

## Effect of an ectoparasite on reproduction in great tits

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### Summary

1. The effect of a haematophagous ectoparasite, the hen flea, on quality and number of offspring was experimentally investigated in the great tit. The experiment consisted of a controlled infestation of a random sample of nests with the parasitic flea and of a regular treatment of control nests with microwaves in order to eliminate the naturally occurring fleas.

2. To assess the effects of fleas on variables related to offspring number, we considered the number of hatchlings and fledglings, the mortality between hatching and fledging, and the hatching and fledging success. For assessment of offspring quality, we measured body mass, tarsus and wing length, and calculated the nutritional condition of nestlings as the ratio of body mass to tarsus length. A physiological variable, the haematocrit level, was also measured.

3. Hatching success and hatchling numbers did not differ between the two experimental groups. Offspring mortality between hatching and fledging was significantly higher in the infested broods ( $\bar{x} = 0.22$  chicks dead per day) than in the parasite-free broods ( $\bar{x} = 0.07$  dead per day). Fledging success was 83% in the parasite-free broods, but only 53% in the infested ones. The number of fledglings in infested broods ( $\bar{x} = 3.7$  fledglings  $\pm 2.1$  SD) was significantly lower than in the parasite-free ( $\bar{x} = 4.9 \pm 1.1$  SD) broods.

4. Body mass of chicks in the infested broods was significantly smaller than in the parasite-free broods both 14 days and 17 days after hatching. The chicks in the infested broods reached a significantly smaller tarsus length than the ones in the parasite-free broods. Close to fledging, the nutritional condition of chicks was significantly lower in infested broods. Haematocrit levels were significantly lower in the infested broods.

5. Brood size correlated differently with body mass and condition of chicks in infested and parasite-free nests. In parasite-free broods both body mass and condition of chicks at age 17 days, i.e. close to fledging, were significantly higher in small broods than in large ones. However, in the infested broods chicks were of the same body mass and condition in large as in small broods. Therefore, in parasite-free broods fitness can potentially be gained through offspring quality or number or both, whereas in infested broods it can be gained through offspring quantity only. In other words, a trade-off between quality and number of offspring is feasible only in the absence of the parasitic hen flea.

6. These results emphasize the need to study the effects of ectoparasites on ecological, behavioural and evolutionary traits of their bird hosts. A knowledge of these effects is essential for the understanding of population dynamics, behaviour and life-history traits of the hosts.

*Key-words:* ectoparasites, great tit, nestling growth, mortality, offspring quality vs. number.

*Journal of Animal Ecology* (1993) **62**, 703–710

## Introduction

The great tit (*Parus major* L.) has been the subject of many long-term studies, where data collected over decades have formed the basis for answering questions arising from ecological, behavioural and evolutionary theory. These studies thus provided a general insight into several important fields including population dynamics (e.g. Kluijver 1951; Lack 1954, 1966; Perrins 1965; Krebs 1971; McCleery & Perrins 1985) life history evolution (e.g. Lack 1966; Boyce & Perrins 1987; Clobert *et al.* 1988; McCleery & Perrins 1988; Pettifor, Perrins & McCleery 1988) quantitative genetics (e.g. Van Noordwijk 1987) and social behaviour (e.g. De Laet 1985; Van Noordwijk *et al.* 1985) of birds and other animals. Møller (1989) has pointed out that all these studies used nest boxes and that their results may, therefore, be afflicted by two kinds of experimental artefacts. First, the design of the nestboxes reduces predation to a fraction of the level encountered in natural cavities. Secondly, since researchers routinely remove the old nests before the next breeding season the load of detrimental ectoparasites may be considerably reduced. Both these factors, predation and ectoparasites, can limit reproductive success and adult survival. Brown & Brown (1986) have demonstrated that the haematophagous swallow bug (*Oeciacus vicarius* Horvath) severely reduces growth of cliff swallow nestlings (*Hirundo pyrrhonota* Vieillot). The haematophagous tropical fowl mite (*Ornithonyssus bursa* Berlese) can affect reproduction (Powlesland 1977; Møller 1990) in the barn swallow (*Hirundo rustica* L.) and in the European starling (*Sturnus vulgaris* L.), and optimal clutch size (Møller 1991) in the barn swallow. These findings demonstrate that a knowledge of the effect of ectoparasites on host behaviour is essential for the understanding of population dynamics, behaviour and life history traits (e.g. clutch size, timing of reproduction) of the hosts. This is particularly important if the effect of ectoparasites is non-random with respect to the phenotypes and genotypes in a host population since then the ectoparasites exert significant selection pressures on behavioural and life-history traits.

In this study we investigate the effect of a common ectoparasite, the hen flea (*Ceratophyllus gallinae*, Schrank), on quality and number of offspring in the great tit. To our knowledge the effect of ectoparasites on reproductive performance of tits has never been experimentally demonstrated. We manipulated the load of the haematophagous hen flea in the nests of the birds, and studied the effects on biometrical, physiological and reproductive parameters of the hosts. We take an experimental approach because of a possible correlation between the reproductive performance of an individual and its vulnerability to parasites.

## Methods

### THE STUDY POPULATION

The forest of the study site is located around the campus of the University of Lausanne, Switzerland. It is composed principally of beech trees, interspersed by a few oaks and hornbeam. There is little undergrowth except at the edge of the forest. A population of great tits has been breeding in the nestboxes since 1989. The experiment reported here was carried out during the breeding season of 1991.

### FLEAS AND THE EXPERIMENTAL PROCEDURE

The ectoparasite used in this study was the naturally occurring hen flea. In great tit nests the hen flea produces two generations per nest as a norm (Harper *et al.* 1992). In our study the second generation started to emerge just a few days before fledging. Many fleas leave with the nestlings, hundreds of fleas wait at the entrance hole for visitors (birds and humans!), and hundreds remain inside the nest in cocoons, attached to the nesting material until the start of the following breeding season.

We collected fleas from old tit nests and, for experimental infestation, transferred them into pipettes containing 20 fleas each. Approximately one-half of the nests were infested with fleas, three times each, between the times the first and the last egg was laid. The other half of the nests were heat-treated at 4-day intervals between hatching and fledging to kill any naturally occurring fleas. For this purpose the nests were taken out of the nest box, put in a closed plastic bag to prevent loss of humidity, and heat-treated for 5 min inside a microwave appliance. This procedure was carried out in the field and a transportable 220-volt generator was used to feed the microwave appliance. The treatment eliminated all fleas: nest checks at 4-day intervals and after fledging revealed in none of the treated nests a presence of fleas or flea larvae.

### OTHER PARASITES

Other haematophagous ectoparasites occur occasionally in tit nests. These are mites (Arachnida), blow fly larvae (Diptera: Protocalliphoridae) and hippoboscids (Diptera: Hippoboscidae). Since the microwave treatment killed all ectoparasites that were present in the nest, and since other ectoparasites than fleas might have been present in the untreated nests, the control and assessment of their number is important. After hatching, all nests, both infested and heat-treated, were thoroughly examined for other ectoparasites at 4-day intervals until fledging. In the habitat under study we never recorded a great tit nest that was infested with mites. Blow fly larvae occurred in three nests of the

present study, but were eliminated when they were still very small (<2 mm). Hippoboscids are known to occur frequently towards the end of the breeding season. The experimental treatment in our study was randomized with respect to the time of breeding and all treatment groups would, therefore, have been affected similarly by this parasite. This parasite does not live in the nest, but on the bird and the heat treatment applied to half the nests in the present study would, therefore, not affect the hippoboscids differently in the two treatment groups. The hippoboscids live in low numbers (Williams 1964; Hutson 1981; personal observation, between one and three individuals) on adults and can be found on chicks only after the growth of feathers. They would, therefore, influence chick development for a very short period at the end of the fledgling stage. Hippoboscids were recorded on the parents of five broods only, three in the infested group and two in the parasite-free group.

Some ectoparasites are also known to be vectors for haematzoa. To our knowledge, the hippoboscids, but not fleas, mites or blood flies, serve as vectors for avian tripanosomes, haemosporina and filaria (Baker 1967). Since these protozoan blood parasites could seriously affect chick development, a blood sample was taken of all chicks and a blood smear prepared. The analysis of the blood smears from 100 chicks of both treatment groups in none of the cases showed an infestation with protozoan blood parasites.

We therefore believe that the effects reported here are principally due to the haematophagous hen flea and not to the presence of other parasites.

#### REPRODUCTIVE, MORPHOLOGICAL AND PHYSIOLOGICAL VARIABLES

Since the timing of breeding can have a significant effect on many breeding parameters, we compared the mean laying date (i.e. day of the first egg laid) between the infested and the parasite-free groups. Since the experimental manipulation of the ectoparasite load started after the first egg was laid, we do not expect a difference in laying date between the two groups. The mean date of laying the first egg was 28 April for infested nests and 2 May for the nests which were kept free of parasites (Mann-Whitney  $U$ -test,  $U_{19,14} = 106$ ,  $P > 0.3$ , NS). Similarly, there was no difference in mean hatching date. The mean hatching date for the chicks was 20 May in infested nests and 24 May in clean nests (Mann-Whitney  $U$ -test,  $U_{20,14} = 125$ ,  $P > 0.5$ , NS).

For each nest we recorded clutch size, brood size at hatching (=day 0) and at the age of 4, 8, 12, 14 and 17 days, and the number of chicks fledged. At the above ages we measured body mass, tarsus and wing length of each chick. At the age of 14 days we collected 20 µg of blood from the brachial vein of

each chick. A small drop of the blood sample was used for a blood smear and the rest was centrifuged for the determination of the haematocrit levels. At this age we also captured both parents, took the same morphological variables as for the chicks, and a blood sample.

During part of the time that the chicks were measured the heat-treatment was applied to the nest. Total handling time of chicks was, therefore, not different for the two experimental groups.

#### NUTRITIONAL CONDITION OF THE NESTLINGS

Since body mass and structural size are often correlated, a higher body mass of nestlings *per se* does not indicate that these nestlings are in a better nutritional state. To test the influence of ectoparasites on the nutritional condition of the nestlings, the ratio given by body mass to tarsus length was used as a measure of condition. This ratio represents a quantitative measure that expresses in relative terms how body mass relates to a unit of linear body size. Tarsus length was preferred to wing length as a measure of reference since tarsus length is fixed at the age of 12 days post-hatching, and because it is also less affected by the growth conditions than wing length.

#### ASSESSMENT OF FLEA LOAD

A day after the chicks fledged each infested nest was cut in half, one half of each nest transferred into a plastic bag, and frozen for 1 hour at  $-70^{\circ}\text{C}$ . The number of adult fleas present was then counted. In the infested nests an average of 37 adult fleas (SD:  $\pm 28$ , range: 3–85) were recorded, but none in the microwaved nests. The flea load was also assessed in a natural, unmanipulated sample of broods in 1990. In that sample the entire content of the nest was collected the day after fledging, sealed in a plastic bag and stored at room temperature for several months before counting the fleas.

#### STATISTICAL ANALYSIS

Only the nests that fledged chicks are included in the analysis of the effects of parasites on the quality and number of offspring. Failure of entire broods was similar in the two experimental groups ( $\chi^2 = 0.17$ ,  $P = 0.68$ ). A total of 34 broods were followed from nest building to fledging, 20 of them were experimentally infested and 14 treated against parasites. In three broods the measurement of body mass and size at age 17 days was omitted, and one brood was excluded from analysis after the age of 14 days because of the death of the male parent when the chicks were 15 days old.

For the statistical analysis of the morphological

variables the mean value from all chicks is calculated for each family. The family means are thus the unit of analysis, and each family mean is considered as an independent data point. This procedure was adopted for two reasons: (i) the value of each chick within a family cannot be truly taken as an independent data point since chicks compete amongst each other for resources; and (ii) large families would have more weight in the analysis than small ones if each chick was taken as a data point.

Analysis of covariance was used to assess the effects of ectoparasites on reproductive, morphological and physiological data. The only factor considered was the experimentally manipulated flea load of nests, i.e. the presence or absence of fleas. The number of chicks at hatching was used as a covariate (denoted as brood size<sub>0</sub>) in the analysis of data describing offspring quality, i.e. morphological and physiological data. The homogeneity of variance and homogeneity of slope assumptions were tested in all ANCOVAs before final analysis. None of the covariate  $\times$  factor interactions were significant at the 5% level. For this interaction only values of  $P < 0.1$  were taken into account for the analysis. Data describing offspring quantity showed significantly non-homogeneous variances for most variables and were, therefore, not broken down into brood size groups. For these data the effect of parasites was assessed by comparing the two experimental groups by *t*-tests only, using a separate variance estimate when appropriate. Proportions and percentages were compared by using non-parametric tests. For graphical representation the mean brood size at hatching was used to partition the broods in two groups, i.e. small broods are those with 3–6 chicks at hatching, and large broods those with 7–10 chicks at hatching.

All significance values are two-tailed unless indicated otherwise. Data analysis was performed using the Systat Statistical Package (Wilkinson 1989).

## Results

### EFFECT ON OFFSPRING QUALITY

#### Haematocrit level

The haematocrit levels of offspring at age 14 days (Fig. 1) were significantly higher in the parasite-free group than in the infested group. Brood size at hatching (thereafter denoted as brood size<sub>0</sub>) had no significant effect on the haematocrit levels (ANCOVA: parasite factor:  $F_{1,31} = 17.67$ ,  $P < 0.001$ ; brood size<sub>0</sub>:  $F_{1,28} = 0.51$ ,  $P = 0.48$ ). The experimental treatment alone explains 38% of the total variance in the haematocrit level.

#### Body mass

Body mass of offspring at age 14 days (Fig. 2) was

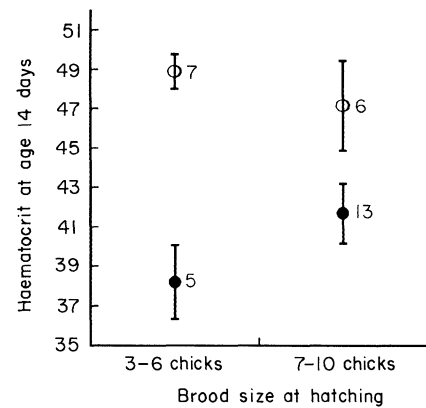


Fig. 1. Mean ( $\pm 1$  SE) haematocrit levels of nestlings at the age of 14 days: (○) = parasite-free broods, (●) = infested broods.

significantly influenced by parasites and by brood size<sub>0</sub> (ANCOVA: parasite factor:  $F_{1,31} = 4.65$ ,  $P = 0.039$ ; brood size<sub>0</sub>:  $F_{1,31} = 8.93$ ,  $P = 0.005$ ). The two variables account for 38% of total variance of body mass of chicks 14 days after hatching.

Between 14 days and 17 days post-hatching the mean body mass of chicks in the parasite-free nests increased sharply in small broods and moderately in large broods (Fig. 2). Surprisingly, in the infested families, it decreased in both small and large broods. Consequently, at the age of 17 days, the chicks in infested small broods at hatching do not show a higher body mass ( $\bar{x} = 14.4 \text{ g} \pm 1.33 \text{ SD}$ ) than the ones in large broods ( $\bar{x} = 14.1 \text{ g} \pm 1.38 \text{ SD}$ ) (Mann-Whitney *U*-test,  $U_{6,13} = 44.5$ ,  $P = 0.63$ ), as observed in the parasite-free families (small broods:  $\bar{x} = 17.7 \text{ g} \pm 1.19 \text{ SD}$ ; large broods:  $\bar{x} = 15.6 \text{ g} \pm 1.38 \text{ SD}$ ;  $U_{7,5} = 31.5$ ,  $P = 0.023$ ). Thus, under a parasite load small family size does not lead to higher fledging mass, as observed in parasite-free broods. Overall, at 17 days post-hatching, the nestlings in

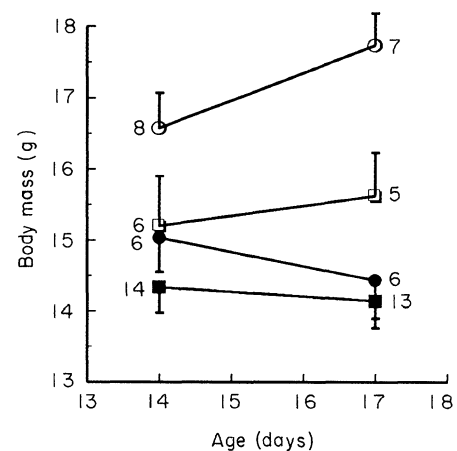


Fig. 2. Mean ( $\pm 1$  SE) body mass of nestlings 14 days and 17 days after hatching: (○) = parasite-free broods that were small at hatching, (□) = parasite-free large broods, (●) = infested small broods, (■) = infested large broods. The number beside the mean indicates sample size (=number of broods). For clarity of presentation error bars are shown on one side only.

the parasite-free broods were on average 18% heavier ( $\bar{x} = 16.9 \text{ g} \pm 1.6 \text{ SD}$ ) than the ones in the infested broods ( $\bar{x} = 14.2 \text{ g} \pm 1.3 \text{ SD}$ ). The difference is highly significant ( $t$ -test,  $t_{19,12} = 4.90$ ,  $P < 0.001$ ).

Both parasites and brood size<sub>0</sub> influence body mass close to fledging (ANCOVA: parasite factor:  $F_{1,27} = 16.31$ ,  $P < 0.001$ ; brood size<sub>0</sub>:  $F_{1,27} = 7.36$ ,  $P = 0.011$ ) and explain 56% of variance in body mass at age 17 days.

#### Body size

Passerine birds reach their final tarsus length well before fledging. In our population, no tarsus growth was observed after a nestling age of 14 days. Tarsus length at the age of 14 days was significantly affected (Fig. 3) by both ectoparasites and brood size<sub>0</sub> (ANCOVA: parasite factor:  $F_{1,31} = 4.38$ ,  $P = 0.045$ ; brood size<sub>0</sub>:  $F_{1,31} = 7.55$ ,  $P = 0.01$ ). The two factors explain 35% of total variance in tarsus length.

Wing length at age 14 days was, at the 5%-level, not significantly affected by ectoparasites or brood size (ANCOVA: parasite factor:  $F_{1,31} = 3.81$ ,  $P = 0.060$ ; brood size<sub>0</sub>:  $F_{1,31} = 3.86$ ,  $P = 0.058$ ).

#### Nutritional condition of nestlings

The nutritional condition of nestlings close to fledging (17 days after hatching) was strongly reduced by ectoparasites, and also slightly influenced by brood size (ANCOVA: parasite factor:  $F_{1,27} = 7.63$ ,  $P = 0.010$ ; brood size<sub>0</sub>:  $F_{1,27} = 3.23$ ,  $P = 0.084$ ; factor  $\times$  covariate interaction:  $F_{1,27} = 3.21$ ,  $P = 0.085$ ). It explains 47% of total variance in nutritional condition of nestlings just prior to fledging. The interaction between the parasite factor and brood size is close to 5%-significance and a comparison within parasite-free and infested broods shows that in parasite-free broods the condition of chicks is higher (Mann-Whitney  $U$ -test,  $U_{7,5} = 30$ ,  $P = 0.042$ ) in small broods (Fig. 4) than in large ones, but in infested broods condition is identical in small and

large ones (Mann-Whitney  $U$ -test,  $U_{6,13} = 36$ ,  $P = 0.79$ ).

#### EFFECT ON OFFSPRING NUMBER

##### *Egg numbers, hatching success and brood size at hatching*

The average clutch size was 1.1 egg larger in the infested nests than in the parasite-free nests (Table 1). This difference is, however, not statistically significant. Hatching success was 91% in the infested nests, and 94% in the parasite-free nests (Table 2). Brood size at hatching was, under an appropriate two-tailed hypothesis, non-significantly larger (Table 1, Fig. 5) in the infested nests.

##### *Chick mortality, fledgling number and fledgling success*

Between hatching to the age of 14 days daily chick mortality (number of chicks dead per day, Table 2) did not increase significantly with ectoparasites. That is, at the age of 14 days the number of chicks in parasite-free and infested broods was identical (Fig. 5). Thereafter, between the age of 14 days and fledging, daily chick mortality increased two-fold in the infested broods, but remained at a very low level in the parasite-free broods. An average of 1.2 chicks less fledged from the infested broods than from the parasite-free broods. Thus, overall chick mortality between hatching and fledging was three times higher (Table 2) with ectoparasites than without ectoparasites (Table 2, Fig. 5).

Fledging success (=number fledged/number hatched) was 30% lower in the infested broods than in the parasite-free broods (Table 2).

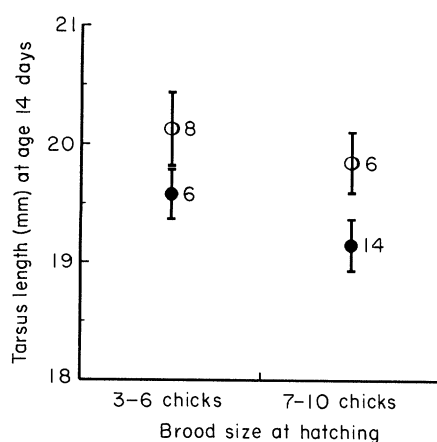


Fig. 3. Mean ( $\pm 1$  SE) tarsus length of nestlings at the age of 14 days. Rest of legend as in Fig. 1.

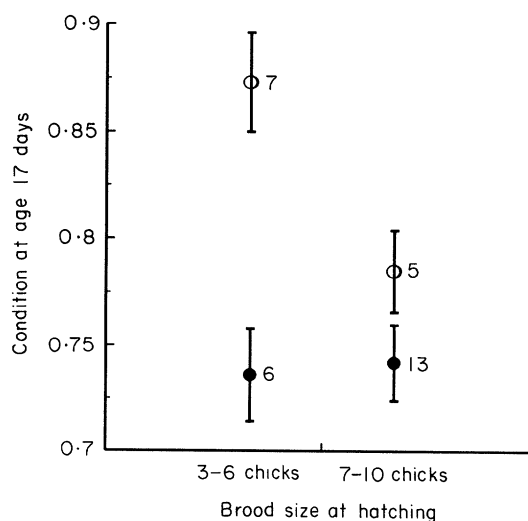


Fig. 4. Mean ( $\pm 1$  SE) condition of nestlings at the age of 17 days. Condition is calculated as the mean body mass of a brood divided by its mean tarsus length. Rest of legend as in Fig. 1.

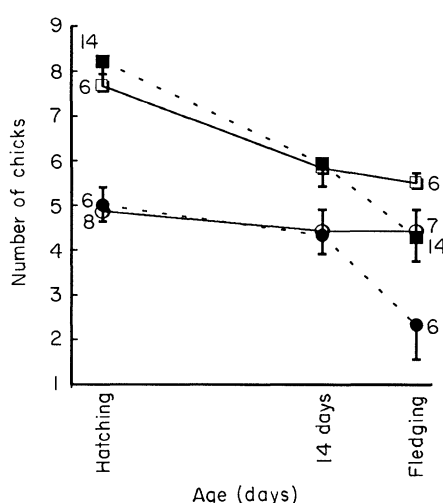
**Table 1.** The number ( $\pm 1$  SD) of eggs and offspring at hatching, at 14 days and at fledging in great tit broods infested with the hen flea, and in parasite-free broods

	Number of eggs	Number hatched	Number survived to age 14 days	Number fledged
Infested broods	7.8 $\pm$ 1.8	7.3 $\pm$ 1.8	5.5 $\pm$ 1.8	3.7 $\pm$ 2.1
Parasite-free broods	6.8 $\pm$ 1.9	6.1 $\pm$ 1.9	5.1 $\pm$ 1.2	4.9 $\pm$ 1.1
<i>t</i> -Test	$t_{20,14} = 1.49$ $P = 0.14$	$t_{20,14} = 1.73$ $P = 0.09$	$t_{20,14} = 0.56$ $P = 0.58$	$t_{20,13} = 2.17^*$ $P = 0.04$

\* Separate variance estimate.

**Table 2.** Mean hatching success, mortality (given as number of chicks dead per day) and fledging success of great tit broods infested with the hen flea, and of parasite-free broods

	% Hatching success	Mortality age 0–14 days	Mortality age 14-day fledging	Overall mortality	% Fledging success
Infested broods	93.9	0.14	0.32	0.22	53.1
Parasite-free broods	90.9	0.07	0.07	0.07	83.6
Mann-Whitney <i>U</i> -test	$U_{20,14} = 159$ $P = 0.38$	$U_{20,14} = 173$ $P = 0.23$	$U_{20,13} = 197$ $P = 0.006$	$U_{20,13} = 203$ $P = 0.006$	$U_{20,13} = 59.5$ $P = 0.009$

**Fig. 5.** Mean ( $\pm 1$  SE) number of nestlings at hatching, and 14 days and 17 days after hatching: ( $\circ$ ) = parasite-free broods that were small at hatching, ( $\square$ ) = parasite-free large broods, ( $\bullet$ ) = infested small broods, ( $\blacksquare$ ) = infested large broods. The number beside the mean indicates sample size (=number of broods). For clarity of presentation error bars are shown on one side only.

## Discussion

This study shows that a haematophagous ectoparasite affects both the number and the quality of fledglings. The quality of offspring is important since it has been shown, that body mass at fledging correlates with post-fledging mortality in tits (e.g. Perrins 1965; Smith Källander & Nilsson 1989; Tinbergen & Boerlijst 1990), and with resource acquisition in tits (Drent 1983) and other species (e.g. Richner 1989a,b, 1992). Tinbergen & Boerlijst (1990) have shown, by experimental manipulation of brood size at hatching, that the relationship

between fledging mass and post-fledging survival is causal. They thus demonstrated that fledging mass *per se* is a strongly fitness correlated parameter. It is, therefore, most likely that in our study the reduced offspring quality resulting from the effect of the ectoparasites on the nestlings will enhance mortality after fledging and further increase the disparity of fitness between parasite-free and infested broods. The effect of ectoparasites on nestlings may strongly influence population demography, behaviour and life-history traits of the host species and for the following reasons we suggest that the effect of parasites on their hosts should be incorporated in future studies.

## INFLUENCE OF ECTOPARASITES ON POPULATION BIOLOGY OF THE HOSTS

As pointed out by Møller (1989), natural cavities may host a variety of ectoparasites which survive to the following breeding season. In nestbox studies, however, these parasites have been eliminated by nest removal and the cleaning procedure applied by the researchers. As shown here, the ectoparasites increase offspring mortality and hereby reduce the fitness of the hosts, and may further influence immigration and emigration if habitats vary in ectoparasite load. Thereby, they may influence the parameters which are relevant to population demography and dynamics. Parasites may affect optimal territory size if the risk of infestation is lower in larger territories and, hence, reduce population densities.

The findings that, in great tits, the fledging mass (Minot 1981) and number of offspring (Dhondt 1977) are negatively correlated with blue tit (*Parus*

*caeruleus* L.) density are most interesting in conjunction with the finding of Harper, Marchant & Boddington (1992) that blue tits are by far the largest source of the hen flea. In this light, interspecific density-dependence of breeding success of great tits may find an explanation not only in the interspecific competition for food, but also in the increased load of detrimental ectoparasites in great tit nests due to high population densities of blue tits.

#### INFLUENCE ON BEHAVIOUR

It is shown here that the parasites influence body mass and size of fledglings. Garnett (1981) suggested that body size (tarsus) can affect dominance behaviour in great tits. It is thus possible that parasites influence the social status of the birds after fledging. Unlike many endoparasites where transmission of the parasite often requires an intermediate host, the ectoparasites can be transmitted directly by contact between individuals. It would therefore pay, even in the absence of heritable resistance to the parasites, for a female to choose a parasite-free male, or a male that can successfully avoid or eliminate parasites. Thus, ectoparasites could influence mate choice, mate fidelity and other behavioural variables.

Another important effect of parasites concerns a possible correlation between parasite load, begging behaviour and predation rates. As shown here, under a parasite load the chicks are in lower body condition than without parasites and this may increase competition among chicks for the food brought by the parents. As a result we expect the broods in infested nests to increase begging rates which in turn can attract more predators.

#### INFLUENCE ON LIFE-HISTORY TRAITS

One of the most intriguing evolutionary problems in the study of birds has been the question of the most productive clutch size (e.g. Lack 1966; Charnov & Krebs 1974; Perrins & Moss 1975; Nur 1986; Boyce & Perrins 1987; Pettifor *et al.* 1988; Price & Liou 1989; Cooke *et al.* 1990). Lack (1966) proposed that natural selection favours individuals laying the clutch size that produces the highest number of recruits into the future breeding population. For an understanding of this evolutionary question, and because of the ubiquity of ectoparasites, it may be important to evaluate the effect of ectoparasites on fitness-related reproductive traits, and in particular to understand to what extent parasites affect the quality of offspring differentially in large and small broods. If the latter is the case, ectoparasites may be an important selective force acting on clutch size. Our study shows that close to fledging the chicks in parasite-free nests of originally small broods are significantly and substantially heavier and in better condition than the ones in originally large broods,

but under a parasite load, this effect disappears (Figs 2 & 4). For infested nests, the fledglings from small broods at hatching are of the same body mass and of identical condition as fledglings from large broods at hatching. Therefore, if parasites are absent, fitness can potentially be gained by both number and quality of offspring, and therefore a trade-off is feasible, but under the presence of parasites, fitness can potentially be gained through quantity of offspring only and not through quality. If ectoparasites are common, we would therefore, counterintuitively, expect selection for larger clutches.

This finding that, in infested nests, the fledglings from small broods at hatching are of the same body mass and of identical condition as fledglings from large broods at hatching cannot be explained by the possibility that originally small broods are related to lower quality parents since, under the parasite-free condition, the fledglings from small broods are substantially heavier than the ones from large broods. It may be important to note, that the hen flea has a generation cycle just 2–3 days shorter than the time that a chick spends in the nest between hatching and fledging. Therefore, a dilution effect can operate over the largest part of the time that offspring spend inside the nest and, hence, during their growth. That is, the number of ectoparasites per chick will be smaller in large than in small broods. Our finding that under a parasite load the quantity only, but not the quality of fledglings can be increased, could therefore be explained by a lower parasite load per chick in large broods, which arises if total parasite number per brood is constant among brood sizes. This condition is fulfilled in our experiment since we added the same total number of parasites to small as to large broods. Indeed, no correlation was found in infested nests between the total number of fleas and brood size at hatching ( $r = -0.31$ ,  $P = 0.27$ ,  $n = 17$ ), but a significantly negative correlation was found between brood size at hatching and the number of fleas per hatchling ( $r = -0.51$ ,  $P = 0.035$ ,  $n = 17$ ). In 1990 no manipulation of the parasite load took place and we also found a negative correlation between brood size at hatching and the number of fleas per hatchling among natural broods ( $r = -0.59$ ,  $P = 0.005$ ,  $n = 21$ ). The advantage given by the parasite dilution effect could potentially select for larger clutch sizes. Indeed, we observed a larger clutch size in infested nests, which is, however, non-significant ( $P = 0.07$ ) under a one-tailed hypothesis formulated a posteriori.

A definite answer to the evolutionary question of whether haematophagous fleas select for bigger clutch size is only possible through simultaneous manipulation of clutch size and parasite load. Furthermore, the effect of fleas on future reproduction of the parents has also to be considered. This will depend on the direct effect of parasites on the body condition and survival of the parents, and also on indirect effects which will depend on the extent that

parents could potentially compensate for the effects of parasites by increasing the rate of food delivery to the brood, which in turn can affect the parental body condition.

### Acknowledgements

We thank the participants of the International Conference on Hole-nesting Birds, held in Sempach in October 1991, for their critical and stimulating discussion of our results. We thank two referees for their constructive comments. The study is supported by the Swiss National Science Foundation, grants 31-26606-89 and 31-27217-89 to H.R.

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Received 7 September 1992; revision received 2 December 1992