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Horizontal transmission and reproductive rates of hen fleas in great tit nests

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Summary

1. The transmission mode and reproductive rates of a parasite are usually associated with its virulence. In this study, two experiments were carried out to quantify horizontal transmission rates and reproductive dynamics of hen fleas infesting a population of great tits. Our results provide experimental data on certain factors affecting the population dynamics of an ectoparasite in a host population.

2. Immigration of adult hen fleas occurred in 72% (29 out of 40) of previously deparasitized great tit nests. The mean infestation intensity was 5·8 adult fleas per nest and did not vary seasonally. Adult hen flea distribution within the host population was aggregated and did not differ from a negative binomial distribution.

3. In nests experimentally infested with 40 adult fleas, two discrete flea cohorts were found at the end of the hosts' breeding attempts. The first cohort consisted of adult fleas, the second cohort was much larger and consisted of second and third instar larvae. No first instar larvae were observed in the second cohort. A small proportion of larvae was found in cocoons.

4. The day in the season and the daily mean temperatures during the birds' 'brooding period' (i.e. from the start of incubation until the last young fledged or died) were not significantly correlated with the number of fleas in the nests. These results suggest that climatic and seasonal factors do not have significant effects on flea reproduction.

5. The number of adult fleas and larvae was not significantly different between nests where all chicks died and nests where at least one young fledged. Host reproductive success affected the number and proportion of larvae in cocoons which was lower in nests of birds that failed compared with nests of birds that fledged young. The proportion of larvae in cocoons increased with the number of days in the 'brooding period' of the birds.

6. Among infested nests, the number of adult fleas and the total number of larvae were positively correlated with the fresh mass of the nests, suggesting that density-dependent mechanisms within nests affect flea numbers. Great tits appeared to increase the mass of their nests following experimental infestations with hen fleas.

7. In nests of birds that fledged at least one young, the number of adult fleas and larvae was not significantly correlated with measures of the hosts' breeding performance (chick mass and number of fledglings). These results suggest that flea reproductive success does not depend on the hosts' reproductive performance.

8. These results emphasize the need to study the effects of host responses on survival and reproductive rates of parasites. A knowledge of these effects is essential for the understanding of population dynamics, dispersal and life-history traits of the parasites.

Key-words: age cohort, *Ceratophyllus gallinae*, density dependence, host-response, nest mass, parasite reproduction, parasite transmission, *Parus major*, virulence.

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Introduction

Parasites are always found in intimate associations with their hosts from which they draw the resources needed for their growth and reproduction (Price 1980). As a result of these interactions, parasites commonly reduce the fitness of their hosts (e.g. reviews on ectoparasites: Møller, Allander & Dufva 1990; Lehman 1993). The virulence of a given parasite is usually considered as the reduction in the lifetime reproductive success of the host (Herre 1993) and results from the interaction between hosts and parasites in which numerous factors acting between and/or within hosts can be important (see Read 1994; Bull 1994 for reviews). Empirical studies commonly use the replication rates of pathogens as a measure of their virulence (Read 1994). It is expected that parasites maximize their fitness, commonly defined as the rate at which new hosts are infected (Anderson & May 1982; Ewald 1983). One way for parasites to increase their transmission rates to new hosts is to increase their reproductive success (Anderson & Gordon 1982). Theoretical analyses on the evolution of virulence have reached the general conclusions that in parasites: (i) there should be a trade-off between infectiousness and virulence; and (ii) increases in horizontal transmission (from host to host) should select for higher virulence. Vertically transmitted parasites (from parent to offspring) are expected to be less virulent for their host (Bull 1994; Read 1994). Empirical evidence in support of these predictions was recently provided in selection experiments involving phages infecting the bacteria *Escherichia coli* (Bull, Molineux & Rice 1991). Bull and collaborators showed that, as predicted, phage virulence can evolve in response to alternative modes of transmission. Further evidence was provided by a field study comparing the virulence of 11 species of parasitic nematodes and their specific fig wasp hosts (Herre 1993). It showed that an increases in the horizontal transmission of the nematodes is correlated with increases in their virulence. In a comparative study of bird ectoparasites, Clayton & Tompkins (1994) found that horizontally transmitted parasites were more virulent than vertically transmitted ones. In rock doves *Columba livia* (Gmelin), Clayton & Tompkins (1995) also found that vertically transmitted feather lice were less virulent than horizontally transmitted mites.

Thus, in order to understand the degree of parasite virulence in a host population, quantification of transmission rates and reproductive performance in association with their hosts' reproductive success are required (Herre 1993; Read 1994). Furthermore, quantification of the population dynamics of a parasite should enable the determination of the likely effects on certain life-history traits of the hosts (Lee & Clayton 1995; Richner & Heeb 1995). Although the impact of ectoparasites on their hosts have recently been studied for many systems (Møller *et al.* 1990; Lehmann 1993; Richner, Oppliger & Christe 1993; Clayton & Tompkins 1994), the reciprocal nature of host–parasite interactions suggests that it is also important to test the effects that host responses have on the survival and reproductive success of parasites (Lee & Clayton 1995).

The hen flea, *Ceratophyllus gallinae* (Schrank) is a haematophagous ectoparasite commonly found in nests of hole-nesting birds in the Western Palearctic where prevalences of 88–92% have been observed (Rothschild & Clay 1952; Humphries 1968; Harper, Marchant & Boddington 1992; Eeva, Lehikoinen & Nurmi 1994; Merilä & Allander 1995). The adult hen fleas feed on the blood of their hosts whilst the larvae are mostly detritivorous, feeding on organic material found inside the nests (Rothschild & Clay 1952; Marshall 1981). The hen flea is bound for most of its life cycle to the nest of its host, and with the exception of dispersal from old nests it spends little time on the hosts; only a few adult fleas leave the nest with the fledglings (Humphries 1968). At the end of the breeding attempts of the birds, nests often contain large numbers of adult fleas, larvae and cocoons (Harper *et al.* 1992; Eeva *et al.* 1994). Dispersal of fleas can take place all year round with a peak during the months of March and April, as shown on blackbirds *Turdus merula* (L) and starlings *Sturnus vulgaris* (L.) (Fowler, Cohen & Greenwood 1983; Peach, Fowler & Greenwood 1987). After spending the winter in the nest as cocoons, the emergence of imagos in spring is triggered by rising temperatures and by visiting birds (Humphries 1968; du Feu 1992). If an infested nest site is re-used by the birds, some of the emerging fleas will stay in the nest and start feeding on the host. If the infested nest sites are not used, fleas will start searching for a new host by waiting at the nest entrance or by moving away from the nest in the expectation of jumping onto a passing bird (Bates 1962; Humphries 1968; du Feu 1992). Although their reproduction is mostly synchronized with that of their hosts (Rothschild & Clay 1952; Humphries 1968), small numbers of active adult fleas, eggs, and larvae have been found all year round in the nests (Jurik 1974).

At present, the quantitative aspects of reproduction and immigration of the hen flea are known only from observational studies where the final number of fleas could have been affected by many factors. For example, it is not known to what degree the high prevalences observed are due to high rates of horizontal transmission and/or to the build up of flea populations within nests over various breeding attempts. Furthermore, the number of generations, or age cohorts, produced by the fleas over one breeding season has not yet been determined (cf. Harper *et al.* 1992).

Hen fleas reduce the breeding success of great tits *Parus major* (L.) by decreasing the quantity and quality of the young produced (Richner *et al.* 1993). Thus, great tits are expected to adopt responses that reduce

the impact of flea parasitism. For example, in winter great tits reduce their risk of flea infestation by choosing ectoparasite-free roosting sites (Christe, Oppliger & Richner 1994), in spring they avoid visiting infested boxes (du Feu 1992). If given a choice between parasite-free or infested boxes for breeding, great tits show a preferrence for parasite-free boxes and when they had to use infested nestboxes they delayed the start of egg laying (Oppliger, Richner & Christe 1994).

The aims of this experimental study were, first, to determine the intensity of immigration by adult hen fleas over one breeding season. Given that hen fleas are mobile and horizontally transmitted parasites, they are expected to infest a large proportion of hosts (high prevalence). The second aim of this study was to quantify hen flea reproduction in controlled infestations that were randomized over host phenotypes and territory qualities. It was of particular interest to determine whether seasonal variations in external temperature or factors associated with the hosts' breeding performance had an effect on flea numbers.

Methods

EXPERIMENTAL PROCEDURE

This study was carried out during the breeding season of 1994 in the 'Bremgartenwald', a forest near the city of Bern (46°57′N, 7°28′E), Switzerland. Nestboxes were put up in 1991 and have been used by great tits since the breeding season of 1992. The internal size of the boxes was 12·5 × 12·5 cm with a height of 21 cm from the bottom to the entrance hole (diameter of 30 mm). Hen fleas occurred naturally in 1992 in over 70% of nestboxes. The forest has little undergrowth and is mainly composed of beech and pine, interspersed by a few oaks and hornbeams.

Old nest material was removed from all the nestboxes before the birds started nest building. Material remaining attached to the box walls was scraped off with a knife and a hard brush. On the morning when the birds laid their second egg, all the nests were placed in a closed plastic bag to prevent loss of humidity. The nests were then heat-treated for 3 min using a microwave appliance fed by a portable 220-volt generator. After the heat treatment the nests were left to cool before randomly assigning them either to the 'infested' ($n = 40$) or 'parasite-free' ($n = 40$) groups. Nests in the 'infested' group were inoculated with 40 adult fleas placed inside the nestcup. For the inoculations, we used hen fleas collected in 1993 from naturally infested tit nests. A few (2–3) of these nests were placed simultaneously in a large aquarium and the adult fleas were then picked at random. The 'parasite-free' nests were kept free of fleas by repeating the heat treatments every 10 days from the start of incubation until the young birds fledged. This procedure ensured that all immigrating adult fleas were killed within a few days after they arrived in the nest, preventing the completion of a reproductive cycle and allowing the determination of flea immigration. There was no significant difference between infested and parasite-free nests in the host laying date ($F_{1,78} = 0{\cdot}12$, $P = 0{\cdot}73$), and clutch size ($F_{1,78} = 0{\cdot}73$, $P = 0{\cdot}40$).

ASSESSMENT OF FLEA NUMBERS

On the day that the last young in the brood fledged, all the nest material was collected and placed in a sealed plastic bag. If the breeding attempt failed, the nest material was collected on the day that the last chick in the brood died. Care was taken to count and recover all the cocoons attached to the nestbox walls. When collecting the nest material, its fresh mass was measured with a Sartorius balance to the nearest 0·1 g. The bags with the nests were then frozen at −18 °C and kept for later inspection. This ensured that all adult fleas, larvae and pupae present in the nest were killed on the day that their hosts became unavailable.

Cotton (1970) determined that, in the laboratory, hen flea development from egg to adult stage takes between 24 and 42 days depending on the external temperature and Harper *et al.* (1992) considered that flea development required 23 days. In our study, great tits completed their breeding attempts in 38·7 ± 0·3 (SE) days (from the start of egg laying to the fledging or dying of the last chick in the brood). Considering the time required for flea development and great tit reproduction, the number of adult fleas counted in infested nests at the end of the birds' breeding attempts should consist of some of the 40 adults initially inoculated, the first generation of adults produced and a few immigrants. We assumed that the number of fleas immigrating and emigrating from the nests is low compared to the number of fleas inoculated and should not have a significant effect on their final numbers (as shown below, this assumption was confirmed by the data from the group of nest boxes that was kept free of parasites).

The fleas were extracted from the nests by manually separating all the nest material over a wire mesh (5 mm wide). Half of the material going through the mesh was then thoroughly searched under a magnifying glass for all adult fleas, larvae and cocoons. We calculated the total larval production by summing the number of larvae and cocoons in the nests. The cocoons that remained attached to the nest material and that did not pass through the mesh were also counted under a magnifying glass. The proportion of larvae in cocoons in relation to the total number of larvae produced was determined as: cocoons/(larvae + cocoons); this proportion gives an indication of the stage of larval development. During the inspection of the nest material, pupae of parasitic flies (genus *Protocalliphora*) were also counted. The number of *Protocalliphora* spp. pupae in parasite-free nests was not significantly different from the numbers in infested nests (parasite-free: 5·6 ± 1·4; infested: 10·4 ± 2·9

(mean ± SE); Mann–Whitney *U*-test, $Z = 682$; $P = 0{\cdot}23$). Other insects counted in the nests were a few small undetermined dipteran larvae and detritivorous rove beetles (family *Staphylinidae*). There was no significant difference in beetle numbers between the two groups of nests (Mann–Whitney *U*-test, $Z = 663$; $P = 0{\cdot}19$). Since the presence of beetles and flies was not experimentally manipulated, they are not included in the analyses.

BREEDING PERFORMANCE OF THE BIRDS

For each breeding pair we measured the following variables: the date of laying the first egg, the clutch size, the date when incubation started, the date when the first egg hatched, the date on which the last young fledged and the number of fledglings. When the chicks were 14 days old, 20 μl of blood from the brachial vein of three chicks in each brood (the lightest, the heaviest and an intermediate one) were collected for the determination of the mean haematocrit level of the brood. On the same day, the mass of each chick in the brood was measured with a Sartorius balance to the nearest 0·1 g and the mean value for the brood was used in the analyses.

In this study we defined the length of the 'brooding period' for each breeding pair as the number of days from the start of incubation until the day the last young of the brood either died or fledged from the nest. Our 'brooding period' corresponds to the 'warm period' used by Harper *et al.* (1992), and describes the period when a nest is kept continuously warm either by the incubating adult or the presence of nestlings.

DAILY TEMPERATURES, STATISTICAL ANALYSES

Daily mean temperatures were obtained from the Swiss Meteorological Institute at the station in Liebefeld near Bern. In 1994, the birds' breeding season started on 13 April when the first egg was laid and ended on 13 June when the last young fledged. The mean daily temperature for that period was $12 \pm 3{\cdot}1$ °C (SD) with a mean daily deviation from the last 10 years' mean of $+0{\cdot}7 \pm 2{\cdot}9$ °C (SD). The mean daily temperature for the 'brooding period' of the birds was estimated as the sum of the mean daily temperatures during the 'brooding period' divided by the number of days in this period. Analyses were performed using the Systat statistical package (Wilkinson 1989). The frequency distribution of adult fleas in sterilized nests was compared to the negative binomial distribution (Anderson 1978; Anderson & Gordon 1982; Poulin & Vickery 1993). Distributions of the flea counts data were normalized by square-root transformations. Parametric analyses were carried out on the normalized data; non-parametric tests were used whenever transformations did not normalize the data. When multiple correlations on non-independent variables were performed, the significance level was adjusted for the number of statistical tests by means of the sequential Bonferroni technique (Rice 1989). All tests were two-tailed.

Results

FLEA IMMIGRATION IN PARASITE-FREE NESTS

Over one breeding season, adult fleas immigrated into 72% of cleaned nests (29 out of 40 nests). Most nests contained between 0 and 5 fleas and the maximum number of fleas counted in one nest was 30 (Table 1). The distribution of immigrant fleas among hosts was aggregated and did not differ significantly from a negative binomial distribution ($\chi^2 = 1{\cdot}16$, d.f. = 2, $P = 0{\cdot}56$; see Fig. 1). The time interval between heat treatments allowed some of the immigrating fleas to produce a small number of larvae (Table 1). However, no cocoons were found in these nests (Table 1), demonstrating that the heat treatments were successful in preventing the completion of a flea reproductive cycle. There was no significant correlation between the date when the birds started breeding and

Table 1. Flea numbers in parasite-free and experimentally infested nests. Mean values (SE)

Treatment	Parasite-free nests	Infested nests
Adult fleas	5·8 (1·0)	142·6 (13·2)
Range	0–30	18–328
Flea larvae	3·1 (1·3)	2180 (204)
Range	0–40	0–6354
Flea cocoons	0	260 (40)
Range	0	0–824
n	40	40

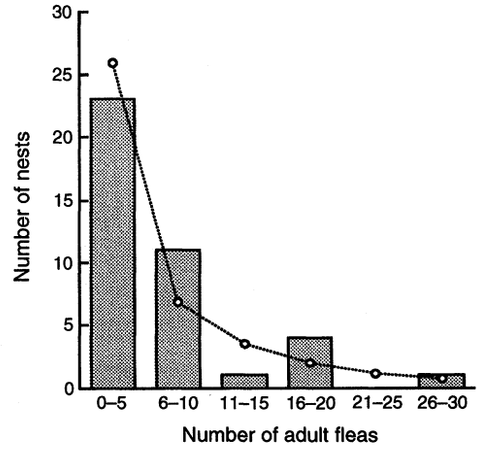

Fig. 1. Frequency distribution of adult hen fleas immigrating into parasite-free nests of great tits over one breeding season. The columns represent the observed frequencies (mean = 5·8, $S^2 = 44{\cdot}0$, $n = 40$ nests). Circles show the expected frequencies from the negative binomial distribution for a mean abundance of 5·8 fleas and an aggregation coefficient $k = 0{\cdot}5$.

the number of adult fleas immigrating in the nests ($r_s = -0{\cdot}14$, $P = 0{\cdot}20$, $n = 40$).

FLEA REPRODUCTION IN EXPERIMENTALLY INFESTED NESTS

Age structure of the flea populations

In our experiment, the inoculated fleas spent on average 37·7 ± 0·6 (SE) days in the nests ($n = 40$), of which 31·7 ± 0·5 (SE) days consisted of the birds' 'brooding period' (see methods for a definition). Over that time, the fleas produced two discrete age cohorts, the first one consisting of adults and the second one of larvae and cocoons. The adult flea population consisted of some of the experimentally inoculated adult fleas, the first generation of adults produced, plus a few immigrants. By excluding 40 fleas (number inoculated) from the total number of adults, it can be estimated that the inoculated fleas produced an average of 2·5 adults (range: 0–8; Table 1). All the counted larvae in the second age cohort were large second and third instars. Dissection of more than 300 cocoons showed that they contained mostly coiled third instar larvae and a few pupae (less than 5%). None of the dissected cocoons contained sclerotized adults ready to emerge. The total number of fleas varied between nests and each age cohort had a distinct and discrete, unimodal distribution (Fig. 2). It can be estimated that the mean number of larvae produced by each of the 40 inoculated adult fleas was 54·5 (range: 0–159; Table 1). Given that the birds may have killed some of the inoculated fleas, the mean number of adults and larvae produced by the surviving fleas could be somewhat higher than our estimates. Although we did not determine how many of the inoculated fleas did reproduce, our estimates indicate the order of magnitude expected for the increases in flea numbers. The number of adult fleas, larvae and cocoons found in the nests were all positively correlated with each other (adults × larvae: $r = 0{\cdot}66$, $P < 0{\cdot}01$; larvae × cocoons: $r = 0{\cdot}57$, $P < 0{\cdot}01$; adults × cocoons: $R = 0{\cdot}46$, $P < 0{\cdot}01$, $n = 40$; Sequential Bonferroni adjusted). These correlations show that, within a given nest, a greater number of adult fleas produced in the first cohort will be associated with higher numbers of larvae and cocoons in the second cohort.

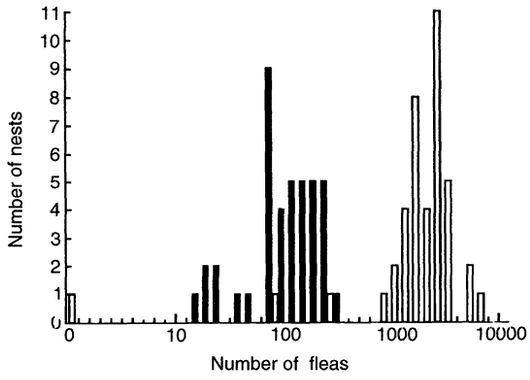

Fig. 2. Frequency distributions of hen fleas in infested great tit nests at the end of the hosts' breeding attempts. Black bars show the frequency distribution of adult fleas. White bars show the frequency distribution of flea larvae and cocoons (pooled data). Log scale rounded to the nearest 0·1.

FACTORS AFFECTING FLEA POPULATION SIZES

Laying dates and mean daily temperatures

The number of adult fleas, larvae or cocoons were not significantly correlated with the laying date of the birds (adult fleas: $r = -0{\cdot}24$, $P > 0{\cdot}10$; larvae: $r = -0{\cdot}28$, $P > 0{\cdot}10$; cocoons: $r = -0{\cdot}28$, $P > 0{\cdot}10$; $n = 40$; Seq. Bonferroni). The mean daily temperatures during the 'brooding period' of the birds was positively correlated with the date when they started egg laying ($r = 0{\cdot}68$, $P < 0{\cdot}0001$, $n = 40$). The number of adult fleas, larvae or cocoons were not significantly correlated with the mean daily temperature during the birds' 'brooding period' (adult fleas: $r = -0{\cdot}33$, $P > 0{\cdot}10$; larvae: $r = -0{\cdot}24$, $P > 0{\cdot}10$; cocoons: $r = -0{\cdot}20$, $P > 0{\cdot}10$; $n = 40$; Seq. Bonferroni).

Host breeding success

The number of adult fleas and larvae did not differ between nests of birds that successfully fledged at least one young and nests of birds which failed during their breeding attempts (adult fleas: $F_{1,38} = 0{\cdot}29$, $P = 0{\cdot}59$; larvae: $F_{1,38} = 0{\cdot}014$, $P = 0{\cdot}90$). In contrast, the number of larvae in cocoons was higher in nests of successful birds than in nests of failed birds (successful: 302 ± 48 (SE), $n = 32$; failed: 92 ± 13 (SE), $n = 8$; Mann–Whitney U-test, $Z = 65$, $P = 0{\cdot}03$). The proportion of larvae in cocoons was also higher in nests of successful birds (successful: 0·116 ± 0·018 (SE); failed: 0·045 ± 0·007 (SE); Mann–Whitney U-test, $Z = 61$, $P = 0{\cdot}028$). The differences in the numbers and proportions of larvae in cocoons were associated with the number of days in the 'brooding period' of the birds: fleas developing in nests of successful hosts had significantly more days with birds in the nest than fleas in nests of birds that failed (successful: 33·0 ± 0·4 (SE) days; failed: 26·5 ± 0·5 (SE) days; Mann–Whitney U-test, $Z = 1$, $P < 0{\cdot}0001$). The proportion of larvae in cocoons was positively correlated with the length of the 'brooding period' (see Fig. 3). In contrast, the number of adult fleas, larvae and cocoons in the nests were not significantly correlated with the length of the 'brooding period' (cocoons: $r = 0{\cdot}36$, $P > 0{\cdot}05$; adults: $r = -0{\cdot}012$, $P > 0{\cdot}05$; larvae: $r = -0{\cdot}04$, $P > 0{\cdot}05$, $n = 40$; Seq. Bonferroni).

In nests of successful birds, the number of adult fleas and the total number of flea larvae (larvae + cocoons) was not correlated with the mean chick mass at 14 days of age (adults: $r = 0{\cdot}22$, $P > 0{\cdot}60$; total larvae: $r = 0{\cdot}23$, $P > 0{\cdot}60$), the mean haematocrit of the brood (adults: $r = -0{\cdot}04$, $P > 0{\cdot}60$; total larvae:

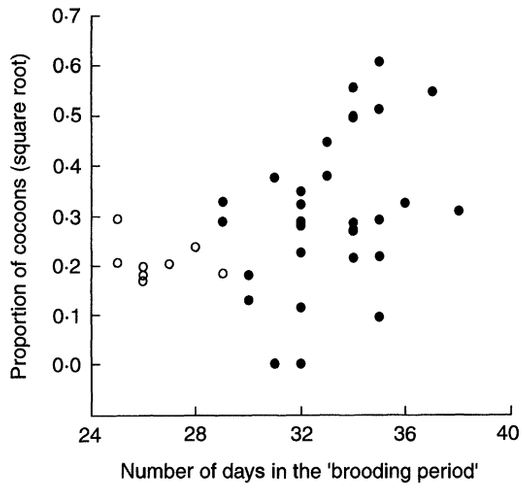

Fig. 3. Relationship between the proportion of larvae in cocoons in infested nests and the number of days in the birds' 'brooding period' (see Methods). Filled circles represent nests of birds which fledged at least one young; open circles represent nests of birds which failed during their breeding attempt. ($r = 0{\cdot}42$, $P = 0{\cdot}007$, $n = 40$).

$r = -0{\cdot}08$, $P > 0{\cdot}60$) or with the number of young fledged by the birds (adults: $r = -0{\cdot}13$, $P > 0{\cdot}60$; total larvae: $r = 0{\cdot}11$, $P > 0{\cdot}60$; $n = 40$; Seq. Bonferroni). In parasite-free nests, the number of young that fledged was positively correlated with the nest mass ($r_s = 0{\cdot}313$, $P = 0{\cdot}05$, $n = 40$). In contrast, the correlation between the number of young fledged and nest mass was not significant in the infested nests ($r_s = 0{\cdot}144$, $P > 0{\cdot}20$, $n = 40$).

Nest mass and flea numbers

There was a significant difference in the fresh mass of the nests between the experimentally infested and the parasite-free nests (see Fig. 4). The fresh mass of the nests decreased over the season ($F_{1,78} = 5{\cdot}07$, $P = 0{\cdot}03$) but there was no significant interaction between this seasonal effect and the experimental treatment ($F_{1,76} = 0{\cdot}52$, $P = 0{\cdot}47$).

In experimentally infested nests, the number of adult fleas and larvae were both positively correlated with the nest mass (see Fig. 5). In contrast, the number of larvae in cocoons and their proportion were not significantly correlated with the nest mass (cocoons: $r = 0{\cdot}25$, $P > 0{\cdot}20$; proportion of cocoons: $r = -0{\cdot}001$, $P > 0{\cdot}20$; Seq. Bonferroni).

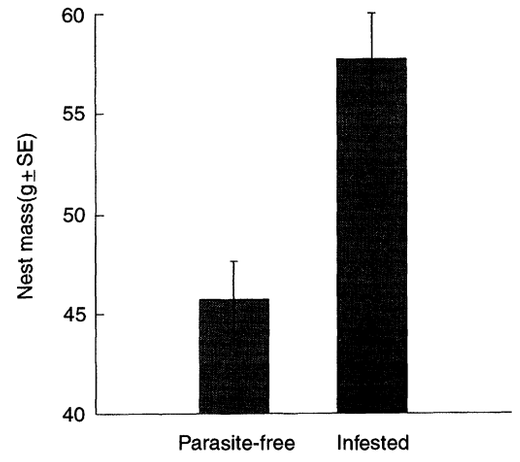

Fig. 4. Mean fresh mass of parasite-free and flea-infested nests. ($F_{1,78} = 13{\cdot}06$, $P = 0{\cdot}001$). Bars denote SE.

Discussion

HORIZONTAL TRANSMISSION OF HEN FLEAS

The first aim of this study was to determine the intensity and prevalence of hen flea infestation through horizontal transmission. Our results show that the distribution of fleas was aggregated among hosts and that 72% of cleaned nests are infested by immigrating fleas over one breeding season. Such high prevalence may not be surprising for a mobile and horizontally transmitted ectoparasite. Anderson & Gordon (1982) suggested that aggregated dispersion of parasites among a host population is due to stochastic factors

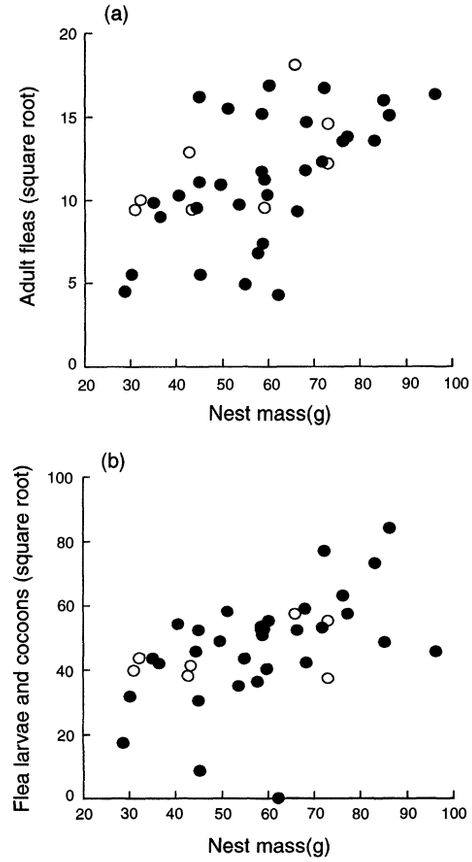

Fig. 5. Relationship between the fresh nest mass and hen flea numbers in infested nests. (a) adult fleas, $r = 0{\cdot}56$, $P < 0{\cdot}002$; (b) larvae and cocoons (pooled data), $r = 0{\cdot}51$, $P = 0{\cdot}002$, $n = 40$; Seq. Bonferroni. Filled circles represent nests of birds which fledged at least one young; open circles represent nests of birds which failed during their breeding attempt.

associated with physical characteristics of the environment, differences in host exposure to parasites, differences in host susceptibility to infection or parasite defence. Previous studies have shown that great tits avoid roosting and nesting in nestboxes containing fleas (Christe *et al.* 1994; Oppliger *et al.* 1994). Since fitness of fleas is likely to depend strongly on dispersal and infestation of new hosts, avoidance of infested nest-sites by potential hosts could influence flea dispersal and population dynamics. The ecological and demographic factors of a host population which influence the hen flea's decision to disperse from a nest have not yet been determined.

In this study, flea immigration occurred between the start of nest building and the end of the hosts' breeding attempt. The mean intensity of flea infestation was rather low and we did not detect any seasonal variation in the number of fleas immigrating into nests. It is likely that most flea immigration coincides with the peak in flea dispersal taking place in spring (Bates 1962; Fowler *et al.* 1983; Peach *et al.* 1987). Harper *et al.* (1992) found a mean infestation of 9·8 fleas in 20 non-experimental great and blue tit nests containing eggs that did not hatch. This result suggests that many fleas immigrate into the nest before the host has completed incubation of the eggs. The best strategy from the fleas' point of view is an early immigration into a nest, since it allows them to produce a new generation of adults before the nestlings fledge. Furthermore, an early start in breeding might allow these fleas to produce larvae that are able to outcompete younger larvae (see below). The higher prevalences described in observational studies of great tit populations could have been due to greater flea numbers dispersing from old nests in natural cavities or to the emergence of some fleas from cocoons already present in the nestboxes (cf. Harper *et al.* 1992; Eeva *et al.* 1994; Mappes, Mappes & Kotiaho 1994).

HEN FLEA POPULATION DYNAMICS

Overall flea reproduction in great tit nests

The second aim of this study was to quantify flea reproduction through controlled, randomized infestations. The 40 adult fleas inoculated in the nests produced two discrete age cohorts over one breeding attempt of their hosts. The mean number of adults observed in the first cohort was assessed as being 2·5 times greater than the initial number of fleas added and the mean number of larvae in the second cohort was measured as being 54·5 times greater. Harper *et al.* (1992) found a mean of 9·8 adult fleas infesting great and blue tit nests before the start of incubation. If each of the fleas in Harpers' *et al.* study produces a similar number of larvae as in our study (54·5 larvae), we would expect to find a mean of 534 adult fleas at the end of the hosts' breeding attempts. This value lies between the mean numbers of adult fleas (368 and 816) found by Harper *et al.* (1992) for naturally infested nests in two great tit populations in Scotland. Our ability to predict a mean number of adult fleas close to the one found by Harper *et al.* (1992) suggests that hen fleas have similar rates of reproduction in Switzerland and Scotland. Furthermore, this comparison also suggests that hen flea emigration from the nests during, or shortly after the breeding attempts of their hosts is not likely to have a significant effect on final flea numbers (cf. Harper *et al.* 1992). Our results suggest that final flea numbers in nests can mostly be attributed to the reproduction of early immigrants.

ENVIRONMENTAL EFFECTS ON FLEA NUMBERS

Laboratory experiments have shown that higher temperatures reduce the time required for flea development (Cotton 1970). In this study, the mean daily temperature during the birds' 'brooding period' was positively correlated with the date when the birds started breeding. If external temperatures or other seasonal factors constitute an important source of variation in flea reproduction and development, intra-seasonal variation in flea numbers and/or the instars present at the end of the breeding attempts would be expected. The absence of significant correlations between number of adult fleas, larvae or the proportion of larvae in cocoons with the season suggest that, in our study, seasonal effects had little influence on flea population dynamics. This suggestion is supported by previous observational studies (Harper *et al.* 1992; Eeva *et al.* 1994) where no significant correlations where found between the time in the season when hosts started breeding and final flea numbers in the nest.

FLEA REPRODUCTION AND HOST BREEDING PERFORMANCE

The number of adult fleas and larvae in nests of great tits that failed to fledge any young were not significantly different from the numbers of fleas in nests of birds that fledged at least one young. In nests of birds which successfully fledged young, none of the parameters associated with host breeding performance (mean chick mass, number of fledglings) were significantly correlated with flea numbers. These results suggest that flea reproduction does not depend on the reproductive performance of the host. Our results support a previous suggestion (Richner & Heeb 1995) that reproduction of ectoparasites with long life-cycles (such as the hen flea) are not limited by the resources provided by the brood of their host. The absence of a significant correlation between the parameters associated with the hosts' breeding performance and the number of fleas produced could result if the birds are able to compensate for the negative effects of the fleas by increasing their own energy expenditure when feeding the young (Johnson & Albrecht 1993). A recent study has shown that male

great tits increase their feeding frequency of the young when the nests were experimentally infested with hen fleas (Christe *et al.*, in press).

The proportion of larvae in cocoons was higher in nests of successful birds than in those that failed to fledge any young. Thus, the stage in development of the flea larvae was correlated with the breeding performance of the hosts since the difference is associated with longer 'brooding periods' in nests of successful birds. Fleas developing in nests of successful birds had more days in nests with brooding birds and a higher proportion of larvae reached the cocoon stage before the hosts left the nest. The absence of correlation between the length of the 'brooding period' and the number of fleas in this study contrasts with the finding of an interspecific comparison (Harper *et al.* 1992) where a positive correlation was found between the length of the 'brooding period' of five species of birds and the number of fleas in the nests after the birds had fledged. Such a correlation, however, could also be due to ecological and life-history differences of the various host species and not to the length of the brooding period *per se*. Different host species are also expected to have evolved different strategies against parasites.

PRESENCE OF DISCRETE AGE COHORTS IN THE FLEA POPULATIONS

Female hen fleas reproduce continuously, laying 2–5 eggs daily throughout their adult life (Marshall 1981). Our laboratory observations have shown that gravid fleas left in glass tubes overnight are able to lay 4 or 5 eggs without further blood feeding (P. Heeb, unpublished data). Given the high and continuous potential for egg production by female hen fleas, a large number of larvae in all developmental stages are expected to be present in the nests at the end of the birds' breeding attempts. The positive correlations found here between nest mass and flea numbers and the presence of two discrete flea age cohorts within the nests are therefore intriguing. The presence of discrete age cohorts within flea populations could be explained if cannibalism and/or competition among flea larvae can affect the size and age structure of the larval populations (see below). As a result of cannibalism, one age class may be partly consumed by a different age cohort (Elgar & Crespi 1992b) and, as it has been shown in polyembryonic parasitoid wasps, siblicide can lead to biased sex ratios (Grbic, Ode & Strand 1992). Alternatively, if the competitive ability of the larvae is positively correlated with body size, cohorts of large larvae might reduce the resources available to younger and smaller larvae, thus lowering their survival. Such an effect has been shown in *Drosophila* larvae (Krebs & Barker 1995).

When the bird host starts incubating its eggs, nest temperatures increase and accelerate flea development (Cotton 1970). Flea eggs and larvae present in the nest before the start of host incubation will therefore develop synchronously and result in a discrete age cohort. Small larval instars developing from later laid eggs would then suffer from cannibalism and/or competition by bigger and older cohorts and thus disappear from the larval population. We then expect that flea larvae from the second cohort will be able to start developing only once they are not in competition with larvae from the first cohort. This suggests that flea competition and/or cannibalism within nests might be one of the most important factors affecting flea population sizes. From a flea point of view, the adult birds, the growing chicks and the nest material need to be considered as forming one single host in which the fleas reproduce. It has been suggested that competition between parasites within a host can be an important selective mechanim for the evolution of parasite virulence (Bull 1994). Herre (1993) argued that parasitic nematodes of fig wasps which show greater horizontal transmission also experience greater within-host competition due to increased mixing of unrelated parasites on a single host. He suggests that competition among different parasite genotypes within individual hosts is the critical factor promoting the evolution of higher virulence. Thus, variations in the competitive ability among fleas within a nest could be a more important fitness determinant than their efficiency in exploiting the hosts. Future studies should thus determine whether the presence of fleas of different genotypes and/or different densities within a nest leads to higher levels of competition affecting their population structure.

NEST MASS VARIATION AND FLEA NUMBERS

As pointed out by Mertens (1977a,b), nest mass variation in great tit populations can play a role in temperature regulation within the nest. In this study, we observed a seasonal decrease in nest mass independently of whether the nests were infested by fleas or not. Lighter and less insulating nests may be built as external temperatures increase over the breeding season. Alternatively, the seasonal decreases in nest mass could be associated with differences in bird phenotypes (Sæther 1990; Lombardo 1994) or territory quality (Soler *et al.* 1995).

Interestingly, great tits experimentally infested with hen fleas had nests with heavier fresh mass at the end of their breeding attempts than great tits with parasite-free nests. Our results also showed that in experimentally infested nests, the number of adult fleas and larvae were positively correlated with the nest mass. Positive correlations between nest mass and adult flea numbers in great tits have also been found in naturally infested nests in Finland (Eeva *et al.* 1994) but not in Scotland (Harper *et al.* 1992). At least seven, not mutually exclusive, hypotheses would predict a correlation between nest mass and flea numbers, and/or changes in nest mass due to ectoparasitism. The first

hypothesis derives from our experimental design, the second and the third are mainly concerned with aspects of flea biology whilst the final four concern aspects of the great tit–hen flea interactions.

1. First, nest mass differences in this study could have resulted from our experimental treatments since nests in the parasite-free group received three more heat treaments than the infested nests. Although during the heat treatments we took care to prevent loss of humidity, we cannot exclude the possibility that the heat treatments modified the water retention properties of the nests. However, another sample of nests from our great tit population showed that the dry mass of nests in both parasite-free and flea-infested nests was strongly, and positively, correlated with their fresh mass (parasite-free: $r = 0{\cdot}97$, $P < 0{\cdot}0001$, $n = 54$; infested: $r = 0{\cdot}928$, $P < 0{\cdot}0001$, $n = 15$). Positive correlations were also found by Eeva in naturally infested nests of great tits in Finland (3 years' data, all P-values $< 0{\cdot}0001$; T. Eeva, unpublished data). These correlations suggest that in our study, flea-infested nests were heavier due to the presence of more nest material and not only due to higher humidity levels. Humidity levels in the nests seem to affect flea numbers since Eeva and collaborators found that, in naturally infested great tit nests, the number of adult hen fleas and larvae was negatively correlated with the water content of the nests. In two years, the water content of the nests was not significantly correlated with their dry mass and, in a third year, there was a negative correlation between the dry mass and the water content of a nest (T. Eeva, unpublished data).

2. A second hypothesis suggest the existence of density-dependent mechanisms acting on flea numbers in infested nests (see above). Cannibalism is particularly common in insects and is generally density-dependent (see Polis 1981; Elgar & Crespi 1992a). Cannibalism has been reported for flea larvae of the genus *Ceratophyllus* and *Xenopsylla* (Reitblat & Belokopytova 1974; cited in Marshall 1981; p. 277). If cannibalism between hen flea larvae is density-dependent, heavier nests with more nest material could provide more space for a greater number of larvae thus reducing their encounter rates. Alternatively, density-dependent competition between flea larvae could occur if the availability of more nest material in heavier nests provides greater resources for the fleas, enabling a larger number of them to reproduce and develop (Pinkowski 1977). This hypothesis predicts a positive correlation between nest mass and flea numbers. Hosts are expected to reduce the mass of their nests if this leads to a reduction in flea numbers.

3. A third hypothesis proposes that nest mass variations are associated with differences in host phenotype (Lombardo 1994; Soler *et al.* 1995). Under this hypothesis, the greater numbers of fleas found in heavier nests could result from the physical conditions present in the nest. For example, heavier nests might provide a more suitable microhabitat for the survival and reproduction of the fleas (in terms of nest humidity or temperature) and/or larger nests may also provide more food resources for the detritivorous flea larvae (Marshall 1981). If nest size is positively correlated with the birds' quality, as it has been proposed for magpies *Pica pica* (L) (Soler *et al.* 1995), great tits with heavier nests might be able to withstand higher flea loads without suffering further reductions in their breeding performance. In this study we found a positive and significant correlation between the mass of parasite-free nests and the number of chicks fledged. This correlation was not significant in infested nests suggesting that flea infestation influenced the nest-building behaviour of the great tits. This hypothesis predicts a positive correlation between nest mass and flea numbers. We expect that an adaptive response to the presence of fleas from the hosts would be to reduce the mass of their nests. Birds of different phenotypic quality are expected to differ in the nest mass changes.

4. A fourth hypothesis (O'Connor 1984; p. 205) proposes that birds with smaller and lighter nests are able to clean them more thoroughly, thus eliminating most ectoparasites. In our study, birds which built light nests could also have been better in their ability to kill fleas through grooming behaviour (cf. Clayton 1991; Hart 1994). However, if large nests provide a more efficient thermal insulation, birds might be obliged to trade-off the benefits of low flea numbers in small nests with the benefits from an efficient thermal insulation in large nests (see below). Each pair of birds is expected to build a nest of a given mass according to their parasite resistance ability. This hypothesis predicts a positive correlation between nest mass and flea numbers. We expect that the birds should respond to flea infestation by decreasing the mass of the nest.

5. A fifth hypothesis proposes that fleas are able to manipulate their great tit hosts into building heavier nests. Host manipulations have been suggested for many internal parasites of intermediate hosts (e.g. Poulin, Brodeur & Moore 1994; Poulin 1994). The greater number of adults and larvae produced by fleas in heavier nests suggest that they could benefit from an increase in nest mass. This hypothesis holds that as a result of parasite manipulation, great tits increase the mass of their nest when infested by fleas.

6. The sixth hypothesis suggests that increases in nest mass could be part of an adaptive response of the hosts to the presence of fleas. The observed correlations between flea numbers and nest mass would then be a fortuitous effect of the change in host behaviour (Poulin *et al.* 1994; Poulin 1994). It has been proposed that green plant material or feathers brought in the nests by some bird species reduces the number of ectoparasites (Wimberger 1984; Winkler 1993). Starling nests provisioned with such green material had lower mite loads at the end of the breeding attempts than nests where this material had been removed (Clark & Mason 1985, 1988). Although blue tits, *Parus caeruleus* (L.), are

known to bring green nesting material into their nests (Cowie & Hinsley 1988; Banbura *et al.* 1995) no such behaviour has been described for great tits (Perrins 1979; Gosler 1993). In this study, the difference in nest mass between infested and parasite-free nests appeared to be due to more of the same nest material being brought into the nest (i.e. moss, dried pine needles, hair, wool) rather than from a change in the type of material used (M. Kölliker, personal observation). If the material brought by the birds in the nest reduces parasitic loads, we expect a negative correlation between nest mass and flea numbers. This hypothesis also holds that when infested by fleas great tits build heavier nests.

7. The seventh hypothesis suggests that great tits would increase the mass of their nests in order to increase thermal insulation. Since greater nest masses are positively correlated with flea numbers, the birds might have to trade-off the benefits obtained through a better nest insulation with the costs due to higher flea numbers. Hypothesis 7 holds that great tits with infested nests should build larger nests that tits of uninfested nests if the benefits of an additional thermal insulation are higher for the weakened parasitized chicks than for non-parasitized ones.

Of all the hypotheses mentioned above, only the manipulation (5) and the thermal insulation hypotheses (7) are supported by our data showing both an increase in nest mass when nests were infested by fleas and positive correlations between nest mass and flea numbers. The hosts' ability to eliminate parasites or to compensate for their effects and the thermal insulation properties of the nests are likely to regulate the changes in nest mass. Clearly, further experimental studies are required to determine which of these two hypotheses explain variations in flea reproductive rates in relation to host responses.

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