they gave up egg-attendance to forage or that males fed them significantly more. It may be that females compensate for the energy lost to fleas by foraging more efficiently when outside the nest. In either case, fleas did not have a significant carry-over effect in terms of the adult bird's body condition. The absence of a detectable effect of fleas on adult body condition is common to all previous studies made on this host-parasite system (Christe *et al.* 1996a, Tripet & Richner 1997a, 1999b, Heeb *et al.* 1998). This would suggest that adult birds pay no costs when increasing their feeding effort or incubating in infested nests. Recent advances, however, show that fleas may influence the likelihood of a bird returning to breed the following year and, more generally, that an increase in current reproductive effort may be traded against future reproduction (Perrin *et al.* 1996, Richner & Tripet 1999).

To our knowledge, this is the first study showing a significant effect of fleas on hatchling weight. Hatchlings in infested nests are often pale, and anaemia is probably the most obvious and earliest sign of the loss of blood to fleas (Tripet pers. obs.). The slight difference in weight that this may cause was not found significant in previous studies probably due to the enormous weight difference between unfed hatchlings and those that have already been fed by adults, a source of variance we circumvented in this study by weighing only freshly hatched young. Adult birds compensated fully for the effect of fleas on nestlings as indicated by the lack of a difference in nestling body mass or tarsus length at day 14 of the nestling period. Although males with low flea burden fed the brood significantly more than females, at high flea density the extra-feeding effort was entirely undertaken by females, which resulted in the sexes feeding equally. A brood-manipulation experiment carried out on Great Tits in the same region also found that females undertook the extra work required to raise an enlarged brood (S. Gebhard pers. comm.). In central Switzerland, Kölliker *et al.* (1998) showed experimentally that female Great Tits were more

responsive to variation in begging intensity of the nestlings than males. Christe *et al.* (1996a), however, found in a Great Tit population in southern Switzerland that males increased their share of work in the presence of fleas. There is, as yet, no theoretical framework that would predict a difference in parental compensatory feeding effort in response to parasites or brood-size manipulations. Our results do not support the hypothesis of a trade-off between the female's energy expenditure during incubation, and her investment in food provisioning during the nestling period. Neither do they suggest that males share the expected flea-mediated costs during incubation by increasing their care to the female during incubation. However, data on the feeding behaviour and courtship feeding outside the nest would be necessary before any conclusion could be reached. Further studies should aim at understanding which ecological factors interact with ectoparasite presence to determine the direction of such asymmetries in extra-parental feeding effort.

The logistic support of the Allschwil local authorities is greatly acknowledged. We thank P. Christe, A. Roulin and M. Kölliker and two anonymous referees for their comments on the manuscript. The work was supported by a Swiss National Science Foundation Grant (31-34020.92 and 31-43570.95 to H.R.).

REFERENCES

- Amlaner, C.R. Jr & Ball, N.J. 1983. A synthesis of sleep in wild birds. *Behaviour* **87**: 85–119.
- Christe, P., Oppliger, A. & Richner, H. 1994. Ectoparasites affect choice and use of roost sites in the great tit, *Parus major*. *Anim. Behav.* **47**: 895–898.
- Christe, P., Richner, H. & Oppliger, A. 1996a. Begging, food provisioning, and nestling competition in great tits infested with ectoparasites. *Behav. Ecol.* **7**: 127–131.
- Christe, P., Richner, H. & Oppliger, A. 1996b. Of great tits and fleas: sleep baby sleep.... *Anim. Behav.* **52**: 1087–1092.
- Clayton, D.H. 1990. Mate choice in experimentally parasitized rock doves: lousy males lose. *Am. Zool.* **30**: 251–262.
- Clayton, D.H. 1991. Coevolution of avian grooming and ectoparasite avoidance. In Loye, J.E. & Zuk, M. (eds) *Bird-Parasite Interactions: Ecology, Evolution, and Behaviour*: 258–289. Oxford: Oxford University Press.
- Clayton, D.H. & Cotgreave, P. 1994. Relationship of bill morphology to grooming behaviour in birds. *Anim. Behav.* **47**: 195–201.
- Cotgreave, P. & Clayton, D.H. 1995. Comparative analysis of time spent grooming by birds in relation to parasite load and other factors. *Behaviour* **131**: 171–187.
- Haftorn, S. & Reinertsen, R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). *Auk* **102**: 470–478.
- Hart, B.L. 1992. Behavioural adaptations to parasites: an ethological approach. *J. Parasitol.* **78**: 256–265.

- Hart, B.L.** 1997. Behavioural defence. In Clayton, D.H. & Moore, J. (eds) *Host-Parasite Evolution. General Principles and Avian Models*: 59–77. Oxford: Oxford University Press.
- Heeb, P., Werner, I., Kölliker, M. & Richner, H.** 1998. Benefits of induced host responses against an ectoparasite. *Proc. R. Soc. Lond. B* **265**: 51–56.
- Heeb, P., Werner, I., Richner, H. & Kölliker, M.** 1996. Horizontal transmission and reproductive rates of hen fleas in great tits. *J. Anim. Ecol.* **65**: 474–484.
- Humphries, D.A.** 1968. The host-finding behaviour of the hen flea *Ceratophyllus gallinae* (Schrank) (Siphonaptera). *Parasitology* **58**: 403–414.
- Kölliker, M., Richner, H., Werner, I. & Heeb, P.** 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Anim. Behav.* **55**: 215–222.
- Lehane, M.J.** 1991. *Biology of Blood Sucking Insects*. London: Harper Collins Academic.
- Marshall, A.G.** 1981. *The Ecology of Ectoparasitic Insects*. London: Academic Press.
- Merilä, J. & Allander, K.** 1995. Do great tits (*Parus major*) prefer ectoparasite-free roost sites? An experiment. *Ethology* **99**: 53–60.
- Nelson, W.A., Keirans, J.E., Bell, J.F. & Clifford, C.M.** 1975. Host-ectoparasites relationships. *J. Med. Entom.* **12**: 143–166.
- Oppliger, A., Richner, H. & Christe, P.** 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). *Behav. Ecol.* **5**: 130–134.
- Perrin, N., Christe, P. & Richner, H.** 1996. On host life-history response to parasitism. *Oikos* **75**: 317–320.
- Richner, H., Oppliger, A. & Christe, P.** 1993. Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.* **62**: 703–710.
- Richner, H. & Tripet, F.** 1999. Ectoparasitism and the trade-off between current and future reproduction. *Oikos* **86**: 535–538.
- Rothschild, M. & Clay, T.** 1952. *Fleas, Flukes and Cuckoos*. London: Collins.
- Toates, F.** 1980. *Animal Behaviour. A Systems Approach*. Chichester: John Wiley.
- Tripet, F. & Richner, H.** 1997a. Host responses to ectoparasites: Food compensation by parent blue tits. *Oikos* **78**: 557–561.
- Tripet, F. & Richner, H.** 1997b. The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*. *Parasitology* **115**: 419–427.
- Tripet, F. & Richner, H.** 1999a. Demography of the hen flea *Ceratophyllus gallinae* in blue tit *Parus caeruleus* nests. *Insect Behav.* **12**: 159–174.
- Tripet, F. & Richner, H.** 1999b. Density-dependent processes in the population dynamics of a bird ectoparasite *Ceratophyllus gallinae*. *Ecology* **80**: 1267–1277.
- Wilkinson, L., Hill, M.A. & Vang, E.** 1992. *SYSTAT: Statistics*, Version 5.2 edition. Evanston, Illinois, USA: SYSTAT.

Received 12 December 2000; revision accepted 23 May 2001