Host defence mediates interspecific competition in ectoparasites

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Summary

1. Interspecific competition influences which, how many and where species coexist in biological communities. Interactions between species in different trophic levels can mediate interspecific competition; e.g. predators are known to reduce competition between prey species by suppressing their population sizes. A parallel phenomenon may take place in host–parasite systems, with host defence mediating competition between parasite species.

2. We experimentally investigated the impact of host defence (preening) on competitive interactions between two species of feather-feeding lice: 'wing' lice *Columbicola columbae* and 'body' lice *Campanulotes compar*. Both species are host-specific parasites that co-occur on rock pigeons *Columba livia*.

3. We show that wing lice and body lice compete and that host defence mediates the magnitude of this competitive interaction.

4. Competition is asymmetrical; wing louse populations are negatively impacted by body lice, but not vice versa. This competitive asymmetry is consistent with the fact that body lice predominate in microhabitats on the host's body that offer the most food and the most space.

5. Our results indicate that host-defence-mediated competition can influence the structure of parasite communities and may play a part in the evolution of parasite diversity.

Key-words: columbiformes, community structure, lice, niche partitioning, preening.

Introduction

Interspecific competition is one of the most important factors influencing community structure (Tilman 1982; Morin 1999). Interspecific competition may lead to niche partitioning, or cause the exclusion of species from the community (Gause 1934; Hardin 1960; Levin 1970; Schoener 1983). Competitive interactions between two species can be influenced by a third species (Chesson 2000; Kneitel & Chase 2004; Holt & Dobson 2006; van Veen, Morris & Godfray 2006). For example, predators facilitate the coexistence of competing prey species by suppressing prey populations, which in turn prevents competitively superior species from monopolizing resources (Paine 1966; Holt 1977; Holt & Lawton 1994; Abrams 1999; Chase *et al.* 2002). Host–parasite systems resemble predator–prey systems, in that host defence can suppress parasite populations. Thus, like predation, host defence has the potential to mediate interspecific competition and influence which, how many and where parasite species coexist.

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Factors influencing the structure of parasite communities are still relatively unexplored, in part, because of the difficulty of manipulating and monitoring parasites in natural settings (Janovy 2002). Although parasites are known to compete (Combes 2001; Poulin 2007), few studies have tested the influence of host defence on competition between parasite species. Moran & Whitham (1990) showed that host-plant resistance influenced the competitive interactions of two distantly related aphid species that exploit the same host. Host-plant resistance prevented the competitive exclusion of one aphid species by the other species. In studies of interspecific interactions of gut helminths parasitizing wild rabbits (Lello *et al.* 2004), and clawed toads (Jackson *et al.* 2006), the authors argue that the observed interactions were likely mediated by responses of the hosts' immune systems.

Studies with immunocompromised rats indicate that intraspecific competition within a single nematode species is regulated by host immune defence (Paterson & Viney 2002). More recently, Raberg *et al.* (2006) showed that host-immune responses mediate intraspecific competition among strains within a single species of malaria. To our knowledge, only one study has looked at the influence of host defence on competition between ectoparasites. Waage & Davies (1986) showed that

competition between species of blood-sucking flies (Tabanidae) was mediated by the tail-flicking defence of their host (Camargue horses). The flies in the Waage and Davies study experienced competition for enemy-free space (Jeffries & Lawton 1984), where the 'enemy' was the host defending itself.

Here we directly quantify long-term fitness consequences of host defence on interspecific competition, using a host–parasite system consisting of rock pigeons *Columba livia* (Gmelin) and their feather-feeding lice (Insecta: Phthiraptera). Feather lice are permanent ectoparasites that spend their entire life cycle on the body of the host, where they feed on the barbules of downy feathers (Marshall 1981). The 3–4-week life cycle begins with the egg, which is glued to the feathers, then progresses through three nymphal instars to the adult stage. Feather lice affect host fitness because the feather damage they cause reduces host mating success (Clayton 1990), thermoregulatory ability (Booth, Clayton & Block 1993), and survival (Clayton *et al.* 1999). Birds defend themselves from lice primarily by preening (Clayton *et al.* 2005).

Rock pigeons are commonly infested with two types of feather lice: 'wing' lice *Columbicola columbae* (Linneaus) and 'body' lice *Campanulotes compar* (Burmeister). Wing lice, which are slender in shape, lay their eggs and spend the majority of their time on the flight feathers of the wings and tail. Body lice, which are oval, lay their eggs and spend virtually all of their time on the abdominal feathers (Nelson & Murray 1971). Wing lice typically escape from preening by inserting their elongate bodies in the furrows between adjacent barbs of the flight feathers (Bush, Sohn & Clayton 2006). Body lice escape from preening by burrowing into the loose downy portions of abdominal contour feathers (Clayton 1991).

Differences between wing and body lice in microhabitat use and morphology may be consequences of historical competition (Clay 1949). Although it is difficult to control for the 'ghost of competition past' (Connell 1980), it is possible to experimentally test for competition in zones where these parasite species currently overlap. Despite some differences in microhabitat use, both wing lice and body lice feed on the downy portions of abdominal contour feathers because only these feathers are fine enough to be ingested by the lice (Bush & Clayton 2006). Wing lice must commute to the abdominal region to feed as they cannot feed on the coarse barbules of the flight feathers. Thus, even though wing lice and body lice are often spatially segregated, they feed on the same feathers and therefore may compete for food. Wing and body lice may also compete for space to mate, reproduce and avoid preening.

To test for competition we infested different groups of rock pigeons with wing lice, body lice or both species of lice. To test the influence of preening on competition, we impaired preening in half of the birds in each group. Thus, we had a 2 × 3 experimental design (normal-preening vs. impaired-preening × wing lice only, body lice only or both lice together). We tested for both numerical and functional responses to competition (Thompson 1980) by comparing parasite population dynamics, food use and the microhabitat distributions of lice on birds in the different experimental treatments.

Methods

POPULATION DYNAMICS AND MICROHABITAT DISTRIBUTION

Forty-two wild rock pigeons were captured with walk-in traps in Salt Lake City, Utah, and housed individually in $30 \times 30 \times 56$ cm wire mesh cages in our animal facility. Cages were separated with plexi-glass partitions to prevent the possibility of contact transmission of lice between birds in adjacent cages. Birds were maintained on a 12-h light/dark photoperiod and provided ad libitum grain, grit and water. The birds were cleared of 'background' louse infestations by housing newly trapped birds at < 25% relative humidity for ≥ 10 weeks. This method kills 100% of lice and eggs (Moyer, Drown & Clayton 2002), while avoiding residues that might result from the use of chemical fumigants. At the start of the experiment the relative humidity in the animal rooms was elevated to the optimum for lice (60–70%; Nelson & Murray 1971; Bush & Clayton 2006).

The 42 louse-free birds were randomly divided among three louse treatments (*n* = 14 birds per treatment) in which birds were seeded with 100 wing lice, 100 body lice, or a combination of 50 wing and 50 body lice (Clayton, Al-Tamimi & Johnson 2003). To test the impact of host defence on competition we experimentally impaired preening in half of the birds within each treatment, by inserting a small C-shaped plastic bit between the upper and lower mandibles of the bill (*n* = 7 birds per louse × preening treatment). Bits spring shut slightly in the nostrils to prevent dislodging, but they do not interfere with feeding and they have no apparent side-effects (Clayton & Tompkins 1994). The bits create a 1–3 mm gap between the mandibles that impairs the forceps-like action of the bill required to remove ectoparasites efficiently (Clayton *et al.* 2005). The increase in louse load caused by impairing preening with bits is within the range of natural variation in louse load observed in wild populations (Clayton *et al.* 1999).

To test for effects of host-mediated parasite competition we compared the relative fitness (survival and reproductive success) of wing and body louse populations among experimental treatments. The number and microhabitat distribution of wing lice and body lice were monitored on all birds every 6 weeks for 42 weeks, which is approximately 10 louse generations (Martin 1934). We used the visual examination method of Clayton & Drown (2001). This sampling method accurately reflects total louse load, yet only requires examination of five plumage microhabitats, which minimizes disturbance to the lice. The visual examination consisted of recording the number and location of wing and body lice during careful examination of the following microhabitats: under-surfaces of one wing and the tail (approximately 60 s each), the back (30 s), keel (30 s) and rump (60 s).

FEATHER CONSUMPTION

We measured the relative consumption of feathers by wing and body lice from each of eight microhabitats (Fig. 1a) at the end of the experiment. For each bird we pulled small clumps of feathers from each microhabitat and weighed the 10 longest feathers to the nearest 0·01 mg on an analytical balance (as in Clayton *et al.* 1999). Flight feathers (wing and tail) were not sampled because they are not consumed by lice (Nelson & Murray 1971; Clayton 1990). To determine the amount of feather material eaten by lice, the mass of feathers from birds in the experiment was compared with feathers pulled from other (louse-free) birds kept in the lab.
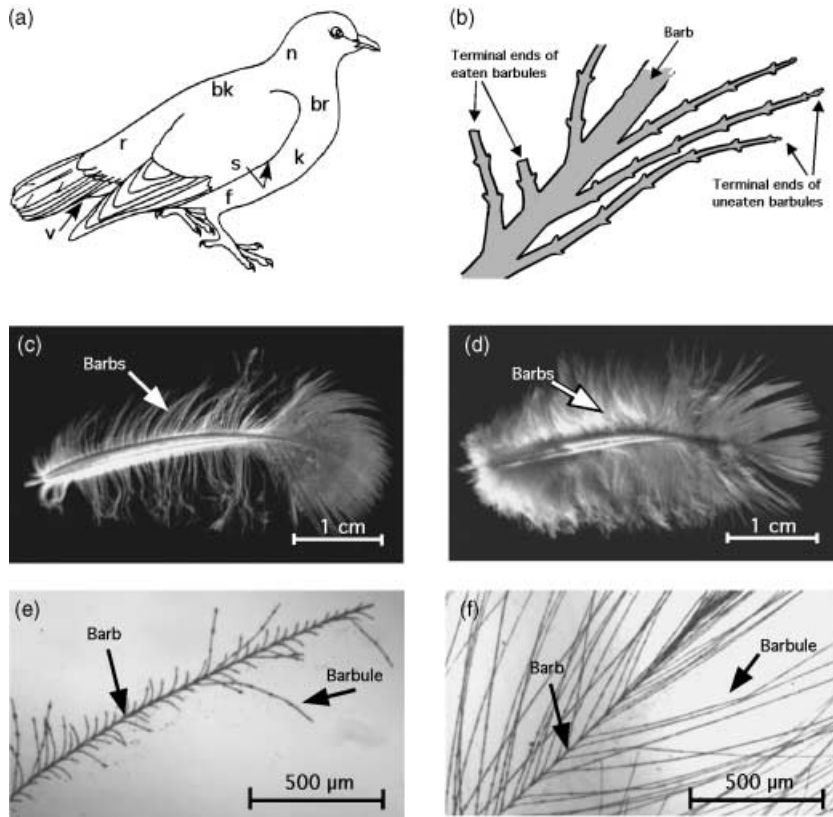
Fig. 1. Feather consumption by wing and body lice. (a) Microhabitats from which feathers were sampled to quantify feather consumption: back (bk), nape (n), breast (br), keel (k), side (s), flank (f), vent (v) and rump (r). (b) Schematic of differences in the terminal diameters of eaten and uneaten feather barbules. (c) Photo of a rump feather severely eaten by lice. (d) Photo of a normal rump feather. (e) Photo of a feather barb with barbules severly eaten by lice. (f) Photo of feather barb with normal barbules.

To determine whether wing and body lice consume the same parts of feather barbules, we measured the terminal ends of the eaten barbules that lice leave behind (Fig. 1b). Feather barbules are tapered, being nearly twice as wide at the base as they are at the tip. Thus, the diameter of the terminal end of the eaten barbule indicates the part of the feather that was not consumed, presumably because that portion is too stout for lice to sever with their mandibles (Clay 1951; Clayton 1991). As we were interested in comparing which parts of the barbules wing lice and body lice consume under extreme conditions, we selected severely eaten rump feathers from several birds (Fig. 1c,e). Feather barbs were haphazardly selected from the centre of each feather and mounted on microscope slides. From these slide-mounted barbs, we haphazardly selected and measured 50 barbules from birds with only wing lice, and birds with only body lice. These measurements were compared with the terminal diameter of barbules from other louse-free birds kept in the lab (Fig. 1d,f). The diameter of the terminal end of each barbule was measured to the nearest 0·2 μm using a Nikon DIC microscope fitted with an ocular micrometer.

Results

POPULATION DYNAMICS

The presence of body lice had a significant negative effect on wing louse populations (Fig. 2a; Repeated Measures ANOVA: d.f. = 1, 20; $F = 11·68$; $P = 0·003$). The magnitude of this effect depended on host defence; there was a significant interaction between the main effects of preening and the presence of body lice (d.f. = 1, 20; $F = 10·11$; $P = 0·005$). On birds that could preen normally, birds with only wing lice tended to have more wing lice than birds also parasitized by body lice; infestations of only wing lice were, on average, 2·8-fold larger than wing louse populations on coinfested birds. However, this difference was not significant (d.f. = 1, 11, $F = 3·13$, $P = 0·10$). When preening was impaired, birds with only wing lice had significantly more wing lice than birds also parasitized by body lice (Fig. 2a; d.f. = 1, 9; $F = 9·08$; $P = 0·01$). Infestations of only wing lice were, on average, four-fold larger than wing louse populations on coinfested birds. When body lice were present, wing louse populations levelled off quickly; in contrast, when body lice were absent, wing louse populations kept increasing until week 24 before levelling off (Fig. 2a). The variation in wing louse load was greatest at week 24 because the population on a single bird increased more rapidly than those on the other birds in the same treatment. By week 36 the wing louse populations on the other birds had caught up, reducing the variation.

The presence of wing lice had no significant effect on body louse populations (Fig. 2b; Repeated Measures ANOVA: d.f. = 1, 20; $F = 0·98$; $P = 0·33$). This was true whether or not host defence was impaired (nonsignificant interaction between the main effects of preening and the presence of wing lice: d.f. = 1, 20; $F = 1·07$; $P = 0·32$). As the effect of competition was strongest on impaired-preening birds, the data we report on resource use (i.e. feather consumption and microhabitat distribution, see below) are restricted to the impaired-preening treatment.
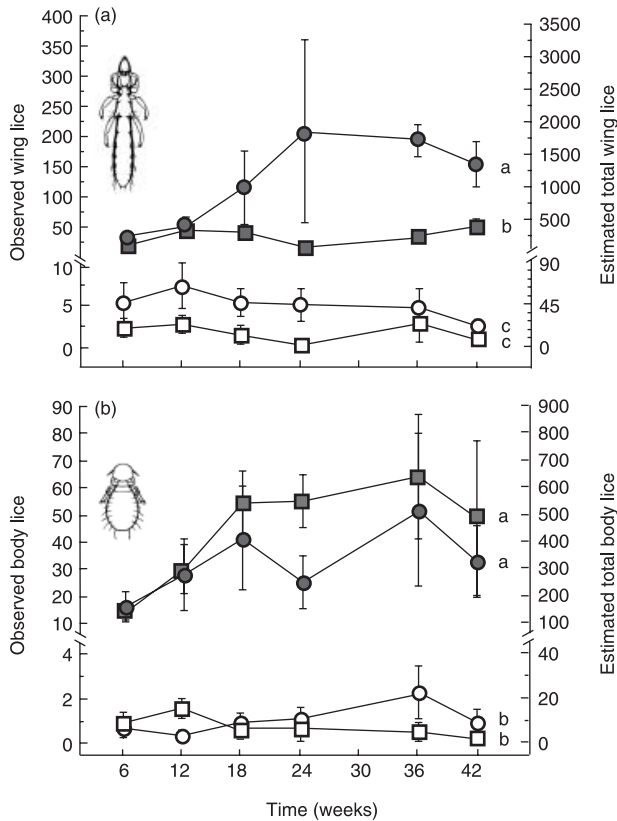
Fig. 2. Population dynamics (mean ± SE) of (a) wing lice and (b) body lice on birds with impaired preening (●■) and normal preening (○□); circles represent birds with a single species of louse; squares represent birds with two species of lice. Left axis is the number of lice observed per bird during visual censuses; right axis is the estimated total number of lice per bird (based on 9× and 10× conversion factors for wing and body lice, respectively; Clayton & Drown 2001). Different lower case letters indicate significant differences (see Results). Not all of the birds 'survived' the 42-week experiment: two died during the experiment probably because they were already old when captured; another four birds from 'single louse species' treatments were excluded because they were found to be contaminated with both species of lice. Final samples are as follows: ●, impaired-preening, alone (n = 5 birds with wing lice and n = 5 birds with body lice); ■, impaired-preening, together (n = 6 birds); ○, normal-preening, alone (n = 7 birds with wing lice and n = 7 birds with body lice); □, normal-preening, together (n = 6 birds).
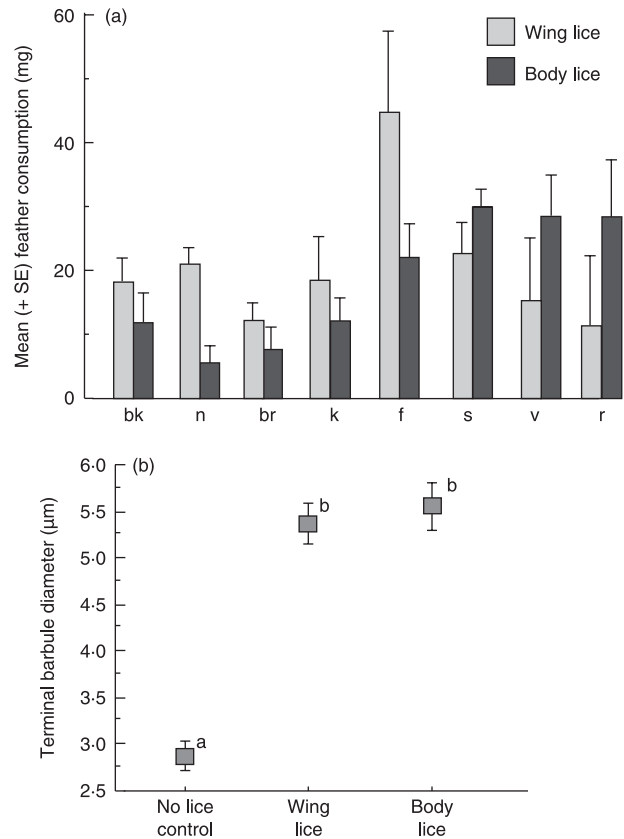

Fig. 3. Feather consumption of wing and body lice. (a) Feather consumption across eight feather microhabitats shown in Fig. 1a. Feather consumption was determined by comparing the mass of feathers with lice to the mass of louse-free controls (zero indicates the mass of the louse-free controls). (b) Mean (± SE) diameter of the terminal ends of uneaten barbules, compared with barbules consumed by wing and body lice. Lower case letters indicate significant differences (see Results).

FEATHER CONSUMPTION

On impaired-preening birds the feathers from birds with lice (body lice, wing lice and both species of lice) weighed significantly less than feathers from control birds without lice (Repeated Measures ANOVA, d.f. = 3, 18; F = 7·65, P = 0·002). The feathers from birds with lice weighed 24% less, on average, than feathers from birds without lice. However, there was no significant difference in the amount of feathers consumed by body lice vs. wing lice (d.f. = 1, 8, F = 0·127, P = 0·73). Both wing and body lice consumed feathers in all eight microhabitats (Fig. 3a). However, there was a significant interaction between louse species and microhabitat (d.f. = 7, 56; F = 3·16, P = 0·007), indicating that wing lice and body lice showed

some partitioning of food resources. Wing lice tended to eat more feathers from the back, nape, breast, keel and flank, whereas body lice tended to eat more feathers from the side, vent, and rump (Fig. 3a).

In addition to testing for microhabitat differences in feather consumption, we also tested for spatial differences in the feather consumption of wing and body lice on a finer scale – along the feather barbules themselves. The terminal diameters of the barbules were significantly larger on feathers with lice compared with control feathers without lice (Fig. 3b; ANOVA, d.f. = 2, 147, F = 46·72, P < 0·0001). However, there was no significant difference in the terminal diameter of the feather barbules eaten by body lice vs. wing lice (Scheffe's post-hoc test P = 0·84).

MICROHABITAT DISTRIBUTION

We quantified the distributions of both species of lice on impaired-preening birds across two very different feather regions: the abdominal feathers and the flight feathers. Wing lice were found on abdominal feathers significantly less often
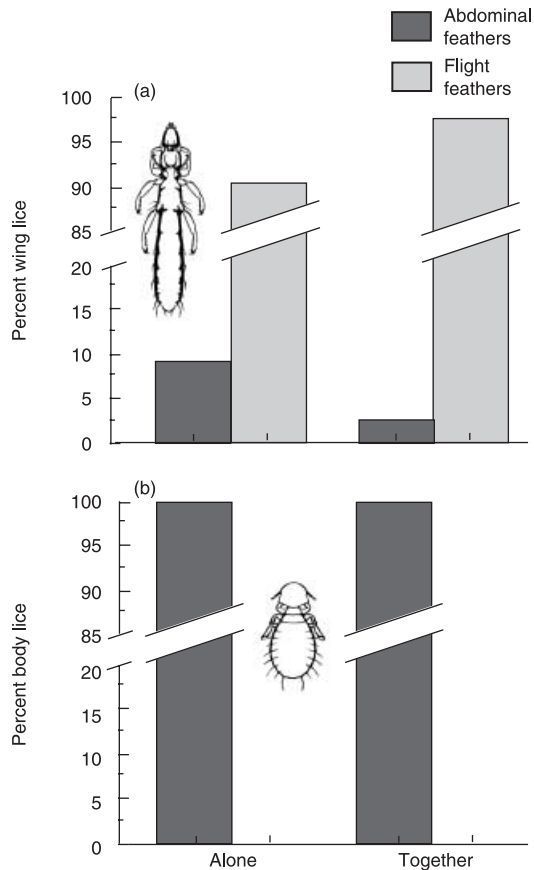
Fig. 4. Distribution of wing and body lice in two major feather regions: abdominal feathers vs. flight feathers. Wing lice (a) shifted microhabitat significantly in the presence of body lice ($P < 0.0001$), whereas body lice (b) remained exclusively on abdominal feathers, regardless of the presence of wing lice ($P = 1.0$).

Fig. 5. Distribution of wing and body lice across three abdominal feather microhabitats: rump, back, and keel. Although wing lice (a) and body lice (b) both showed significant microhabitat shifts in the presence of the other louse, the response by wing lice was much greater than that by body lice (see Results).

when body lice were present, than when body lice were absent (Fig. 4a; Fisher's exact test, $n = 4781$, $P < 0.0001$). In contrast, the presence of wing lice did not impact the microhabitat distribution of body lice (Fig. 4b; Fisher's exact test, $n = 2546$, $P = 1.0$), which were found on the abdominal feathers, regardless of the presence of wing lice.

Within the abdominal body region, the microhabitat distribution of wing lice shifted significantly away from the rump when body lice were present (Fig. 5a; $\chi^2 = 9.23$, d.f. = 2, $n = 337$ lice, $P = 0.01$). Similarly, the microhabitat distribution of body lice shifted away from the rump when wing lice were present (Fig. 5b; $\chi^2 = 40.97$, d.f. = 2, $n = 2546$ lice, $P < 0.01$), but less dramatically. Only 11% of the body louse population was displaced from the rump in the presence of wing lice, compared with 29% of the wing louse population displaced from the rump in the presence of body lice.

Discussion

Host-mediated competition may influence the community structure of a diverse array of host–parasite systems. However, despite the fact that parasites represent a large portion of
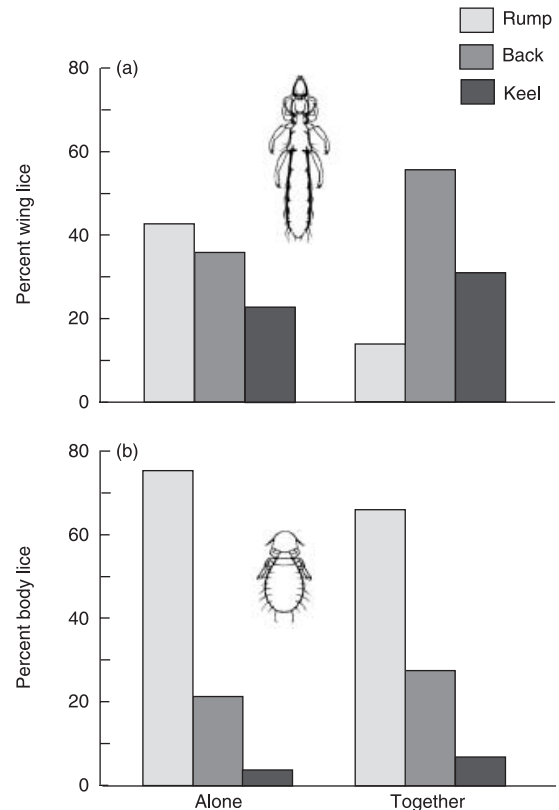
global biodiversity (Price 1980), host-mediated competition has seldom been tested. In this paper we describe the results of a study showing that host defence mediates interspecific competition in ectoparasitic feather lice. Our experiment compared the long-term relative fitness of wing lice and body lice among treatments that manipulated the presence of a potential competitor, as well as host defence. Our results show that: (1) wing and body lice compete; (2) competition is asymmetrical; and (3) the magnitude of competition is dependent on host defence.

Competition was strongest when preening was impaired. Under this circumstance we found that the presence of body lice suppressed wing louse populations. When body lice were absent, wing lice experienced competitive release and the size of wing louse populations increased dramatically (Fig. 2a). In comparison, wing lice had no significant effect on the size of body louse populations (Fig. 2b). On birds that could preen normally, wing louse populations on birds without body lice tended to be larger than the wing louse populations on birds with body lice, but the effect was not significant. The experimental impairment of host defence did not lead to competitive exclusion of wing lice over the course of the experiment, but host defence still mediated the magnitude of competition. We found that host defence kept louse populations small, minimizing competition for resources.
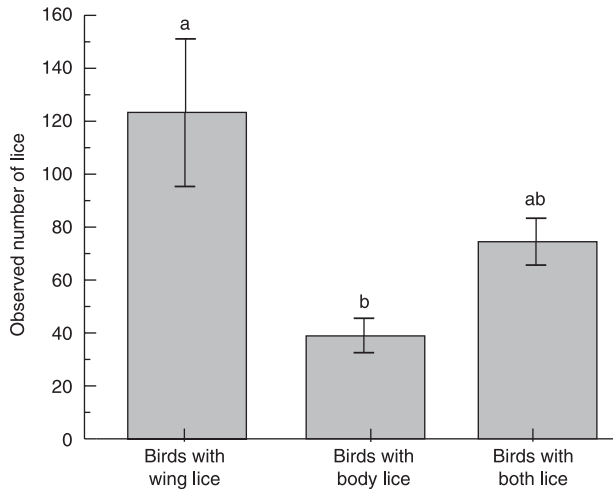
Fig. 6. Grand mean (± SE) number of lice on impaired-preening birds over the course of the 42 week experiment. The number of lice differed significantly among treatments (ANOVA; d.f. = 2, 93; $F = 6.04$; $P = 0.003$); lower case letters indicate significant differences. Birds with only wing lice had significantly more lice than birds with only body lice (Scheffe's post-hoc test $P = 0.003$). If lice were not competing, then the number of lice on birds with both species should have been equivalent to the total number of lice on birds with wing lice added to the number of lice on birds with body lice. However, the number of lice on coinfested birds did not differ significantly from birds with either wing or body lice (Scheffe's post-hoc tests $P = 0.12$), which is indicative of competition.

It is likely that the impact of body lice on wing lice is the result of indirect competition for limiting resources such as food or space. We found that wing and body lice eat similar parts of the feather barbules, which provides an opportunity for resource competition. More importantly, we found that both wing and body lice ate feathers from all eight sampled feather microhabitats (Fig. 3), indicating that the food resources of wing and body lice overlap. This overlap in the use of resources sets the stage for competition for food. However, the population dynamics observed on impaired-preening birds in our experiment suggest that wing and body lice are not merely competing over limited food resources. Pigeons only moult new feathers once a year. As feathers are not continually renewed, louse populations limited only by food should crash when the food is depleted. In our study, the louse populations did not crash even though new feathers did not grow during the course of the experiment. Instead, both wing and body louse populations reached and maintained a carrying capacity. This pattern suggests that wing and body lice are competing for some resource instead of, or in addition to, food.

We provide evidence suggesting that wing and body lice compete for space. Wing lice are found on the abdominal feathers and flight feathers, whereas body lice are restricted to the abdominal feathers (Fig. 4). If space is a limiting resource, we would expect that lice restricted to a smaller portion of the host's body will have a smaller population than the lice using more of the host's body. Indeed, we found that birds with only body lice had smaller louse populations than birds with only wing lice (Fig. 6). Moreover, if body lice can outcompete wing lice for space on the abdominal feathers, then wing louse

populations should be depressed when body lice are present, whereas body louse populations should not be affected by the presence of wing lice. We observed both of these patterns. Wing louse populations were severely depressed when body lice were present (Fig. 2a), but there was no significant effect of wing lice on body louse populations (Fig. 2b).

We found that wing lice shifted their microhabitat distributions considerably when body lice were present. First, wing lice were found less frequently on the abdominal feather region when body lice were present (Fig. 4a). In contrast, body lice did not shift their distribution among feather regions when wing lice were present (Fig. 4b). Among microhabitats on the abdomen, both species of lice were most common on the rump feathers when the other louse species was absent (Fig. 5). This is not surprising because rump feathers weigh nearly twice as much as feathers from either the back or the keel and thus provide the most food and space (mean ± SE mass of a feather from the: rump, 13.5 mg ± 0.8; back, 6.3 mg ± 0.2; and keel, 8.2 mg ± 0.2). Under competitive circumstances, we found that both wing lice and body lice shifted their distribution away from the rump (Fig. 5). The proportion of body lice on the rump only decreased from 75% in the absence of wing lice to 64% when wing lice were present. Although body lice shifted away from the rump, wing lice experienced the most dramatic shift. The proportion of wing lice on the rump decreased from 43% in the absence of body lice to just 14% when body lice were present. The shifts in microhabitat that we observed with wing lice are consistent with interspecific competition for food and space; however, these results are not independent of intraspecific competition. The absence of body lice and concomitant increase in wing louse populations are inseparable. In the future, experiments manipulating louse density may be able to separate the effects of interspecific vs. intraspecific competition.

It is unclear how body and wing lice defend spatial resources. It is unlikely that space is defended physically. In the many hours we spent observing lice, we never observed direct aggression between wing and body lice. Alternatively, the interaction could be mediated chemically. Chemotaxis is known to occur in lice; human body lice *Pediculus humanus* (Linneaus) are attracted to conspecific faeces (Mumcuoglu, Galun & Ikan 1986). It is also possible that chemical compounds in faeces or pheromones repel other species of lice.

Competition between wing and body lice may have played a fundamental role in the diversification of feather lice. Clay (1949) speculated that competition with body lice on the abdomen of the bird caused ancestral 'wing' lice to adapt to the harsher microhabitats of the flight feathers. Our data are consistent with this hypothesis. Interestingly, 'wing' louse and 'body' louse ecomorphs are not restricted to Columbiformes; they occur on many avian orders (Price *et al.* 2003). Recent molecular evidence indicates that wing and body lice have evolved repeatedly within many of the major louse lineages parasitizing different bird orders (Smith & Johnson, pers. comm.). Our results suggest that interspecific competition mediated by host defence may have been important in the diversification of feather lice.

Traditionally, research seeking to understand the evolution of parasite diversity has focused on two aspects of parasite biology: the interaction between hosts and their parasites, and the interaction among parasites (Combes 2001; Poulin 2007). Studying host–parasite interactions or parasite–parasite interactions in isolation obscures the influence that the host may have over parasite–parasite interactions. As a host individual is ultimately a finite resource for which all of its parasites are competing (Janzen 1973), it is crucial to understand how hosts influence competition among their own parasite communities. As in feather lice, host-mediated parasite interactions are likely important in the diversification of other host–parasite and host plant–herbivore systems.

Acknowledgements

References

Abrams, P.A. (1999) Is predator mediated coexistence possible in unstable systems? *Ecology*, **80**, 608–621.

Booth, D.T., Clayton, D.H. & Block, B.A. (1993) Experimental demonstration of the energetic cost of parasitism, in free-ranging hosts. *Proceedings of the Royal Society of London B*, **253**, 125–129.

Bush, S.E. & Clayton, D.H. (2006) The role of body size in host specificity: reciprocal transfer experiments with feather lice. *Evolution*, **60**, 2158–2167.

Bush, S.E., Sohn, E. & Clayton, D.H. (2006) Ecomorphology of parasite attachment: experiments with feather lice. *Journal of Parasitology*, **92**, 25–31.

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M. & Case, T.J. (2002) The interaction between predation and competition: a review and synthesis. *Ecology Letters*, **5**, 302–315.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Clay, T. (1949) Some problems in the evolution of a group of ectoparasites. *Evolution*, **3**, 279–299.

Clay, T. (1951) The Mallophaga as an aid to the classification of birds with special reference to the structure of feathers. *Proceedings of the International Ornithological Congress*, **10**, 207–215.

Clayton, D.H. (1990) Mate choice in experimentally parasitized Rock Doves: lousy males lose. *American Zoologist*, **30**, 251–262.

Clayton, D.H. (1991) Coevolution of avian grooming and ectoparasite avoidance. *Bird–Parasite Interactions: Ecology, Evolution and Behaviour* (eds J.E. Loye & M. Zuk), pp. 258–289. Oxford University Press, Oxford.

Clayton, D.H., Al-Tamimi, S.E. & Johnson, K.P. (2003) The ecological basis of coevolutionary history. *Tangled Trees: Phylogeny, Cospeciation and Coevolution* (ed. R.D.M. Page), pp. 311–341. University of Chicago Press, Chicago, IL.

Clayton, D.H. & Drown, D.M. (2001) Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). *Journal of Parasitology*, **87**, 1291–1300.

Clayton, D.H. & Tompkins, D.M. (1994) Ectoparasite virulence is linked to mode of transmission. *Proceedings of the Royal Society of London B.*, **256**, 211–217.

Clayton, D.H., Lee, P.L.M., Tompkins, D.M. & Brodie, E.D. III (1999) Reciprocal natural selection on host-parasite phenotypes. *American Naturalist*, **154**, 261–270.

Clayton, D.H., Moyer, B.R., Bush, S.E., Jones, T.G., Gardiner, D.W., Rhodes, B.B. & Goller, F. (2005) Adaptive significance of avian beak morphology for ectoparasite control. *Proceedings of the Royal Society of London B*, **272**, 811–817.

Combes, C. (2001) *Parasitism: the Ecology and Evolution of Intimate Interactions.* University of Chicago Press, Chicago, IL.

Connell, J.H. (1980) Diversity and the coevolution of competitors, of the ghost of competition past. *Oikos*, **35**, 131–138.

Gause, G.F. (1934) *The Struggle for Existence.* Williams & Wilkins, Baltimore, MD.

Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292–1298.

Holt, R.D. (1977) Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.

Holt, R.D. & Dobson, A.P. (2006) Introduction: Extending the principles of community ecology to address the epidemiology of host-pathogen communities. *Disease Ecology: Community Structure and Pathogen Dynamics* (eds S.K. Collinge & C. Ray), pp. 6–27. Oxford University Press, Oxford.

Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.

Jackson, J.A., Pleass. R.J., Cable, J., Bradley, J.E. & Tinsley, R.C. (2006) Heterogeneous interspecific interactions in a host–parasite system. *International Journal for Parasitology*, **36**, 1341–1349.

Janovy, J. (2002) Concurrent infections and the community ecology of helminth parasites. *Journal of Parasitology*, **88**, 440–445.

Janzen, D.H. (1973) Host plants as islands. II. Competition in evolutionary and contemporary time. *American Naturalist*, **107**, 786–790.

Jeffries, M.M. & Lawton, J.H. (1984) Enemy-free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.

Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, **7**, 69–80.

Lello, J., Boag, B., Fenton, A., Stevenson, I.R. & Hudson, P.J. (2004) Competition and mutualism among the gut helminths of a mammalian host. *Nature*, **428**, 840–844.

Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, **104**, 413–423.

Marshall, A.G. (1981) *The Ecology of Ectoparasitic Insects.* Academic Press, London.

Martin, M. (1934) Life history and habits of the pigeon louse (*Columbicola columbae* [Linnaeus]). *Canadian Entomologist*, **66**, 6–16.

Moran, N.A. & Whitham, T.G. (1990) Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. *Ecology*, **7**, 1050–1058.

Morin, P.J. (1999) *Community Ecology.* Cambridge University Press, Cambridge.

Moyer, B.R., Drown, D.M. & Clayton, D.H. (2002) Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos*, **97**, 223–228.

Mumcuoglu, Y., Galun, R. & Ikan, R. (1986) The aggregation response of human body louse (*Pediculus humanus*) (Insecta: Anoplura) to its excretory products. *Insect Science and its Application*, **7**, 629–632.

Nelson, B.C. & Murray, M.D. (1971) The distribution of Mallophaga on the domestic pigeon (*Columba livia*). *International Journal for Parasitology*, **1**, 21–29.

Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.

Paterson, S. & Viney, M.E. (2002) Host immune responses are necessary for density dependence in nematode infections. *Parasitology*, **125**, 283–292.

Poulin, R. (2007) *Evolutionary Ecology of Parasites.* Princeton University Press, Princeton, NJ.

Price, P.W. (1980) *Evolutionary Biology of Parasites.* Princeton University Press, Princeton, NJ.

Price, R.D., Hellenthal, R.A., Palma, R.L., Johnson, K.P. & Clayton, D.H. (2003) *The Chewing Lice: World Checklist and Biological Overview.* Illinois Natural History Survey. Special Publication 24. Illinois Natural History Survey, Champaign, IL.

Raberg, L., Roode, J.C., Bell, A.S., Stamou, P., Gray, D. & Read, A.F. (2006) The role of immune-mediated apparent competition in genetically diverse malaria infections. *American Naturalist*, **168**, 41–53.

Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, **122**, 240–285.

Thompson, J.D. (1980) Implications of difference sorts of evidence for competition. *American Naturalist*, **116**, 719–726.

Tilman, D. (1982) *Resource Competition and Community Structure.* Princeton University Press, Princeton, NJ.

van Veen, F.J.F., Morris, R.J. & Godfray, H.C.J. (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, **51**, 187–208.

Waage, J.K. & Davies, C.R. (1986) Host-mediated competition in a blood-sucking insect community. *Journal of Animal Ecology*, **55**, 171–180.