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Dynamics of Hen Flea *Ceratophyllus gallinae* Subpopulations in Blue Tit Nests

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The hen flea is a common parasite in bird nests, in particular, in tit species, and imposes considerable fitness costs for the host. These costs are expected to lead to selection for increased host defense, which in turn should select for better-adapted parasites. Our understanding of the coevolution of this host–parasite system is currently limited by the insufficient knowledge of both the timing of flea generations and their reproductive behavior within the nesting period of their hosts. In the present study we (1) followed the demography of experimental flea subpopulations during the host's breeding cycle, (2) assessed the importance of time–temperature effects in the nest by recording temperatures within the nest material, and (3) investigated the influence of variation in host timing and duration of the breeding period on flea development. We found the following. (1) Fleas completed either one or two generations within the birds' nesting cycle, leading to two well-defined periods of cocoon formation. (2) Within-nest temperatures during the warm period of the host breeding cycle—i.e., the incubation and nestling periods—depended on both outdoor temperatures and heat production from the breeding birds. Day-degree availability, a measure of physiological time, during the host incubation was significantly explained by the duration of incubation period and its timing in the season. Similarly, day-degrees during the warmer nestling period were significantly explained by its duration and its timing in the season. (3) The number of flea larvae found in the nests correlated with the host's timing and duration of the warm period available for their development; this was not the case, however, for the number of adult fleas. These results underline the importance of time–temperature effects as determinants of flea demography within the nests. The life-cycle and time–temperature effects are discussed in the light of potential host selection on parasite behavior and life histories.

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INTRODUCTION

The hen flea *Ceratophyllus gallinae* (Schrank) is one of the most common ectoparasite of European birds (Nordberg, 1936). It has been recorded in the nests of 72 wild bird species (Tripet and Richner, 1997a) and regularly invades poultry houses (Titchener, 1983). Blue tits *Parus caeruleus* and great tits *P. major* are the main hosts (Rothschild and Clay, 1952; Tripet and Richner, 1997a), with prevalences of infestations often reaching 90 to 100% of the nests (Nordberg, 1936; Ash, 1952; Harper *et al.*, 1992).

A number of recent studies have focused on the fitness costs that these parasites impose on their tit hosts and on the hosts' responses to flea infestation. These experiments have shown that *C. gallinae* can adversely affect the growth and survival of tit nestlings (Richner *et al.*, 1993) and that adult tits increase their current reproductive effort in response to infestation, probably in an attempt to compensate for the effect of fleas on nestlings (Perrin *et al.*, 1996; Christe *et al.*, 1996a; Tripet and Richner, 1997b). Parasite costs on host fitness are expected to select for increased host defenses, which in turn should select for better-adapted parasites, leading to an evolutionary arms race between the two (Dawkins and Krebs, 1979). Our present understanding of the interactions between fleas and tits and their potential coevolution, however, is limited by our knowledge of the ecology and population dynamics of fleas within the breeding period of their hosts. Difficulties inherent to sampling flea subpopulations in nests without causing disturbances to the breeding host may account for the fact that most of the information on flea demography available today has been inferred from rearing experiments in the laboratory and by analysis of nest contents after the birds' breeding period. As a result, *C. gallinae*'s life cycle is not fully understood and speculations are still going on concerning the number and time of appearance of flea generations during the host breeding period (Rothschild and Clay, 1952; Harper *et al.*, 1992; Eeva *et al.*, 1994). Another problem arises because of the overdispersed patterns of flea number per nests (Heeb *et al.*, 1996; Tripet, unpublished data). Aggregated distributions in parasite populations are considered the result of heterogeneity in host exposure and resistance (Anderson and Gordon, 1982; Hudson and Dobson, 1997). This suggests that inferences from correlational studies are limited because the population demography of fleas may be tied with environmental qualities of the breeding site or phenotypic qualities of the host.

The aim of the present study was therefore to investigate the demography of *Ceratophyllus gallinae* subpopulations in a random sample of experimentally

infested blue tit nests. Fleas, like all ectotherm organisms, require a certain combination of time and temperature, referred to as "physiological time," to complete their development (Begon *et al.*, 1990). We therefore also recorded the number of day-degrees—i.e., the product of time and temperature—available for flea development in each nest. This allowed us to assess the importance of host timing and duration of the breeding period in relation to flea development. Variation in these host behavioral traits are likely to correlate with variation in flea demography because of time–temperature effects. These data are therefore important for our understanding of host selection on parasite behavior and life-history traits and the evolution of complex host behavioral defenses.

STUDY SPECIES

C. gallinae spends little time on the host itself but rather settles in its nest (Marshall, 1981; Lehane, 1991). It breeds during the bird nesting period when the host and its young are available for regular blood meals. The larvae develop in the nest material and feed on detritus and undigested blood excreted by the parents (Marshall, 1981; Lehane, 1991). Elevated temperatures speed up flea development as shown by laboratory experiments (Cotton, 1970). It has been suggested that adult fleas produce a new adult generation during one reproductive cycle of the host, but whether this generation could lay eggs and produce larvae before the birds leave the nest is still subject to controversy (Rothschild and Clay, 1952; Harper *et al.*, 1992). Adult fleas have been observed leaving the nest shortly after fledging. Some are carried away on the nestlings themselves (Humphries, 1968; personal observation). The flea larvae remaining in the deserted nests complete their larval development, spin cocoons, pupate, and molt to the adult stage. Most of the imagos remain quiescent in the cocoons until the next spring (Humphries, 1968; Du Feu, 1987). Emergence from the cocoon is triggered by the spring rise in temperatures and mechanical disturbances (Humphries, 1968).

Blue tits are common European passerine birds, breeding in deciduous and mixed woods habitats. Blue tit pairs build their nest in natural tree-holes and also readily use nestboxes. In spring the female lays a mean clutch of 9 to 12 eggs, depending on the habitat (Glutz Von Blotzheim and Bauer, 1993). The eggs are incubated solely by the female and hatch on average 13 days later. The hatchlings are fed by both parents with caterpillars collected on neighboring deciduous trees and they fledge on average 20 days later. Blue tits nests are often and heavily infested by *C. gallinae* (Tripet and Richner, 1997a). They are known to avoid visiting heavily infested nestboxes (Du Feu, 1992). Video recordings of nests experimentally infested with *C. gallinae* but void of other ectoparasites showed that female blue tits spent considerable amount of time cleaning the nest and that their cleaning behavior is dependent on the density of fleas (Tripet, unpublished data).

METHODS

Bird–flea interactions were studied in a population of blue tits breeding in nestboxes and natural cavities in a 60-ha forest 8 km southwest of Basel, Switzerland (47°32′N, 7°32′E). Work done on this blue tit population before 1990 has shown high natural infestation rates by the hen flea, *Ceratophyllus gallinae* (Zhandt, personal communication). Between 1990 and 1994 both bird and flea populations were left unmanipulated. In January 1994 we replaced the old nestboxes with new ones. The nests which contained fleas were stored in plastic bags for later use.

At the beginning of the blue tits' breeding period we visited the nestboxes daily and recorded the onset of laying, number of eggs laid, start of incubation, length of incubation (i.e., the number of days elapsed from the first day we detected warm eggs spread in the nestcup to the hatching of the first nestling), and first day of hatching (referred to as day 0 of the nestling period). Since nest mass could influence flea development (Eeva *et al.*, 1994; Heeb *et al.*, 1996), we standardized nest size during egg laying by birds to a height of 8 ± 1 cm by adding or removing material from the column of moss present under the nestcup. This corresponds to the average nest size in 1994. This manipulation was well accepted by the birds and never led to nest desertion. When the birds laid their second egg we heat-treated the nests using a microwave oven to kill all existing parasites (Fig. 1). There was a possibility that desiccation would alter flea development and we therefore placed the nests in plastic bags during the heat treatment. We also sprayed the nests with 4 ml of water after the heat treatment. On the second day of incubation the nests were randomly infested with 6, 20, and 50 adult fleas (Fig. 1). Fleas used for infestation were picked at random from nest material combined from three to five nests. The male/female ratio at infestation was 0.41. Immigration of wild fleas brought in by the adult birds can occur. In great tits a mean immigration of 5.8 fleas per nest has been found between nest-building and fledging of the young (Heeb *et al.*, 1996). In our experiment, fleas infesting the nests before egg laying were killed by our heat treatment, which further reduces the number of uncontrolled fleas.

Population Growth

We counted the number of flea larvae in the nests at hatching (= end of incubation) and on day 10 of the nestling period (= midnestling period) (Fig. 1). The following procedure was applied when counting parasite larvae at day 0. We first divided the nest into two parts. The top part of the nest holding the nestcup was kept intact and gently shaken above a plastic dish until no more larvae fell from it. It was then placed back in the nestbox so that the adult birds could feed and incubate their young during the rest of the manipulations. The bottom part of the nest was thoroughly mixed above a metal mesh. The fraction of nest material

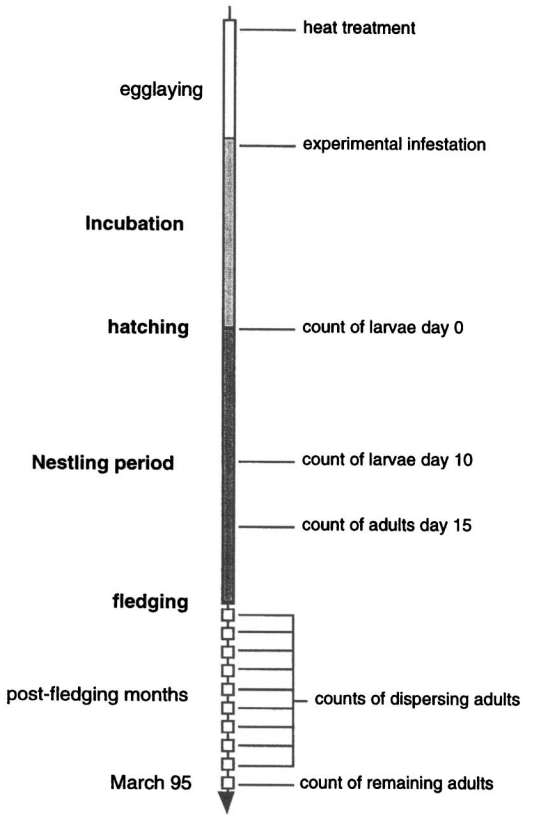

Fig. 1. Sequence of measurements made on the experimental flea populations (right-hand side of the graph) in blue tit nests. Bird events during the nesting period are listed on the left-hand side of the graph. The shaded area and bold letters indicate the warm period in the nests.

that contained the larvae and the larvae from the nestcup were then mixed, spread on the plastic dish, and divided into eight sectors. We counted the live larvae from two randomly chosen sectors. Following our measurement, we rebuilt the bottom part of the nest and reintroduced the larvae under the nestcup. The same method was used on day 10 of the nestling period. At that stage the nestcup is considerably destroyed by the female bird's cleaning activities and trampling by the nestlings. We therefore inspected all of the nest material at once.

Adult fleas were counted on day 15 of the nestling period (Fig. 1). They are more conspicuous than larvae and were counted visually from both fine and coarser fractions of the nest material. We then rebuilt the nest and reintroduced the fleas into the nest material.

To estimate the final number of larvae present at the end of the bird's breed-

ing period, we sealed all cracks in the nestbox with tape and set a flea trap at its entrance hole after fledging of the young. The flea traps were built following the instructions in Bates (1962) and prevented birds from entering the nestboxes. We collected dispersing fleas monthly during summer, autumn, and winter (Fig. 1). Fleas remaining in the nests were sampled in March 1995 using the method used for larvae counts (Fig. 1). The estimated number of larvae present in the nests at the end of the nestling period equals the sum of dispersing adult fleas and adult fleas remaining in the nest material, from which should be substracted the number of adult fleas present in the nest during the nestling period. These adults disperse in the days that follow fledging of the young birds (personal observation) and we therefore excluded adults dispersing within 2 weeks after fledging from our count of the final larvae number.

Density-dependent effects on flea population dynamics will be discussed elsewhere (Tripet and Richner, 1999), and we therefore present the data of population growth as mean values over the three experimental groups.

The original sample size was 49 nests. Three nests were deserted by the birds before the end of incubation and two broods failed just after hatching. Overall nestling mortality was very low and 97.2% of the nestlings fledged successfully. The numbers of flea larvae at the end of incubation and the midnesting period were counted in 46 and 44 nests, respectively. Adult fleas were counted from 43 nests. One bird pair started a second brood before we set the flea trap, two nestboxes were stolen, and one flea trap was destroyed. The final number of fleas produced could therefore be recorded from only 41 nests.

Nest Temperatures and Physiological Time

The number of day-degrees above 0°C available for parasite development during the bird incubation and nestling period was measured for each nest by placing a "temperature recorder" under the nestcup. The "temperature recorders" consisted of 5-ml plastic tubes filled with a sucrose solution which turns at a temperature-dependent rate into glucose (Berthet, 1960). The tubes were stored at −20°C before and after use. The final glucose concentration was measured with a polarimeter and allowed calculation of the average temperature for the period concerned. All manipulations and calculations were made following the methods described by Berthet (1960). "Within-nest day-degrees" were calculated from the temperature obtained with the temperature recorders, and outdoor day-degrees from temperature charts provided by a nearby meteorological station.

Flea Reproduction and Timing and Length of the Warm Period

The importance of the variables timing and length of warm period on the number of offspring produced per founder flea was analyzed using general linear models in GLMstat (Beath, 1995). Due to heteroscedasticity, the models on the number

of larvae produced until hatching and the midnestling period required Poisson error distributions. Other models are based on Normal error distributions. Because the nests were infested with three flea densities, we accounted for density-dependent effects on offspring production by including a factor referred to as "density correction" in the models. Density-dependent effects will be discussed elsewhere, hence we do not give the P values of the density correction factor.

All other statistical analysis were performed using the Systat Statistical Package (Wilkinson, 1992). Data were checked for normality and heterogeneity of variances. Where transformations were needed, they are described in the text. Significance levels are two-tailed.

RESULTS

Population Growth

The number of larvae increased significantly from the end of incubation to the midnestling period (Fig. 2) and from midnestling to the end of the nestling period (repeated-measures ANOVA: breeding stage, $F_{2,78} = 165.8$, $P < 0.001$). Note that the number of larvae at the end of the nestling period is inferred from the total number of offspring counted in winter (see Methods) and does not take into account larval and pupal mortality. Cocoons were present under the nestcup when counting the larvae at the end of incubation but not at the midnestling period. Cocoons were then found again in some nests when counting adult fleas on day 15 of the nestling period. The number of imagos (Fig. 3) increased significantly (Wilcoxon: $Z = 4.3$, $n = 39$, $P < 0.001$) from the start of incubation to the 15th day of the nestling period.

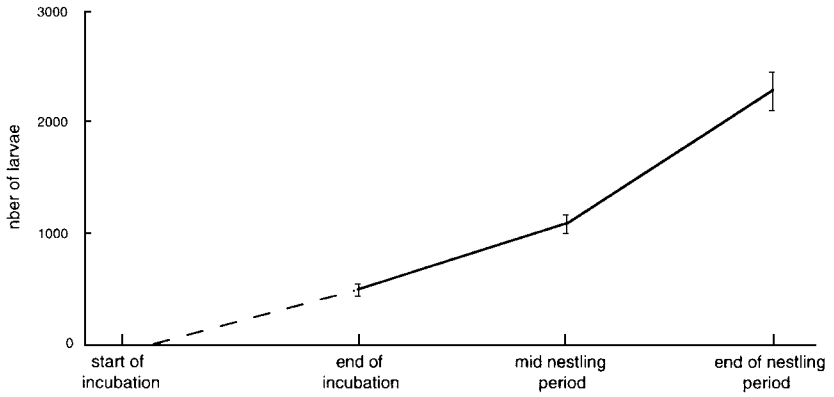

Fig. 2. Growth of the larval cohort during the blue tit breeding cycle. Vertical bars are standard errors of estimates.

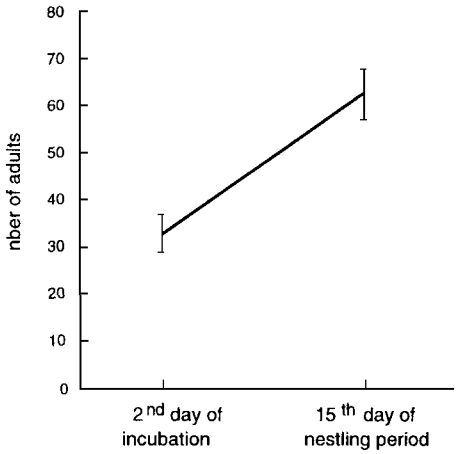

Fig. 3. Growth of the cohort of adult fleas from infestation to the 15th day of the nestling period. Vertical bars are standard errors of estimates.

Nest Temperatures and Physiological Time

The mean temperature measured within the nest material during incubation was 21.5 ± 3.0°C (SD). This was 12.1°C higher than the mean outdoor temperature (Wilcoxon: $Z = 5.8$, $n = 45$, $P < 0.001$). Incubation temperatures within the nest material correlated with outdoor temperatures ($r = 0.574$, $n = 45$, $P < 0.001$) and increased seasonally (linear regression: $T = 3.7$, $n = 45$, $P < 0.001$) (Fig. 4). Physiological time, expressed as day-degrees, available for flea development was on average 337 ± 69 for a mean incubation length of 15.6 ± 1.9 days. Variation in the amount of day-degrees inside and outside the nests occurred because of variation in the bird length of incubation. We performed a repeated analysis of covariance on the day-degrees inside and outside the nests (repeat), with the length of incubation as a covariate. Note that there is no constant in the model. Due to the higher temperatures within the nest material, day-degrees inside the nests added up at a faster rate than outdoors (repeated-measures ANCOVA: length of incubation, $F_{1,45} = 2178$, $P < 0.001$; repeat * length of incubation, $F_{1,45} = 994$, $P < 0.001$) (Fig. 5). Day-degrees were therefore significantly explained by the length of the bird incubation period and by its timing of incubation in the season (multiple regression: length, $T = 8.6$, $P < 0.001$; timing, $T = 3.7$, $n = 45$, $P = 0.001$).

During the nestling period the average temperature in the nest material was 30.7 ± 4.0°C, 17.4°C higher than the mean outdoor temperature (Wilcoxon: $Z = 5.6$, $n = 42$, $P < 0.001$) and 9.2°C higher than within-nest incubation temperatures (paired t test: $t = 10.0$, $n = 41$, $P < 0.001$). Average nest temperatures during

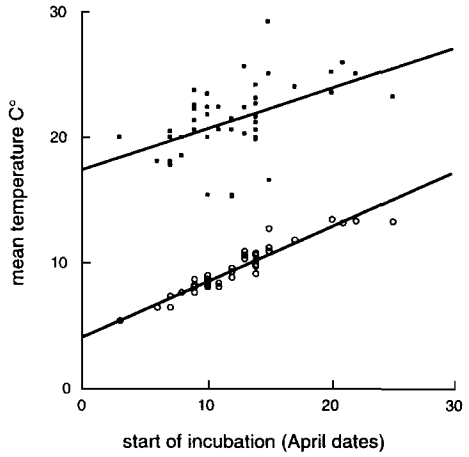

Fig. 4. Relationship between the start of the bird's incubation period (April dates) and the average temperatures during incubation outdoors (○) and in the nest (●).

the nestling period did not correlate with mean outdoor temperatures ($r = 0.048$, $n = 42$, $P = 0.763$) and decreased seasonally (linear regression: $T = -3.4$, $n = 42$, $P = 0.001$), while outdoor temperatures neither increased nor decreased significantly (linear regression: $T = 1.2$, $n = 42$, $P = 0.246$). The amount of day-degrees available to fleas was on average 630.5 ± 88.5 during the 20.5 ± 1.0-day-long

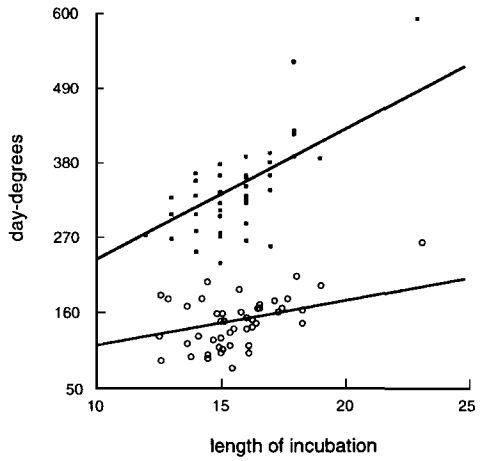

Fig. 5. Relationship between the length of the bird's incubation period (days) and the amount of day-degrees (above 0°C) outdoors (○) and in the nest (●).

nestling period. Day-degrees were significantly explained by the length of the bird nestling period and by its timing in the season (multiple regression: length, $T = 3.1$, $P = 0.004$; timing, $T = -3.4$, $n = 41$, $P = 0.002$).

There was a significant negative correlation between the mean nest temperatures during the incubation and those during the nestling period ($r = -0.347$, $n = 41$, $P = 0.026$). The entire warm period, i.e., incubation and nestling period, lasted on average 36.2 ± 2.2 days, for a total of 967.9 ± 101.8 day-degrees. The variation in the amount of day-degrees was not significantly affected by the timing of the warm period but varied with its length (multiple regression: timing, $T = -1.1$, $n = 41$, $P = 0.277$; length, $T = 4.6$, $P < 0.001$).

Flea Reproduction and Timing and Length of the Warm Period

As shown above, timing and duration of the warm period are likely to correlate with parasite demography through their effects on day-degree availability. The importance of those variables on the number of offspring produced per founder flea was analyzed using general linear models. The number of larvae at the end of incubation and at the midnestling period increased with the season and with the length of the warm period (Tables I and II). However, the final number of larvae present at the end of the nestling period did not depend on these factors. There was, nevertheless, still a trend for offspring numbers to correlate with the length of the warm period (Table III). The timing and length of incubation had no significant effect on the number of adult fleas produced until day 15 of the nestling period (Table IV).

DISCUSSION

The Life Cycle of *C. gallinae*

Flea subpopulations in the nests showed two distinct periods of cocoon formation, giving rise to two cohorts of imagos (Fig. 6). At the end of incubation,

Table I. Effect of the Timing and Length of Incubation on the Number of Larvae Produced per Flea Until Hatching (Day 0)[a]

Model	Deviance	df	ΔD	Δdf	P
Null	104.1	45			
Density correction	*73.3*	*43*	*32.3*	*2*	
Length of incubation	61.8	42	20.8	1	<0.001
Timing of incubation	62.2	42	21.2	1	<0.001
Min.	41.0	41			

[a]Interactions were not significant. Also included in the model is the factor "density correction," accounting for density-dependent effects inherent to our infestation with three flea densities.

Table II. Effect of the Timing and Length of the Warm Part of the Bird's Breeding Cycle on the Number of Larvae Produced per Flea Until the Middle of the Bird Nestling Period (Day 10)[a]

Model	Deviance	df	ΔD	Δdf	P
Null	132.6	43			
Density correction	*111.4*	*41*	*72.4*	*2*	
Length of warm period	55.4	40	16.4	1	<0.001
Timing of warm period	46.6	40	6.6	1	<0.02
Min.	39.0	39			

[a]Interactions were not significant. Also included in the model is the factor "density correction," accounting for density-dependent effects inherent to our infestation with three flea densities.

Table III. Effect of the Timing and Length of the Warm Part of the Bird's Breeding Cycle on the Final Number of Larvae Present at the End of the Nestling Period (Log-Transformed Data)[a]

Model	Deviance	df	ΔD	Δdf	P
Null	107.4	40			
Density correction	*101.8*	*38*	*65.8*	*2*	
Length of warm period	39.7	37	3.7	1	<0.1, >0.05
Timing of warm period	37.1	37	1.1	1	>0.1
Min.	36.0	36			

[a]Interactions were not significant. Also included in the model is the factor "density correction," accounting for density-dependent effects inherent to our infestation with three flea densities.

Table IV. Effect of the Timing and Length of the Incubation Period on the Number of Adult Fleas at the Nestling Stage [$\log(x + 1)$-Transformed Data][a]

Model	Deviance	df	ΔD	Δdf	P
Null	83.0	39			
Density correction	*82.2*	*37*	*47.2*	*2*	
Length of incubation	35.1	36	0.1	1	>0.5
Timing of incubation	35.5	36	0.5	1	>0.1
Min.	35.0	35			

[a]Interactions were not significant. Also included in the model is the factor "density correction," accounting for density-dependent effects inherent to our infestation with three flea densities.

a fraction of the larvae spun cocoons under the nestcup, pupated, and gave rise to first-generation fleas. This led to an overlap of parental and first-generation adult fleas. The second peak at the end of the nestling period was formed by the cocooning of the remaining first-generation larvae and the larvae produced by

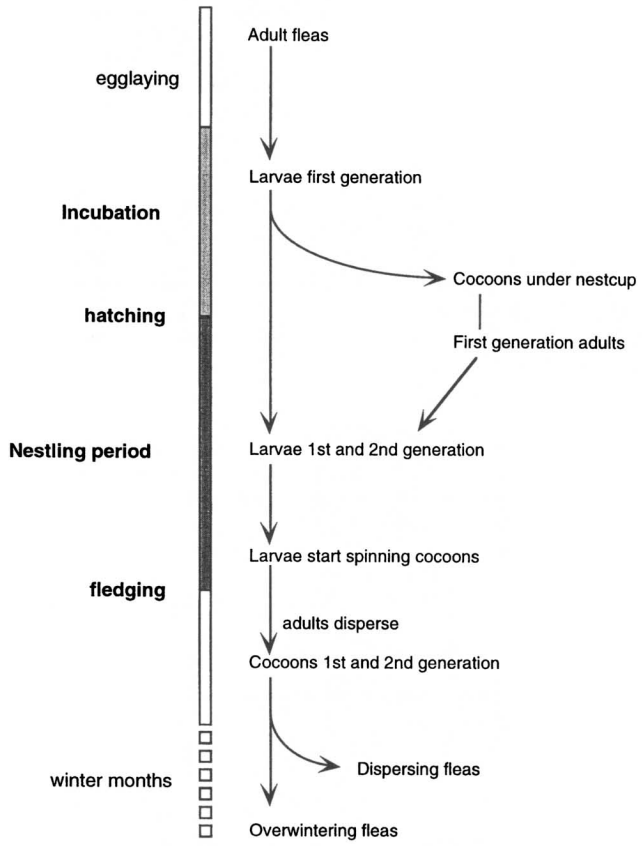

Fig. 6. The life cycle of *C. gallinae* in the nests of *Parus caeruleus*. Bird events during the nesting period are listed on the left-hand side of the graph; flea events, on the right-hand side. The shaded area and bold letters indicate the warm period in the nests.

both generations of adult fleas during the nestling period. Imagos from these cocoons did not hatch before fledging of the young birds and these fleas either overwintered in cocoons or dispersed from the nests. Few or no cocoons were found in nests at day 10 of the nestling period.

One striking feature of the life cycle of fleas in blue tit nests is the near-completion of two generations within the nesting period of the host's breeding cycle. The time of appearance of first-generation adults and whether they can feed and lay eggs before the departure of the birds have been discussed by many authors (e.g., Rothschild and Clay, 1952; Cotton, 1970; Harper *et al.*, 1992; Eeva *et al.*, 1994). It shows that the rate of development of the *C. gallinae* under

natural conditions has so far been underestimated. We compared our results with those of Cotton (1970), who measured rates of development of hen fleas in the laboratory at 21 and 28°C. Based on the mean of his two measurements, one can calculate that fleas required a minimum of 556 day-degrees to complete one generation and a further 410 day-degrees until the cocoon stage of the following generation. This gives a total of 966 day-degrees, which is consistent with the average 968 day-degrees measured in our nests.

Under natural conditions fleas sometimes feed and manage to develop eggs during the birds' egg-laying period (personal observation). Since we heat-treated the nest at the start of the bird egg-laying period, in some nests a few wild fleas may have immigrated before our experimental infestations (Heeb *et al.*, 1996). Given the low nest temperatures at the bird egg-laying stage, at the beginning of incubation these flea eggs should have a 1- or 2-days advance in development compared to those laid by the founders of our experimental populations. Similarly, given that temperatures are much higher during the nestling period, this initial difference should shrink to even smaller proportions. Thus, even if immigration may occur during the bird egg-laying stage, it should not have an important effect on the patterns of the flea life cycle reported here.

Constraints on the Timing of Flea Generations

First-generation larvae that cocoon under the nestcup at the end of the birds' incubation period seem to develop at their maximum rate for the amount of day-degrees available. This is clearly not the case for those first-generation larvae which delay metamorphosis and spin cocoons at the end of the nestling period together with second-generation larvae. These larvae do not appear to behave in a way that maximizes their rate of development. We suggest that further cocoon formation under the nestcup might be prevented by the female bird's cleaning behavior. Video recordings made during the nestling period showed that female tits spent considerable amount of time cleaning the nest (Christe *et al.*, 1996b; Tripet, unpublished data). Females regularly dive head-first in the nestcup, vigorously searching and shaking the nest material. The shaking movements probably make larvae fall farther down into cooler regions of the nest material, and they may therefore develop at a slower rate. Also, for flea larvae, the searching and killing of larvae by females could lead to a trade-off between their survival and speed of development. The farther from the female they build their cocoon, the less likely they are to be killed. However, to cocoon farther from the nestcup also means less heat to complete their development and a lower chance to feed as adults and lay eggs that will develop before the host's departure. It might, then, be more advantageous for the larvae to delay metamorphosis and overwinter under optimal conditions in cocoons rather than to hatch as imagos near or after the departure of the birds. Heeb *et al.* (1996) also found larvae and

imagos, but few cocoons, in great tit nests collected immediately after fledging. It was suggested that cannibalism or competition could affect the age structure of the larvae populations and lead to discrete age cohorts. We found larvae at all stages (first, second, and third instar) together with cocoons at the end of incubation. There is therefore no evidence that older larvae prevent the development of younger larvae before pupating. However, there remains the possibility that, once a threshold larval density is reached, crowding around the nestcup forbids further cocoon formation and pupation. Furthermore, first-instar larvae kept under crowded conditions in the laboratory have been observed dismantling freshly spun cocoons and devouring their contents (Tripet, personal observation). Competition for suitable pupation sites may therefore prevent older larvae from spinning cocoons near the heat source of the nestcup, thereby inciting them to delay metamorphosis.

Parasites and Timing and Length of the Warm Period

Temperatures in the nest material during incubation depended on both the heat produced by incubating females and the outdoor temperatures. Outdoor temperatures increased seasonally during that period. Thus early- and fast-incubating birds minimized the heat and time available for parasite development, and those behavioral traits correlated negatively with the number of flea larvae (Table I). Variation in the amount of day-degrees available for flea development also had a strong influence on the timing of appearance of first-generation fleas. First-generation fleas, for example, were observed at hatching time only in the two nests which benefited from more than 500 day-degrees during incubation. Effects on the number of larvae produced were measured at the end of incubation and the midnestling period but not later (Tables I–III). Mean temperatures in the nest material during the nestling period decreased seasonally, and this led to a negative correlation between nest temperatures during incubation and the nestling period. At present we have no straightforward explanation for this decrease in nest temperature. There was no correlation between nest temperatures and number of nestlings (Pearson correlation, $P > 0.1$) or between the hatching date and the number and body mass of the nestlings ($P > 0.5$ and $P > 0.1$, respectively). It may be that early-incubating females which had the cooler nests during incubation brooded more during the nestling period than late-breeding females. The resulting negative relationship between incubation and nestling nest temperatures may explain why, overall, the timing of the bird breeding cycle had no effect on the final number of larvae produced. It may, however, also be that temperature effects are progressively overridden by others factors such as density effects. Harper *et al.* (1992) found a positive correlation between the flea load and the length of the warm period across five bird species. They also found that birds with long warm periods bred earlier and harbored more fleas. Our results suggest

that (1) within species, fleas could maximize their reproductive rates by infesting the host at the very beginning of its breeding period to produce two generations and to maximize the duration of the warm period; and (2) there seems to be an initial advantage to infest late breeding individuals to benefit from higher outdoor temperatures. However, under the conditions of our experiment this effect disappeared with time.

The simplest way for a flea to infest a host early during its breeding season is to overwinter in the nest and to wait and see if the nest is reused the following year. If such is the case, imagos may emerge from the pupal cocoon directly to feed on the new coming host, thereby skipping the hazardous dispersal and host searching phases. This advantage might, however, be overridden by important drawbacks. For one thing, if hosts avoid infested nests (Du Feu, 1992; Oppliger *et al.*, 1994), fleas face the danger of not finding a host at all unless they disperse. Those that manage to jump on a suitable host will then face the drawbacks of a late host infestation compared to an early one [see above (1)]. Very little is known of *C. gallinae*'s dispersal behavior and how flea individuals balance these conflicting selective forces. The existing data on *C. gallinae*'s emergence and dispersal from hole nests suggest that, although there is a peak of emergence coinciding with the period of greatest hole visiting activity by tits, there remains considerable variation in the time of emergence and dispersal of fleas from nestboxes (Bates, 1962; Du Feu, 1987). One would expect between-habitat genetic differentiation in flea populations' dispersal patterns in relation to differences in nest site availability, avian community structure, and environmental conditions (Tripet and Richner, 1997a). Future studies should aim at determining whether the observed variance in dispersal is maintained by gene flow between spatially distinct populations and subpopulations from different nests or, rather, is linked to phenotypic variation.

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