

The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*

F. TRIPET* and H. RICHNER

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

(Received 24 December 1996; revised 21 April 1997; accepted 21 April 1997)

SUMMARY

Hosts exert selection pressures on their parasites and it is often assumed that host–parasite coevolution with each host is less intense in a generalist parasite than for a parasite with a narrow host range. Selection pressure on the parasite, however, is rather determined by host specificity, i.e. the relative importance of each host, than simply by the range of hosts. The determination of host specificity requires an assessment of the prevalence and intensity of parasite infestation within each host's nests, as well as the local abundance of each host species. Since the hen flea, *Ceratophyllus gallinae*, is a rather generalist parasite of birds it could be concluded that there has been weak coevolution with each of its hosts. By reviewing the literature on the prevalence and intensity of hen flea infestations in bird nests we estimated the number of individuals produced in the nest of each host species. The comparative analysis shows (1) that the prevalence of infestation is highest in hole-nesting avian families, (2) that prevalence and intensity of infestation among bird families are highly correlated, and (3) that hole-nesting Paridae have the highest intensities of infestation and harbour the majority of the flea population. These results underline the fleas' potential for coevolution with Paridae despite their extensive host range.

Key words: host specificity, *Ceratophyllus gallinae*, niche exploitation, specialization, Paridae.

INTRODUCTION

The hen flea *Ceratophyllus gallinae* (Schrank) is probably the commonest bird flea of the western Palearctic and has been reported from the bodies or nests of numerous avian species. Rothschild (1952) in a synthesis of the British records reported 65 host species and Smit (1957) listed 75 avian species and 15 species of mammals including *Homo sapiens*! These records, however, are of limited use when considering the evolution of host–parasite relationships because (1) hosts which *C. gallinae* regularly uses for reproduction are not distinguished from those used accidentally for phoresis and opportunistic feeds and that do not provide breeding opportunities to the parasite, and (2) the relative importance of each host's selective force on parasite traits is not evaluated (Holmes, 1983). Thus, the relative prevalence and intensity of infestation for each host species, as well as the relative abundance of each host species are essential in our understanding of parasite specificity (Holmes, Hobbs & Leong, 1977; Rohde 1980).

There have been several attempts to determine which are the main hosts among the bird species that offer suitable breeding conditions to the common hen flea (Thompson, 1937; Rothschild & Clay, 1952; Bates, 1956). It was concluded that *C. gallinae* showed little specificity and preferred forest birds

nesting in cavities and semi-cavities, or some height above the ground (Nordberg, 1936; Ash, 1952; Rothschild, 1952; Jurik, 1974). Hole-nesting tits (Paridae) have occasionally been proposed as main hosts (Rothschild & Clay, 1952; Harper, Marchant & Boddington, 1992) but populations of hen fleas are invariably found in nests of other species.

Recent research on the hen flea–Paridae system which has been concerned with the cost of parasitism (Richner, Oppliger & Christe, 1993) and host-responses to parasites (Christe, Oppliger & Richner, 1994; Oppliger, Richner & Christe, 1994; Perrin, Christe & Richner, 1996; Tripet & Richner, 1997) have underlined potential mechanisms of parasite selection on host behaviour and life-history traits (Richner & Heeb, 1995). The reciprocal tit selection pressure on fleas is, however, difficult to infer from data on parasite behaviour. If we assume that *C. gallinae* is a true generalist, we do not expect it to coevolve with any particular host species but rather to undergo diffuse coevolution with its several hosts (Futuyma & Slatkin, 1983). On the other hand, even in the face of an extensive host range, coevolution with tits could still be extensive provided that the majority of fleas reproduce in their nests (Holmes, 1983).

We therefore reevaluate the 'generalist' label of this widespread avian parasite. The present comparative study analyses the currently available data in an attempt to determine *C. gallinae*'s primary and secondary hosts. *C. gallinae*'s potential specialization and the factors likely to maintain an extensive host

* Corresponding author. Tel: +41-31 631 91 28. Fax: +41-31 631 91 41. E-mail: tripet@esh.unibe.ch

Table 1. List of studies reporting the mean prevalence p or the mean intensity i of *Ceratophyllus gallinae* infestation from bird nests

Reference	Location	Year	Species	Data
(a) Nordberg (1936)	Helsinki, Finland	1929–1933	56	p
(b) Ash (1952)	Berkshire, England	1950	30	p, i
(c) Langer & Tilgner (1957)	Frankfurt, Germany	1955	4	p
(d) Kime (1962)	Durham, England	1954, 1955, 1960	6	p, i
(e) Raes (1969)	Gent, Belgium	1967	3	p
(f) Jurik (1974)	Former Czechoslovakia	1965, 1966	69	p, i
(g) Kiziroglu (1984)	Munich, Germany	?	1	p
(h) Harper <i>et al.</i> (1992)	2 Study sites	1974–1983	7	p, i
(i) Harper <i>et al.</i> (1992)	Herefordshire, England		7	
(j) Eeva <i>et al.</i> (1994)	Harjavalta, Finland	1991, 1992	2	p
(k) Merilä & Allander (1995)	Gotland Island, Sweden	1993	3	p, i
(l) Rothschild (1952)	Review of British records			

spectrum in the hen flea and other ‘generalist’ bird fleas are discussed.

MATERIALS AND METHODS

C. gallinae, like most bird fleas, 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 bloodmeals. The larvae develop in the nest material and feed on detritus and undigested blood excreted by the parents (Marshall, 1981; Lehane, 1991). Adult fleas leave the nest shortly after fledging. Some are carried away on the nestlings themselves (Humphries, 1968; and personal observations). The flea larvae remain in the deserted nests and within a few days complete their larval development. The third larval instars spin cocoons, pupate and moult to the adult stage. Most of the imagoes remain quiescent in the cocoons until the next spring (Humphries, 1967; Du Feu, 1987). There are no data available on the optimal temperature and humidity requirements of *C. gallinae*’s developmental stages. Larvae of this species are known to tolerate a broad range of humidity (Bates, 1956) and high relative humidity seems beneficial to the survival of imagoes overwintering in cocoons (Humphries, 1967). Emergence from the cocoon is triggered by the spring rise in temperatures and mechanical disturbances (Humphries, 1968).

In theory, *C. gallinae*’s main hosts are those avian species in the nests of which the majority of flea offspring surviving to the next breeding event are produced. The majority of the new flea generation overwinters in cocoons in the abandoned nests (Heeb *et al.* 1996). Thus, for a given bird species (s) the number of fleas produced in 1 breeding season and surviving to the next spring is roughly equal to:

$$N(s) = p(s) \cdot i(s) \cdot d(s), \quad (1)$$

where p is the mean prevalence or percentage of infested nests; i the mean intensity of infestation or

number of fleas overwintering in infested nests; and d is the density of hosts’ nests. Thus for the flea population as a whole the total number of recruits W surviving to the next breeding event is the sum of recruits from the nests of the different host species

$$W = \sum \beta(s) \cdot N(s), \quad (2)$$

with β as the transmission rate or probability of an offspring finding and infesting a new host’s nest.

Although there are no data on transmission rate currently available in the literature; there are a number of studies reporting p (percentage of infested nests), and i (number and fleas per infested nest) of flea infestations in bird nests. We found 11 such studies (Table 1) concerning a total of 99 different avian species and 2668 bird nests. There were also a few bird species reported by Rothschild (1952) for which they are no other data available other than records of occurrence. *C. gallinae* was recorded from the nests of 72 avian species (Table 2).

Except for a few non-specified cases described by Jurik (1974), all p and i values in these studies were measured either after fledging of the young birds or in the autumn or winter month between 2 bird breeding events. The fleas were either counted directly from discarded nests (studies c, d, g), or extracted using Berlese funnels (b), Tullgren funnels (a), and variations of these methods (h, i, j, k); or thermoelectors (e, f).

Given that most parasite infestations exhibit overdispersion, the precision of the p and i values increases with the number of nests examined. We therefore weighed those values by the number of nests involved in the study when calculating the mean p and i over all studies. Phylogenetic effects were also taken into account by working at the family rather than species level. P and i values for families for which less than 4 nests were analysed were considered not precise enough to be included in the analysis.

All bird species were assigned to 7 nest categories according to their most common breeding habits.

Table 2. List of bird species whose nests were examined for the presence of *Ceratophyllus gallinae*

(Species whose nests scored positive for the presence of hen fleas are marked with a black dot. Letters in the 'Study' column refer to Table 1.)

Order	Family	Host species	Study	
Accipitriformes	Accipitridae	<i>Accipiter gentilis</i> ●	a	
		<i>Accipiter nisus</i> ●	a	
		<i>Buteo buteo</i> ●	a	
		<i>Haliaeetus albicilla</i> ●	a	
		<i>Circus pygargus</i> ●	b	
		<i>Pernis apivorus</i> ●	f	
Anseriformes	Anatidae	<i>Mergus merganser</i> ●	a	
		<i>Anas platyrhynchos</i>	f	
		<i>Somateria mollissima</i>	a	
Apodiformes	Apodidae	<i>Apus apus</i> ●	l	
Charadriiformes	Charadriidae	<i>Vanellus vanellus</i>	b	
Ciconiiformes	Ciconiidae	<i>Ciconia ciconia</i>	f	
	Ardeidae	<i>Ixobrychus minutus</i>	f	
Falconiformes	Falconidae	<i>Falco peregrinus</i> ●	a	
		<i>Falco tinnunculus</i> ●	a, f	
		<i>Columba oenas</i> ●	a	
Columbiformes	Columbidae	<i>Columba livia</i> ●	a, f	
		<i>Columba palumbus</i>	a, b, f	
		<i>Streptopelia decaocto</i>	f	
		<i>Streptopelia turtur</i>	f	
		<i>Gallus domesticus</i> ●	l	
		<i>Perdix perdix</i> ●	b	
Galliformes	Gallinaceae	<i>Phasianus colchicus</i> ●	l	
	Phasianidae	<i>Gallinula chloropus</i> ●	l	
		<i>Fulica atra</i>	a, b, f	
Gruiformes	Ralidae	<i>Larus fuscus</i> ●	a	
		<i>Larus canus</i>	a	
		<i>Larus ridibundus</i>	f	
Lariformes	Sternidae	<i>Sterna hirundo</i>	a	
		<i>Sterna paradisaea</i>	a	
		<i>Alauda arvensis</i> ●	a, f	
	Passeriformes	Alaudidae	<i>Lullula arborea</i>	b
			<i>Corvus corone</i> ●	a, b, f
		Corvidae	<i>Corvus monedula</i> ●	a, f
			<i>Pica pica</i> ●	a, b, f
			<i>Garullus glandarius</i>	b, f
		Certhiidae	<i>Certhia familiaris</i> ●	a, b, d
			<i>Certhia brachydactyla</i>	f
Cinclidae		<i>Cinclus cinclus</i> ●	l	
Emberizidae		<i>Emberiza citrinella</i> ●	l, f	
		<i>Emberiza schoeniclus</i>	b	
Fringillidae	<i>Emberiza hortulana</i>	a		
	<i>Carduelis cannabina</i> ●	b, f		
	<i>Carduelis chloris</i> ●	l, f		
	<i>Fringilla coelebs</i> ●	a, b, f		
	<i>Pyrrhula pyrrhula</i> ●	a		
	<i>Serinus serinus</i> ●	f		
	<i>Carduelis carduelis</i>	f		
	<i>Coccothr. Coccothraustes</i>	f		
	Hirundinidae	<i>Delichon urbica</i> ●	a, f	
		<i>Hirundo rustica</i> ●	a, f	
<i>Riparia riparia</i> ●		a, f		
Laniidae	<i>Lanius cristatus</i>	f		
Motacillidae	<i>Anthus pratensis</i> ●	a, b		
	<i>Anthus spinoletta</i> ●	a, f		
	<i>Motacilla alba</i> ●	a, f		
	<i>Anthus trivialis</i>	f		
Muscicapidae	<i>Muscicapa striata</i> ●	a, b, f		
	<i>Ficedula albicollis</i> ●	f		
	<i>Ficedula hypoleuca</i> ●	a, c, d, h, i, j, k		

Table 2. (cont.)

Order	Family	Host species	Study
	Paridae	<i>Aegithalos caudatus</i> ●	b
		<i>Parus ater</i> ●	a, d, f, h, i
		<i>Parus caeruleus</i> ●	b, c, d, e, f, h, i, k
		<i>Parus major</i> ●	a, b, c, d, e, f, g, h, i, j, k
		<i>Parus montanus</i> ●	a
		<i>Parus palustris</i> ●	f, h, i
	Passeridae	<i>Passer domesticus</i> ●	a, f
		<i>Passer montanus</i> ●	e, f
	Prunellidae	<i>Prunella modularis</i> ●	b, f
	Sittidae	<i>Sitta europea</i> ●	b, f, h, i
	Sturnidae	<i>Sturnus vulgaris</i> ●	a, b, f
		<i>Oriolus oriolus</i>	f
	Sylviidae	<i>Phylloscopus collybita</i> ●	f, l
		<i>Phylloscopus trochilus</i> ●	a, b
		<i>Regulus regulus</i> ●	a
		<i>Sylvia borin</i> ●	a, f
		<i>Sylvia communis</i> ●	a, f
		<i>Acrocephalus arundinaceus</i>	f
		<i>Acrocephalus scirpaceus</i>	f
		<i>Acrocephalus palustris</i>	f
		<i>Hippolais icterina</i>	f
		<i>Locustella fluviatilis</i>	f
		<i>Sylvia attricapilla</i>	f
		<i>Sylvia curruca</i>	f
		<i>Sylvia nisoria</i>	f
	Troglodytidae	<i>Troglodytes troglodytes</i> ●	b, f
	Turdidae	<i>Erithacus rubecula</i> ●	a, b, f
		<i>Oenanthe oenanthe</i> ●	a
		<i>Phoenicurus ochruros</i> ●	f
		<i>Phoenicurus phoenicurus</i> ●	a, c, d, f, h, i
		<i>Saxicola rubetra</i> ●	a
		<i>Turdus merula</i> ●	a, b, f
		<i>Turdus musicus</i> ●	a
		<i>Turdus philomelos</i> ●	a, b, f
		<i>Turdus pilaris</i> ●	a
	Upupidae	<i>Upupa epops</i>	f
Piciformes	Picidae	<i>Dendrocopos major</i> ●	a, b
		<i>Dryocopus martius</i> ●	a
		<i>Jynx torquilla</i> ●	f
Podicepidiformes	Podicepididae	<i>Podiceps auritus</i> ●	a
		<i>Podiceps cristatus</i>	a, f
Procellariiformes	Hydrobatidae	<i>Hydrobates pelagicus</i> ●	l
Strigiformes	Strigidae	<i>Aegolius funereus</i> ●	a
		<i>Asio otus</i> ●	l
		<i>Athene noctua</i> ●	b
		<i>Bubo bubo</i> ●	a, f
		<i>Strix aluco</i> ●	l
		<i>Tyto alba</i> ●	l

Nest categories were respectively: 'tree holes' for nests in tree holes and nest boxes, 'crevices' for nests built in partial hollows in wood or rock structures, 'tree' for open nests high in trees, 'bushes' for open nests in small trees and shrubs, 'ground' for nests on or near the ground, 'mud nests' for the mud nests and excavations of Hirundinidae, and 'floating nests' of Ralidae and Podicepididae.

Parasite reproduction $N(s)$ per species

Estimations of the number of flea individuals $N(s)$ produced/km² of lowland forest for the commonest

host species were calculated using eqn (1). Because of the overdispersion of flea infestations more importance was given to between-nest variations rather than between-study variations. Thus the p and i means from each study were first multiplied by the number of nests analysed in that study. These products were then summed up and divided by the total number of nests analysed when calculating the mean p and i of infestation over all studies. Data on densities of bird breeding pairs in lowland oak dominated forest habitat are mean values calculated from Glutz von Blotzheim & Bauer (1980) for central Western Europe.

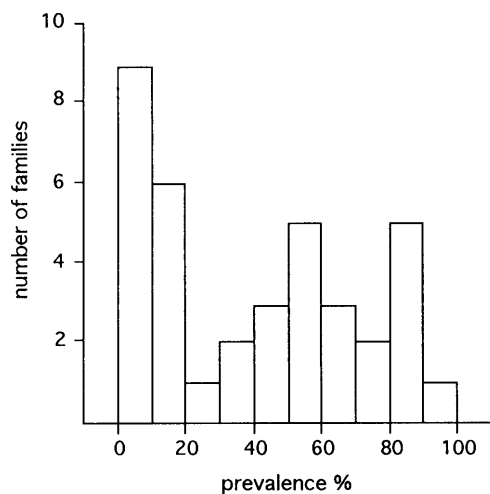


Fig. 1. Distribution of prevalence p of infestation of *Ceratophyllus gallinae* in the nests of avian families.

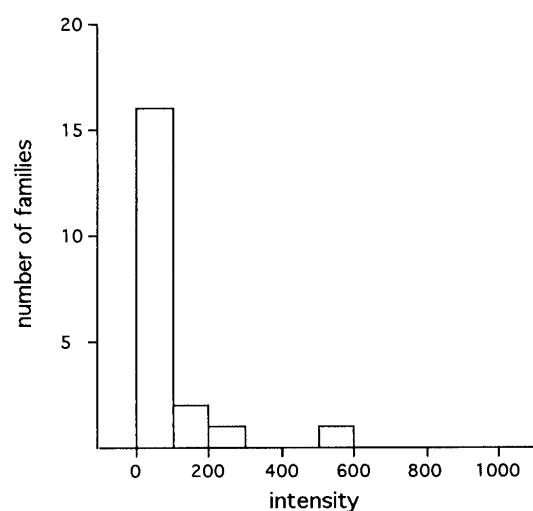


Fig. 2. Distribution of the intensity i of infestation of *Ceratophyllus gallinae* in infested nests. Data were available for 20 avian families only. The measure of i is based on infested nests only (see Materials and Methods section). Families which do not harbour fleas are therefore excluded from the figure.

Statistical analyses were made using SYSTAT (Wilkinson, 1992). Data were checked for non-normality and heterogeneity of variance. General linear models were performed on GLMstat (Beath, 1995).

RESULTS

Among the studies surveyed here, *C. gallinae* was detected in 93% of the examined nests (2469 infested out of 2668). *C. gallinae* was found in 61% of the species (60 out of 99) for which p or i was recorded (Figs 1 and 2).

Prevalence and host nest type

The relationship between the prevalence of infestation of bird families and the nest type of the taxa

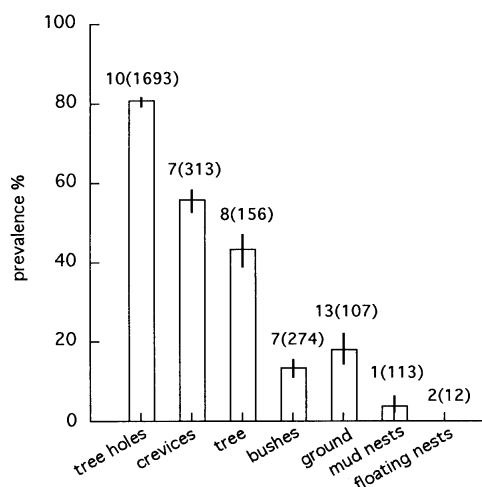


Fig. 3. Prevalence of hen flea infestation according to host nest type. Vertical bars are standard deviations derived from the GLM (see Results section and Table 3). Above the standard deviation bars are the number of families examined and the number of nests analysed (parentheses).

Table 3. Influence of the avian host nest type on the prevalence of infestation by *Ceratophyllus gallinae*

(Within nest category p values are family means in order to minimize phylogenetic bias.)

Model	Deviance	D.F.	ΔD	$\Delta D.F.$	P
Null model	1024	47			
Nest type	151.9	41	872	6	< 0.001

was investigated by using a general linear model with binomial error distribution. Nest type had a strong influence on prevalence of infestation (Fig. 3) (Table 3). No *C. gallinae* individuals were found in floating nests.

Prevalence and intensity of infestation

There is a positively exponential correlation between the mean prevalence and per-nest intensities (\log_e value) of infestations ($r = 0.857$; $n = 20$; $P < 0.001$) (Fig. 4) among bird families. Avian families using tree hollows and those using various crevices have the highest p and i values. At a comparable prevalence of infestation, the Paridae have the highest intensity of flea infestation among the hole nesting families.

Parasite reproduction $N(s)$ per species

Estimations of the number of flea individuals $N(s)$ produced/km² of lowland forest which is the habitat of the commonest host species show that in that habitat 93% of the parasite population (140552 out

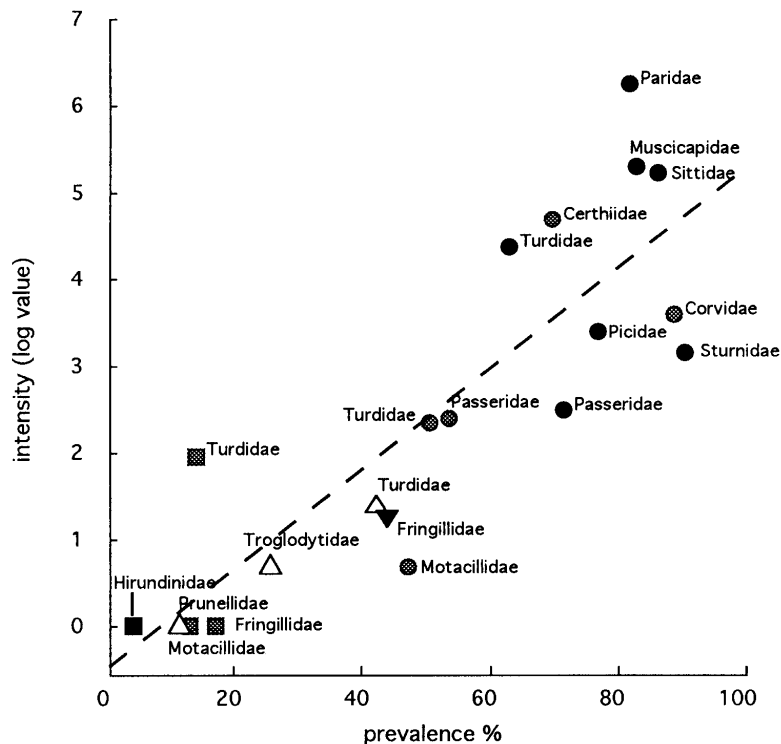


Fig. 4. Relationship between mean intensity and prevalence of infestation. In order to minimize phylogenetic effects, within nest types, p and i values are family means calculated from the species data. Excluded from this graph are families for which p and $i = 0$ (Ralidae, Podicepididae, Anatidae, Sternidae, Lanniidae and Columbidae). Symbols are ● nest-holes, ● crevices, ▼ tree crowns, ▨ bushes, △ ground and ■ mud nests.

of 150743 individuals) is produced in the hole-nesting Paridae (Fig. 5, shaded bars).

Altogether, 99.8% of the hen flea population overwinters in the 9 hole-nesting species (Fig. 5). Blue and great tits harbour most of the *C. gallinae* individuals because they are the most common tit species in that habitat. For these two species there were 8 and 6 studies respectively in which p and i were measured. Although there was no significant difference in prevalence between the two species (Wilcoxon signed rank test: $Z = 1.214$; $n = 16$; $P = 0.225$), a pairwise comparison shows that blue tits tend to have higher intensities of infestation (Wilcoxon signed rank test: $Z = 1.782$; $n = 12$; $P = 0.075$). There are too few studies to compare these p and i values with those of coal tits and marsh tits. These species, however, have p and i values of the same order of magnitude (Fig. 6).

DISCUSSION

Host spectrum of *Ceratophyllidae*

Although the hen flea is a frequent ectoparasite of most forest bird species nesting in cavities and crevices, the Paridae seem to offer optimal conditions for its reproduction. This does not exclude that in habitats where tit species are less common *C. gallinae* can successfully maintain itself on alternative host species. There is some evidence that in North-

America *C. gallinae* first infested poultry houses before invading indigenous wild bird species (Rothschild & Clay, 1952). Furthermore, there are reports in the literature suggesting that *C. gallinae* may locally breed in great numbers in tree crown nests of crows (Rothschild & Clay, 1952). Nest sites that offer suboptimal conditions for *C. gallinae* are often ecological niches of other ceratophyllid bird fleas. *Dasyptyllus gallinulae* commonly infests birds nesting in shrubs and low trees, *C. garei* moist nests on or near the ground, and *C. vagabundus insularis* cliff nests (Traub, Rothschild & Haddow, 1983). Other Ceratophyllidae are known specialists. *C. rossittensis rossittensis* parasitizes crows, *Corvus corone*, *C. affinis affinis* swallows, *Hirundo rustica*; whilst 4 other species, *C. caliotes*, *C. delichoni*, *C. fareni fareni* and *C. hirundinis*, are all parasites of the house martin *Delichon urbica* (Traub *et al.* 1983). Apart from these specialists, many bird fleas have been recorded in a variety of host's nests and hence apparently exhibit extensive overlap in host exploitation.

Width of the host spectrum of *Ceratophyllus gallinae*

Overall, our survey shows that hole-nesting birds are the main hosts of *C. gallinae* and appearance in the nests of other species seems less predictable. The host spectrum maintained among the hole and

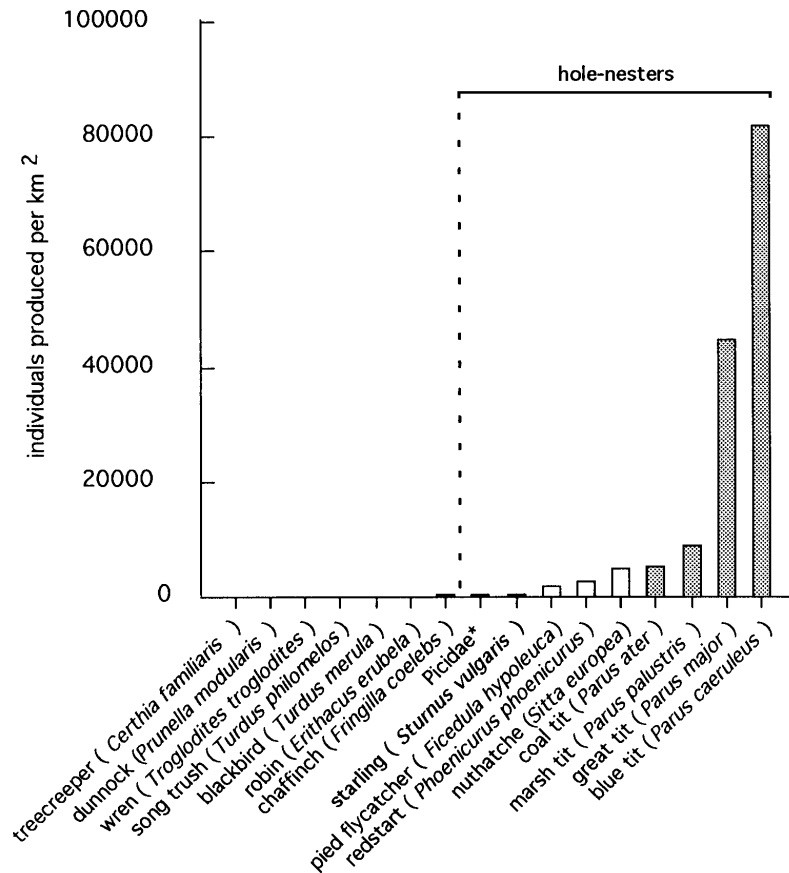


Fig. 5. Number of fleas produced in the nest of different species ($N(s)$) in a hypothetical lowland forest community. Shaded bars are hole-nesting Paridae. *Picidae family means were used because no data are available for the great spotted woodpecker (*Dendrocopos major*).

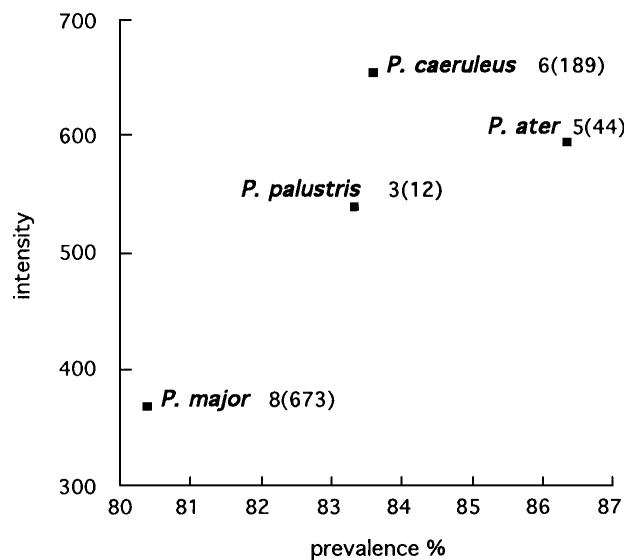


Fig. 6. Relationship between mean intensities and prevalence of infestation in hole-nesters of the family Paridae. Next to the species' names are the number of studies involved and the number of nests analysed (parentheses).

crevice nesters is considerable, however, and contrasts with the rather narrow spectrum of the ceratophyllid species typical for colonial breeding

birds such as, for example, swallows and house martins. The spatial and temporal distribution of the main hosts of bird ectoparasites is likely to determine the potential for gene flow among subpopulations from different host species, and is therefore of importance for the evolution and maintenance of host spectrum width.

When the main host is overdispersed, as is the case in the colonially breeding swallow and house martin, both flea immigration rates and variation in ecological conditions within the host colony will be low. These two conditions lead to little gene flow and narrow selection pressures, and will therefore favour parasite specialization on a single host species. In contrast, if the main hosts are underdispersed, as is the case for territorial hole-nesters, variation in ecological condition among nests is larger and gene flow between flea subpopulations and meta-populations from different habitats is higher. A broad tolerance of nest texture, temperature and humidity by the egg, larval and adult flea stages may be favoured, which also facilitates the exploitation of additional host species. Under these conditions a wider host-spectrum will be maintained even if the majority of parasites breed on the main host. Furthermore, specialization on an underdispersed host would increase the risk of not finding a suitable

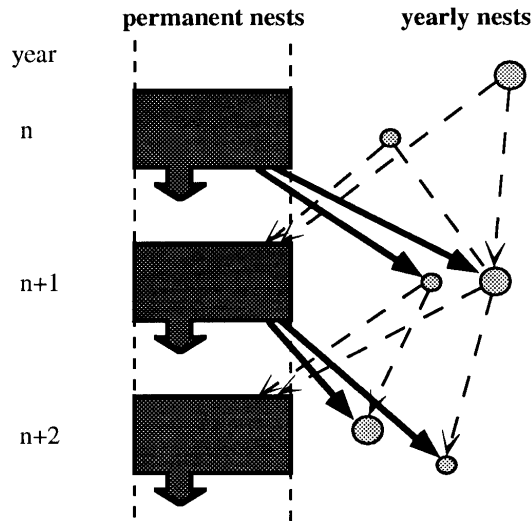


Fig. 7. The contrast between the number of parasites produced in permanent nest sites (hollows, crevices) and in yearly nests. Arrows symbolize the transmission of recruits from each type of nest.

host, and the fleas' host spectrum may therefore reflect the trade-off between the benefits from a high reproductive rate on an optimal host and the cost of not finding the optimal host for reproduction.

There is also a temporal scale which may be of importance for the question why a wide host spectrum is maintained among the hole nesting bird species. Most of these bird species do not excavate a breeding site but use naturally occurring tree holes, which generally appear when dead branches fall off the tree trunk. The holes are small first and become bigger over time. The body size related dominance hierarchy of potential host species leads to the pattern that smaller bird species occupy the nesting hole first, and larger species later. Other holes are excavated by woodpeckers and later used by other forest birds. *C. gallinae* subpopulations maintain themselves in hole nests from one year to another (Fig. 7), and may therefore encounter a new host species every following year. These naturally occurring changes in host species will therefore prevent specialization on one single host species.

Experiments have also shown that birds avoid infested nest sites (Oppliger *et al.* 1994; Christe *et al.* 1994). Hen fleas dispersing from unused nest boxes invariably migrate upwards in trees (Humphries, 1968). This behaviour increases the encounter rate with foraging tits, but it will also favour encounters with other tree-foraging bird species. Also, it is not known if hen fleas are phenotypically plastic in their dispersal behaviour and if individuals bred from ground and bush nests, which are used only for one season disperse earlier in search of a host than hen fleas bred from repeatedly used nest holes. Although the present data seem unequivocal concerning the coevolutionary potential between hen fleas and Paridae, evidence for coadaptations and trade-offs

(Futuyma & Moreno, 1988; Thompson, 1994) that would decrease the fitness of fleas infesting secondary hosts is slim.

Relationship between intensity and prevalence

There are different mutually non-exclusive mechanisms that might account for the relationship between i and p exhibited by hen fleas. (1) Host-parasite compatibility: low intensities of infestations in unsuitable hosts may be coupled with apparent low prevalence if the nest conditions are poor both for developmental stages and for adult survival. (2) Nest type: ground and bush nests are usually not used from one year to the next. Cavities and nestboxes on the contrary are often in limited supply and occupied by birds year after year. Once infested by fleas, they probably remain so for several flea generations (Fig. 7), hence higher prevalence. (3) Host choice: selection is predicted to favour individuals that maximize their encounter rate with suitable hosts. This should lead to the evolution of complex non-random dispersal and host searching behaviour, which may account for some of the variation in prevalence of *C. gallinae* among its host species.

Further studies

A growing number of studies show that parasites can specialize despite an apparent long list of hosts (Thompson, 1994). This study reveals that hole-nesting Paridae are the main hosts of the 'generalist' *C. gallinae*. The spatial and temporal scale of this study, however, allows few inferences at lower levels of organization. A better understanding of the interaction of the hen flea with its host-complex would require experimental data on the reproductive rates and the transmission rate β of individual fleas on different hosts and in different habitats. Although the mobility of bird fleas does not favour extensive genetic differentiation between habits, the understanding of bird-flea interactions would gain from a genetic approach. To this end, the estimation of the degree of genetic differentiation between spatially distinct parasite populations, and the evaluation of within-population variance and phenotypic plasticity are fundamental.

The work was supported by a Swiss National Science Foundation Grant (31.43570.95 to H.R.).

REFERENCES

- ASH, J. (1952). Siphonaptera bred from birds' nests. *Entomologists' Monthly Magazine* **88**, 217–222.
 BATES, J. K. (1956). Host selection in bird fleas. *Journal of Animal Ecology* **25**, 475–476.
 BEATH, K. J. (1995). *GLMStat User Manual*. Version 1.5.1.

- COTTON, M. J. (1970). The life history of the hen flea, *Ceratophyllus gallinae* (Schrank) (Siphonaptera, ceratophyllidae). *Entomologist* **103**, 45–48.
- CHRISTE, P., OPPLIGER, A. & RICHNER, H. (1994). Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*. *Animal Behaviour* **47**, 895–898.
- DU FEU, C. R. (1987). Some observations on fleas emerging from tit nestboxes. *Ringling and Migration* **8**, 123–128.
- EEVA, T., LEHIKONEN, E. & NURMI, J. (1994). Effects of ectoparasites on breeding success of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in an air pollution gradient. *Canadian Journal of Zoology* **72**, 624–635.
- FUTUYMA, D. J. & SLATKIN, M. (1983). *Coevolution*. Sinauer Associates, Sunderland, MA, USA.
- FUTUYMA, D. J. & MORENO, G. (1988). The evolution of ecological specialisation. *Annual Review of Ecology and Systematics* **19**, 207–233.
- GLUTZ VON BLOTZHEIM, U. N. & BAUER, K. M. (1980–1993). *Handbuch der Vögel Mitteleuropas*, vols 9–13, Aula-Verlag GmbH, Wiesbaden, Germany.
- HARPER, G. H., MARCHANT, A. & BODDINGTON, D. G. (1992). The ecology of the hen flea *Ceratophyllus gallinae* and the moorhen flea *Dasypsyllus gallinulae* in nestboxes. *Journal of Animal Ecology* **61**, 317–327.
- HEEB, P., WERNER, I., RICHNER, H. & KÖLLIKER, M. (1996). Horizontal transmission and reproductive rates of hen fleas in great tits. *Journal of Animal Ecology* **65**, 474–484.
- HOLMES, J. C. (1983). Evolutionary relationships between parasitic helminths and their hosts. In *Coevolution* (ed. Futuyma, D. J. & Slatkin, M.), pp. 161–185. Sinauer Associates, Sunderland, MA, USA.
- HOLMES, J. C., HOBBS, R. P. & LEONG, T. S. (1977). Populations in perspective: community organisation and regulation of parasite populations. In *Regulation of Parasite Populations* (ed. Esh, G. W.), pp. 209–245. Academic Press, New York.
- HUMPHRIES, D. A. (1967). The behaviour of fleas (Siphonaptera) within the cocoon. *Proceedings of the Royal Entomological Society of London, A* **42**, 62–70.
- HUMPHRIES, D. A. (1968). The host-finding behaviour of the hen flea, *Ceratophyllus gallinae* (Schrank) (Siphonaptera). *Parasitology* **58**, 403–414.
- JURIK, M. (1974). Bionomics of fleas in birds' nests in the territory of Czechoslovakia. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovaca*, **Brno** **8**, 1–54.
- KIME, R. D. (1962). A study of two bird fleas, *Ceratophyllus gallinae* (Schrank) and *Dasypsyllus gallinulae* (Dale), in the nests of hole-nesting birds. *Entomologists' Monthly Magazine* **98**, 54–59.
- KIZIROGLU, I. (1984). Untersuchungen über Insekten, insbesondere Flöhe als Bewohner von Nestern der Kohlmeise, *Parus major* L. in Nistkästen in einem Fichtenwald. *Anzeiger für Schädlingskunde und Pflanzenschutz* **57**, 70–72.
- LANGER, R. & TILGNER, W. (1957). Der Flohbesatz in den künstlichen Nisthöhlen des Frankfurter Stadtwaldes. *Vogelwelt* **78**, 176–181.
- LEHANE, M. J. (1991). *Biology of Blood Sucking Insects*. Harper Collins Academic, London.
- MARSHALL, A. G. (1981). *The Ecology of Ectoparasitic Insects*. Academic Press, London.
- MERILÄ, J. & ALLANDER, K. (1995). Do great tits (*Parus major*) prefer ectoparasite-free roost sites? An experiment. *Ethology* **99**, 53–60.
- NORDBERG, S. (1936). Biologisch-ökologische Untersuchungen über die Vogelnidicolen. *Acta Zoologica fennica* **21**, 1–168.
- OPPLIGER, A., RICHNER, H. & CHRISTE, P. (1994). Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). *Behavioral Ecology* **5**, 130–134.
- PERRIN, N., CHRISTE, P. & RICHNER, H. (1996). On host life-history response to parasitism. *Oikos* **75**, 317–321.
- RAES, H. (1969). Onderzoek over Siphonaptera in nesten van koolmees, pimpelmees en ringmus. *Natuurwetenschappelijk Tijdschrift* **51**, 90–93.
- ROHDE, K. (1980). Host specificity indices of parasites and their implication. *Experientia* **36**, 1370–1371.
- ROTHSCHILD, M. (1952). A collection of fleas from the bodies of british birds, with notes on their distribution and host preferences. *Bulletin of the British Museum, Natural History, Entomology* **2**, 187–232.
- ROTHSCHILD, M. & CLAY, T. (1952). *Fleas, Flukes and Cuckoos*. Collins, London.
- RICHNER, H. & HEEB, P. (1995). Are clutch and brood size patterns in birds shaped by ectoparasites. *Oikos* **73**, 435–441.
- RICHNER, H., OPPLIGER, A. & CHRISTE, P. (1993). Effect of an ectoparasite on reproduction in great tits. *Journal of Animal Ecology* **62**, 703–710.
- SMIT, F. G. A. M. (1957). The recorded distribution and hosts of siphonaptera in Britain. *Entomologist's gazette* **8**, 45–75.
- THOMPSON, G. B. (1937). The parasites of British birds and mammals. XV. Bird-fleas and their hosts. *Entomologists' Monthly Magazine* **73**, 137–142.
- THOMPSON, J. N. (1994). *The Coevolutionary Process*. The University of Chicago Press, Chicago.
- TRAUB, R., ROTHSCCHILD, M. & HADDOW, J. F. (1983). *The Ceratophyllidae: Key to the Genera and Host Relationships*. Cambridge University Press, Cambridge.
- TRIPET, F. & RICHNER, H. (1997). Host responses to ectoparasites: Food compensation by parent blue tits. *Oikos* (in the Press).
- WILKINSON, L. (1992). *SYSTAT: Statistics*, Version 5.2 Edition. Evanston, IL, USA.