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COMPARATIVE TRANSMISSION DYNAMICS OF COMPETING PARASITE SPECIES

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Abstract. Competition–colonization trade-off models explain the coexistence of competing species in terms of a trade-off between competitive ability and the ability to colonize competitor-free patches of habitat. A simple prediction of these models is that inferior competitors will be superior dispersers. This prediction has seldom been tested in natural populations because measuring dispersal is difficult. Host–parasite systems are promising in this regard, especially those involving "permanent" parasites that complete their entire life cycle on the body of the host. Because of this close association with the host, the dispersal, i.e., transmission, of these parasites can be monitored very accurately. We tested the dispersal prediction of the competition–colonization model by documenting the transmission dynamics of feather-feeding lice, which are permanent, relatively host-specific parasites of birds. We compared two groups known as "wing" lice and "body" lice that are common parasites of Rock Pigeons (*Columba livia* Gmelin). The two groups are ecologically similar, and they compete for resources on the host. Previous work shows that body lice are competitively superior to wing lice, leading us to predict that wing lice should be better than body lice at dispersing to new host individuals. We tested this prediction by comparing the ability of wing and body lice to disperse between hosts using vertical- and horizontal-transmission mechanisms, including phoretic hitchhiking on parasitic flies (Diptera: Hippoboscidae). A series of experiments with both captive and wild birds confirmed that wing lice are much better than body lice at colonizing new hosts. Wing lice showed significantly greater vertical transmission to nestlings, and they were quite capable of phoretic transmission to new hosts on flies. In contrast, body lice were not phoretic. These results provide the first rigorous demonstration of phoretic transmission in lice, and they underscore the importance of a community-level approach to understanding the ecology of parasite transmission dynamics.

Key words: *bird lice;* Campanulotes compar; *coexistence; colonization;* Columba livia; Columbicola columbae; *competition; dispersal; parasite; phoresis; specificity;* Pseudolynchia canariensis.

INTRODUCTION

A central tenet of community ecology is that niche partitioning facilitates the coexistence of potential competitors. Niche partitioning can occur through specialization on different resources or by temporal or spatial differences in the use of the same resource (MacArthur and Levins 1967, Armstrong and McGehee 1980, Chesson 2000). One model for how competing species may partition space invokes a competition–colonization trade-off. The basic idea is that inferior competitors gain an advantage by being better at colonizing competitor-free patches of habitat (Levins and Culver 1971, Tilman 1994, Amarasekare 2003). For example, plant species with large seeds may outgrow and outcompete species with small seeds. However, small-seeded species may have an advantage in being able to disperse over greater distances, allowing them to exploit "open" patches with few competitors (Turnbull et al. 1999).

Although competition–colonization models have received a good deal of attention in recent years, realistic tests of these models are still few in number. One reason for this is that measuring dispersal under natural conditions is difficult. Consequently, dispersal ability is often estimated using proxies, such as seed size (Turnbull et al. 1999). However, this approach depends on the assumption that the proxy is a true reflection of dispersal ability. Another problem is that dispersal is often treated as a simple trait, despite the fact that some organisms use rather different modes of dispersal over different spatial scales (Higgins and Cain 2002, Nathan 2006). More realistic tests of the dispersal-related prediction of competition–colonization trade-off models require tractable systems in which the dispersal of competing species can be directly measured and manipulated.

Host–parasite systems are promising in this regard. This is particularly true of "permanent" parasites that complete their entire life cycle on the body of the host (Marshall 1981). Such parasites are so closely tied to

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their hosts that it is relatively easy to monitor their dispersal, i.e., transmission, by measuring the rate at which they move between parasitized and non-parasitized host individuals (Fenton et al. 2002). In such cases, transmission between hosts is directly analogous to dispersal between spatially isolated patches of habitat. Some hosts have more than one species of permanent parasite, and some of these species are known to compete for resources (Poulin 2007). Here, we used permanent parasites to test the simple prediction that competitively inferior species are better colonizers than competitively superior species.

We tested this prediction using birds and feather lice (Insecta: Phthiraptera: Ischnocera), which are permanent, relatively host-specific parasites that pass their entire life cycle on the host. Feather lice both feed on feathers and attach their eggs to feathers. Upon hatching, the lice complete a direct life cycle, consisting of three nymphal instars and the adult stage. Many feather lice are so specialized for life on feathers that they cannot move onto the host's skin, and they are virtually immobile off the host (Clayton et al. 1999). Feather louse populations are relatively easy to quantify and manipulate on captive or wild birds (Clayton et al. 1999, Clayton and Drown 2001).

The experiments reported in this paper were conducted with a model system consisting of Rock Pigeons (*Columba livia* Gmelin) and lice. Rock Pigeons have two distinct groups of feather lice, generally known as "wing" lice and "body" lice (Bush and Clayton 2006). Rock Pigeon wing lice (*Columbicola columbae* (L.) and *C. tschulyschman* Eichler) feed on the host's abdominal feathers, but spend most of their time, and lay their eggs, on the host's wings and tail. Rock Pigeon body lice (*Campanulotes compar* (Burm.)) feed and lay their eggs on the host's abdominal feathers, and are seldom, if ever, found on the wings or tail (Nelson and Murray 1971). Although they are distantly related, the ecology of these two genera of lice is quite similar. They feed on the same regions of the abdominal contour feathers (Bush and Malenke 2008), and the feather damage they cause has a negative effect on host mating success (Clayton 1990), thermoregulatory ability (Booth et al. 1993), and survival (Clayton et al. 1999). Pigeons defend themselves against wing and body lice with diligent preening that removes the lice, or kills them in situ (Clayton et al. 2005).

Transmission to new hosts is often vertical, from parent to offspring in the nest (Clayton and Tompkins 1994). Transmission may also be horizontal, although this has not been measured. Horizontal transmission could be direct, such as between mated adults, or it could be indirect, via phoresis. Phoresis occurs when one species hitches a ride on a more mobile species for transport between resources or hosts (Marshall 1981). Lice have often been observed hitchhiking rides on hippoboscid flies, which are winged parasites of birds and mammals (Keirans 1975). The literature contains several records of Rock Pigeon lice on hippoboscid flies, suggesting that phoresis is an important transmission route (Martin 1934, Hathaway 1943, Ansari 1947, Ward 1953, Iannacone 1992, Clayton et al. 2004, Macchioni et al. 2005). Interestingly, all of these records involve wing lice (Fig. 1), suggesting that Rock Pigeon body lice may not be phoretic; in contrast, body lice from other Columbiform species, such as Mourning Doves (*Zenaida macrourae*), have been removed from hippoboscid flies (Couch 1962). We tested this hypothesis by comparing the extent of phoresis-mediated transmission by wing and body lice in an experiment using captive birds.

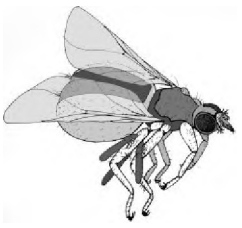

FIG. 1. Drawing of three *Columbicola columbae* attached to a fly captured inside one of the sheds used in this study. Drawn by S. E. Bush; reprinted from Clayton et al. (2004) with permission from Systematic Biology.

Columbiform lice are known to compete both on Rock Pigeons (Bush and Malenke 2008) and Mourning Doves (*Zenaida macroura*) (Malenke 2008). On Rock Pigeons, body lice are competitively superior to wing lice (Bush and Malenke 2008). Both groups depend on the downy portions of abdominal contour feathers for food, which appears to be one of the limiting resources mediating competition in this system. Wing and body lice also compete for space, although the exact way in which space is limiting is unclear (Bush and Malenke 2008). The asymmetric competitive impact of body lice on wing lice, coupled with the preponderance of records of phoretic wing lice, led us to predict that wing lice are better at colonizing new hosts than body lice.

Differences in colonization ability can result from uneven transmission between hosts, uneven establishment once on a host, or a combination of the two. Bush and Clayton (2006) showed that wing and body lice are roughly equal in their ability to establish populations when experimentally transferred to new host individuals (or species). In the current study, we explored the relative ability of the two types of lice to disperse from infested to uninfested hosts. We conducted four main experiments. First, we used captive breeding Rock Pigeons to compare rates of vertical transmission by wing and body lice between parent hosts and their offspring in the nest. Second, we used captive Rock Pigeons to measure direct horizontal transmission by contact between adult birds. We then repeated this experiment using free-ranging Rock Pigeons under field conditions. Finally, we used captive Rock Pigeons to

quantify indirect horizontal transmission by wing and body lice via phoresis on hippoboscid flies. The phoresis experiments involved the pigeon fly *Pseudolynchia canariensis* (Macquart), a common parasite of Rock Pigeons (Bequaert 1953, Marshall 1981).

Methods

Direct vertical transmission

Vertical-transmission rates of wing and body lice were measured in a captive breeding colony of 43 mated pairs of wild caught Rock Pigeons housed in a $9.2 \times 3.7 \times 2.5$ m free-flight enclosure (see Clayton and Tompkins 1995). We determined the number of lice on adult birds and their nestlings using timed visual examinations, as described in Clayton and Tompkins (1994). Wing and body lice were visually examined on nestlings and their parents when nestlings were 20–29 d old, at which point they had relatively mature plumage and were near fledging age. The louse loads of nest-mates were averaged to avoid pseudoreplication. Parent louse loads were also averaged for each nest.

Adult birds in the breeding colony had a range of louse loads, created by a two-step manipulation prior to collection of the transmission data. First, to increase initial parasite loads, all birds were fitted with "bits," which are small C-shaped pieces of steel or plastic inserted between the upper and lower mandibles. While harmless to the bird, the bit creates a 1–3 mm gap between the mandibles that impairs the forceps-like action required for efficient preening (Clayton et al. 2005). Bits do not interfere with feeding or provisioning of nestlings and they have no other side effects (Clayton and Tompkins 1995). Second, to create a range of louse loads prior to the transmission study, 20 "low-load" pairs were chosen at random and fumigated with a 1.0% aqueous solution of pyrethrum, which has no side effects on birds (Clayton and Tompkins 1995). The remaining 23 "high-load" pairs were sham-fumigated with water. We collected data on vertical transmission of lice for pairs of birds that reared offspring to fledging age during the subsequent study period.

Direct horizontal transmission

We trapped wild Rock Pigeons using walk-in traps placed on rooftops and under bridges in Salt Lake City, Utah (UT), USA. Upon capture, birds were housed individually in wire mesh cages ($30 \times 30 \times 56$ cm, with a mesh size of 1.2×2.5 cm) and provided *ad libitum* food, water, and grit. In order to accurately measure rates of transmission, it was important to kill 100% of the "background" lice on freshly trapped birds prior to the experiments. To do this we used the non-chemical "drying" technique of Moyer et al. (2002), in which birds are housed at low ambient humidity (<40% relative humidity) over a period of 10 weeks, which kills the lice and their eggs by desiccation. To confirm that the drying method kills all lice, we conducted the test described in the next section.

Test of drying method.—We used 24 Rock Pigeons that had been in captivity for many months and were known to be 100% free of lice (C. Harbison, *unpublished data*). Each bird was "seeded" with 100 lice removed from culture pigeons as described in Moyer et al. (2002). The birds were housed in separate cages and divided between four rooms. Two rooms were kept at high humidity (>60%) and two rooms at low humidity (<40%). After 10 weeks, all birds were euthanized. Their lice were then recovered by body washing, which removes ~85% of the lice from a bird and is highly correlated with total louse load ($r^2 = 0.99$; Clayton and Drown 2001). None of the 12 birds kept at low humidity had any lice by the end of the 10-week period, whereas all 12 birds kept in the humid rooms maintained viable populations of lice (42.8 ± 16.0 lice/bird, mean ± SE). In short, the drying method proved 100% effective.

Captive birds.—For an initial measure of direct horizontal transmission, we captured adult Rock Pigeons ($n = 56$), and cleared them of lice by drying. The extermination of natural louse loads was verified with a visual examination of each bird (Clayton and Drown 2001). Birds were divided randomly into "donor" and "recipient" groups. Donor birds were each seeded with 50 adult wing and 50 adult body lice; recipient birds were not seeded with lice. Seven donor birds and seven recipient birds, chosen at random, were released into a circular outdoor aviary (4.5 m diameter × 5 m tall). The 14 birds were allowed to interact freely for 21 d, at which point they were removed and euthanized. The louse loads of all donor and recipient birds were then determined by body washing (Clayton and Drown 2001). The experiment was replicated a total of four times in identical aviaries.

The experimental period of 21 days was chosen because it allowed us to distinguish transmission of lice from recruitment (at 37°C wing lice take 24.4 ± 0.3 d [mean ± SE] to develop from newly laid eggs to the adult stage (Martin 1934). In an experiment lasting >24 days, adult P1 and adult F1 lice can co-occur on recipient birds. In our 21-day experimental design, all adult lice on recipient birds would have arrived via transmission, whereas immature lice could have been born on the recipient birds. Our analyses were therefore restricted to adult lice.

No hippoboscid flies were observed on or around the captive birds, nor recovered by washing at the end of the experiment. Thus, all movement of lice had to be via direct transmission between birds in physical contact.

Wild birds.—Hippoboscid flies are patchily distributed among wild breeding colonies of Rock Pigeons (Sol et al. 2000; C. Harbison, *unpublished data*). This fact made it possible to repeat the direct horizontal-transmission experiment with wild birds, while still controlling for indirect transmission by phoresis. The experiment was conducted using a flock of 350–400 pigeons under a highway overpass in Lehi, UT. Flies had never been observed during past work at this site. We confirmed the

TABLE 1. The number of flies and lice on donor and recipient birds in phoresis experiments, with the total number of recipient birds colonized by lice in each shed indicated in parentheses (na, not applicable).

Year	Shed	Flies†	Donor bird lice‡		Recipient bird lice§	
			Wing lice	Body lice	Wing lice	Body lice
1	1	67 ± 7	366 ± 28	586 ± 86	17 (11)	1 (1)
1	2	0	405 ± 50	677 ± 76	0 (0)	0 (0)
2	2	33 ± 3	303 ± 38	394 ± 88	10 (3)	0 (0)
2	1	0	303 ± 34	468 ± 78	0 (0)	1 (1)
3	2	70 ± 10	440 ± 50	589 ± 132	17 (11)	2 (1)
3	1	67 ± 8	593 ± 72	na	39 (20)	na

† Number of flies (mean ± SE) from visual examinations carried out once every two weeks.
‡ Number of lice (mean ± SE) from monthly visual examinations.
§ Total number of adult lice recovered from recipient birds by body washing.

absence of flies in two ways: (1) by carefully examining and washing 62 adult birds, and (2) by euthanizing and ruffling the feathers of 13 randomly chosen nestlings. No flies were found on any of these adult or nestling birds. In contrast, flies were recovered from 19 of 29 (65%) adult birds, and 8 of 13 (61.5%) nestling birds, at another breeding colony with a known history of fly infestation 30 km away on the same highway.

At the Lehi bridge we captured 70 adult birds and used the drying technique to exterminate their lice, and then we examined them carefully to confirm elimination of their background lice. The louse-free birds were then banded and released back into the native flock (June 2004). These "recipient" birds re-associated with the flock and were observed interacting with birds that had not been captured. Recipient birds were recaptured 14–23 d after their release using individual walk-in traps and canopy mist nets suspended beneath the overpass. All were recaptured within 23 d to ensure accurate measures of transmission for adult lice, as explained under the captive experiment. Of 69 birds originally released, 32 were recaptured. We captured an additional 30 unmarked birds from the flock to estimate natural background lice on potential donor birds. All birds were euthanized and washed (Clayton and Drown 2001). We also collected data on host body mass, sex, breeding condition, and length of the maxillary overhang of the bill, which is related to preening efficiency (Clayton et al. 2005).

Indirect transmission (phoresis)

To compare phoretic transmission by wing and body lice, we measured the number of lice that transmitted from donor birds housed on one side of a shed to recipient birds housed on the opposite side. We conducted experiments over the course of three years using two identical wooden animal sheds that measured 2.5 × 9.0 m. We housed recently caught birds in individual adjacent cages along the walls of each shed. Twenty donor Rock Pigeons infested with lice were placed along one wall of each shed, with 10 louse-free (dried) recipient pigeons along the opposite wall. Cages were separated with plexiglass dividers to prevent contact between the feathers of adjacent birds. Throughout each experiment, both donor and recipient birds were prevented from preening using C-shaped bits, as described under the vertical-transmission experiment.

During the first week, pigeon flies (*Pseudolynchia canariensis*) were released into the experimental shed from a laboratory culture started with wild-caught flies. Additional flies were periodically added to maintain fly levels at 1–2 flies per bird. Natural pigeon populations range from 0–6 flies per bird (Klei 1975, Dranzoa et al. 1999, Sol et al. 2000). The flies could move freely between donor and recipient birds in the experimental shed. In years 1 and 2, the control shed (reversed between years) received no flies; in year 3, both sheds received flies (Table 1). Each of the three experiments lasted six months (October–March; 2003–2004, 2004–2005, 2006–2007).

Phoretic transmission of lice to "recipient" birds was measured in two steps. Lice were initially detected during a 15-min visual examination once every two weeks of each recipient bird, which detects wing and body lice equally well (Clayton and Drown 2001). When lice were seen on a recipient bird, that bird and the corresponding bird in the control shed (i.e., the bird whose cage was in the same position), were immediately euthanized. Both birds were replaced with new louse-free (dried) birds. A reciprocal procedure was followed when lice were detected on recipient birds in the control shed. Euthanized birds were washed to quantify their lice. The number of wing and body lice on donor pigeons was also monitored monthly with a 5-min visual examination (Clayton and Drown 2001).

We also kept track of the number of flies seen on recipient birds. At the start of the experiment, this number was ~21% of the total number released in the shed. We used this percentage to extrapolate the total number of flies present at biweekly (once every two weeks) intervals over the course of each experiment (Table 1). In year 1, 100 flies were introduced to the experimental shed. In year 2, we introduced 50 flies to the experimental shed. In year 3, both sheds received 100 flies, but in one shed the donor birds had wing and body

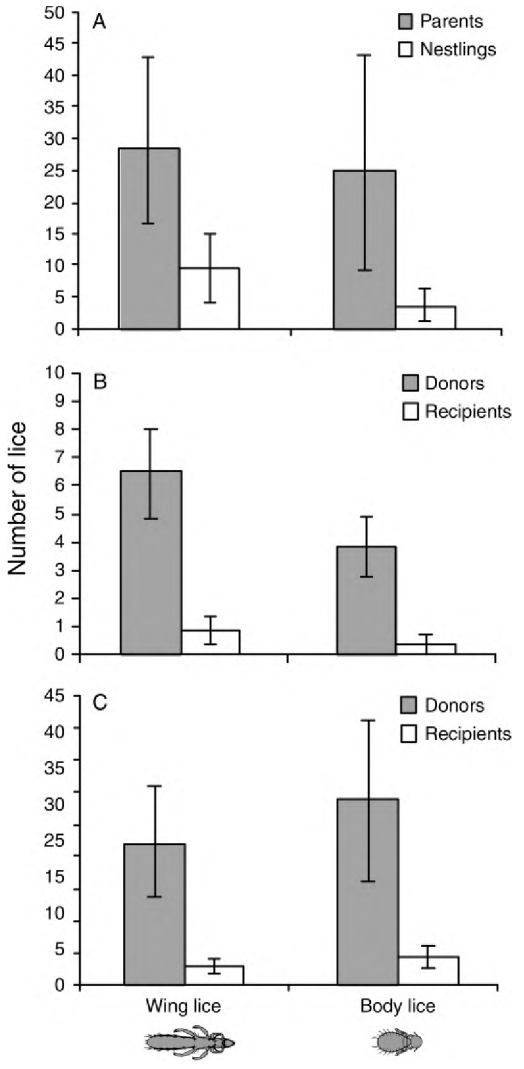

FIG. 2. (A) Direct vertical transmission of lice from captive parent to nestling Rock Pigeons (n = 15 nests). (B) Direct horizontal transmission of adult lice between captive birds (n = 28 donors, 28 recipients). (C) Direct horizontal transmission of adult lice between wild birds (n = 30 donors, 32 recipients). Data are means; error bars indicate 95% confidence intervals.

lice, while donor birds in the other shed had only wing lice (Table 1).

RESULTS

Direct vertical transmission

Of the monitored nests, 15 had nestlings during the study period. Parents in all 15 nests were infested with wing lice; nestlings from 14 (93%) of these nests became infested with wing lice before fledging. Parents in 14 of the 15 nests had body lice; nestlings from 10 (71%) of these nests became infested with body lice before fledging. The mean number of wing lice on nestlings was 42% of that on parents, while the mean number of body lice on nestlings was 21% of that on parents (Fig. 2A). Vertical transmission of wing lice was significantly greater than that of body lice (Wilcoxon signed-ranks test, $P = 0.013$).

Direct horizontal transmission

Captive birds.—To compare the direct horizontal transmission of wing and body lice, we quantified the number of lice on recipient birds, relative to the number of lice on donor birds at the end of the experiment (Fig. 2B). Data from the four replicates were combined for analyses. Overall, recipient birds had 25 wing and 9 body lice, compared to 183 wing and 108 body lice on donor birds. There was no significant difference in the rates of transmission of wing and body lice to recipient birds relative to donors (Fisher's exact $P = 0.26$; power = 0.95, $w = 0.20$; Cohen 1977).

Wild birds.—Transmission was independent of host body size (wing lice, Spearman rho = 0.29, $P = 0.10$; body lice, rho = 0.18, $P = 0.32$), host sex (Wilcoxon rank sum test; wing lice, $P = 0.75$; body lice, $P = 0.23$), and length of the bill overhang (wing lice, Spearman rho = 0.21, $P = 0.26$; body lice, rho = 0.57, $P = 0.76$). The relationship of host breeding condition to louse transmission could not be tested because nearly all birds were in breeding condition.

Both wing and body lice transmitted readily to recipient birds (Fig. 2C); by the time of recapture, 94% of recipients were infested with lice. Of the 32 recipient birds, 44% had both wing and body lice, 25% had only wing lice, and 25% had only body lice. Overall, recipient birds had 98 wing and 144 body lice and donor birds had 657 wing and 871 body lice. There was no significant difference in rates of transmission of adult wing and body lice to recipient birds (Fisher's exact $P = 0.49$; power = 1.0, $w = 0.20$; Cohen 1977).

Indirect transmission (phoresis)

Flies were observed on both donor and recipient birds in sheds with flies. Flies were never observed on birds in the fly-free control sheds. The number of lice on donor birds varied between years (Table 1), but never exceeded levels documented for wild Rock Pigeons, which can support thousands of lice (Clayton et al. 1999). Donor birds had more body lice than wing lice in all sheds with dual infestations (Table 1).

The year-1 experiment provided strong evidence for phoresis by wing lice, which colonized 11 recipient birds in the experimental "fly" shed, but no birds in the control shed (Fisher's exact, $P < 0.001$; Fig. 3A, B). Two of these birds were colonized by more than one individual wing louse. Overall, 17 wing lice colonized the 11 recipient birds in the experimental shed compared to no wing lice on birds in the control shed (Fisher's exact, $P < 0.001$; Table 1). In contrast, there was little evidence for body louse phoresis, as only one bird was colonized by a single body louse in the experimental shed, and no body lice colonized recipient birds in the control shed (Fisher's exact, $P = 1.0$; Fig. 3A, B, Table 1).

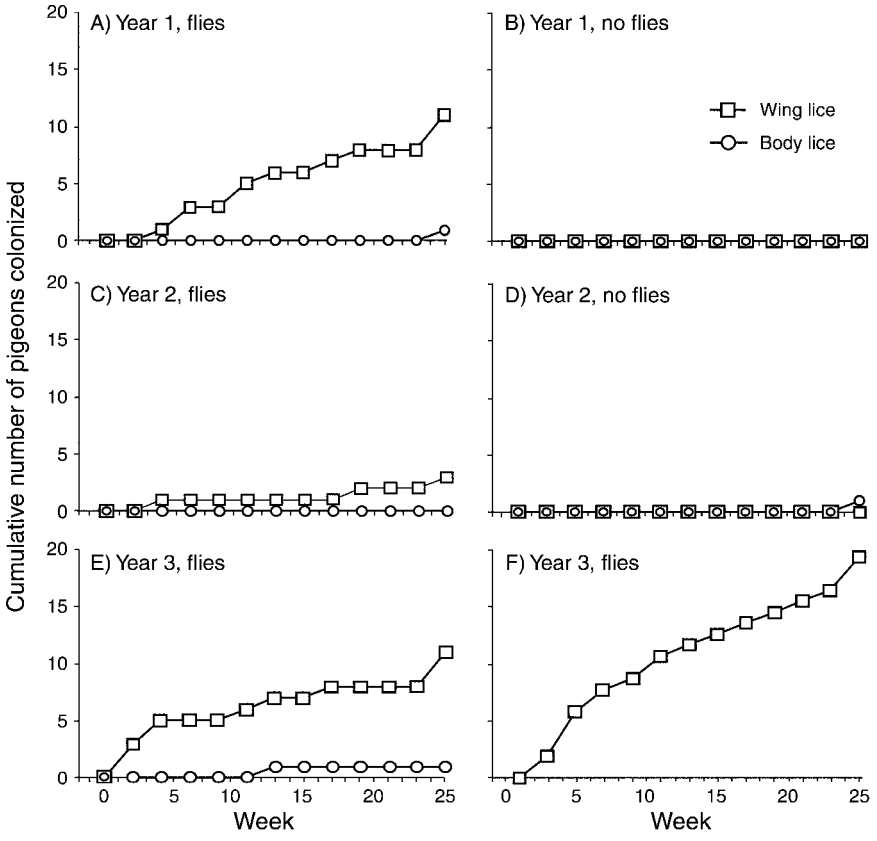

FIG. 3. Cumulative number of recipient pigeons colonized by wing and body lice in phoresis experiments: in year 1, (A) experimental (fly) and (B) control (no fly) sheds; in year 2, (C) experimental (fly) and (D) control (no fly) sheds; and in year 3, (E) shed containing flies, wing lice, and body lice, and (F) shed containing flies and wing lice.

The year-2 experiment, which had fewer flies, and fewer donor lice (Table 1), provided weaker evidence for phoresis. Three recipients were colonized by wing lice in the experimental shed, while no birds were colonized by wing lice in the control shed (Fisher's exact, $P = 0.22$; Fig. 3C, D). All three birds were colonized by more than one individual wing louse. Overall, 10 wing lice colonized the three recipient birds in the experimental shed, while no birds were colonized by wing lice in the control shed (Fisher's exact, $P = 0.03$; Table 1). No birds were colonized by body lice in the experimental shed, and one bird was colonized by a single body louse in the control shed (Fisher's exact, $P = 1.0$; Fig. 3C, D, Table 1).

In year 3, we replicated the year-1 fly shed as closely as possible by introducing the same number of flies and attempting to culture similar numbers of wing and body lice on the donor birds (Table 1). The results were virtually identical to those of year 1, with wing lice colonizing 11 recipient birds with a total of 17 lice, and body lice colonizing a single recipient bird with a total of two lice (Fisher's exact, $P = 0.001$; Fig. 3E, Table 1).

In contrast to years 1 and 2, year 3 did not have a fly-free shed. Instead, the other shed (shed 1) contained donor birds with wing lice, but no body lice. We predicted that, in the absence of body lice, the rate of wing louse phoresis would decline. This prediction, however, was not supported. Only 11 birds were colonized by wing lice in the wing–body-lice shed (Fig. 3E), compared to 20 birds in the wing-lice-only shed (Fisher's exact, $P = 0.40$; Fig. 3F). In the wing–body-lice shed, 4 birds were colonized by more than one individual wing louse, while 11 birds were colonized by more than one individual wing louse in the wing-louse-only shed. Overall, 17 wing lice colonized birds in the wing-body lice shed compared to 39 wing lice on birds in the wing-lice-only shed (Fisher's exact, $P = 0.24$; Table 1). In summary, there were no significant differences in phoresis between the year-3 sheds.

Across the three years, there was a significant positive relationship between the number of wing lice on donor and recipient birds (Spearman rho $= 0.95$, $P = 0.05$; Fig. 4). This result suggests the limiting factor in phoresis was the number of wing lice on donor birds, not the number of flies in the shed. The rate of phoresis varied considerably even among the three sheds that all received 100 flies (Table 1, Fig. 4).

DISCUSSION

Our results are consistent with the dispersal prediction of the competition–colonization trade-off model. Prior

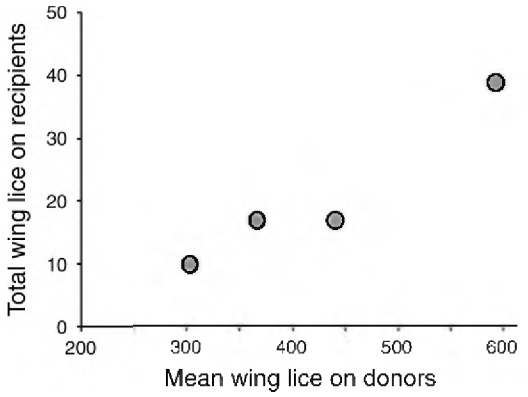

FIG. 4. Number of wing lice on recipient pigeons in relation to the mean number on donor pigeons in the phoresis experiment sheds with flies (Table 1).

work demonstrates that wing lice are competitively inferior to body lice, suggesting that wing lice are better at transmission between hosts than body lice. We confirmed this prediction, demonstrating greater vertical and indirect (phoretic) transmission by wing lice, despite there being no difference in direct horizontal transmission of wing and body lice. Our results further show that louse transmission dynamics are complex. Rock Pigeon wing lice are capable of several modes of transmission driven, in part, by community interactions with other kinds of parasites, such as pigeon flies.

Most studies of feather louse transmission have focused on vertical transmission from parent hosts to their offspring (Dubinin 1947, Rothschild and Clay 1952, Eveleigh and Threlfall 1976, Marshall 1981, Clayton and Tompkins 1994, Lee and Clayton 1995). Although the potential role of horizontal transmission has received less attention, recent work on the feather lice of pheasants, cuckoos, and bee-eaters suggests that it may be more important than previously thought (Hillgarth 1996, Lindholm et al. 1998, Darolova et al. 2001). We therefore tested both the vertical and horizontal components of transmission by Rock Pigeon wing and body lice. First we compared vertical transmission from parent to offspring: the prevalence of lice on nestlings at the time of fledging was higher for wing lice (93%) than body lice (71%), and the number of wing lice on infested nestlings was twice that of body lice (Fig. 2A). Because nestlings are free of lice upon hatching, higher transmission by wing lice to nestlings can provide a refuge from competition with body lice.

We also documented significant horizontal transmission of lice during periods of direct contact between unrelated adult hosts, both in captive and wild birds. In our captive experiment, donor and recipient birds often came into direct physical contact when feeding, allopreening, mating, fighting, and roosting (C. Harbison, *unpublished data*). Horizontal transmission could have taken place during any of these encounters. While lice dispersed to recipient birds in both experiments, there was no significant difference in the rates of direct horizontal transmission by wing and body lice in either captive birds (Fig. 2B), or wild birds (Fig. 2C).

Finally, we documented that lice also disperse by phoretic hitchhiking on hippoboscid flies. Wing lice consistently colonized recipient birds via phoresis (Fig. 3). In contrast, we found little evidence that body lice are phoretic, even though body lice outnumbered wing lice on donor birds in every experiment (Table 1). The difference in wing and body lice phoresis was not an artifact of flies spending more time in microhabitats preferred by wing lice. Wing lice spend a majority of their time on the flight feathers of the wings and tail, whereas body lice rarely leave the host's abdominal feathers (Nelson and Murray 1971). Flies were most common in the abdominal regions preferred by body lice. The mean (±SE) number of flies on abdominal feathers (0.75 ± 0.09) was significantly greater than the number on the flight feathers of the wing and tail (0.20 ± 0.05; Wilcoxon signed-ranks test, $P < 0.001$). The observed distribution of the flies is not surprising, since the flies are going to the abdominal regions to feed on blood (Bequaert 1953).

Overall, 20 (44%) of 45 recipient pigeons infested by wing lice harbored multiple wing lice. These birds could have received their lice from several flies, or from a single fly carrying multiple lice, which is a common phenomenon (Keirans 1975). Indeed, one published account reported 31 lice attached to a single fly (Peters 1935). Although a single gravid female can establish a new louse population (Marshall 1981), transmission events involving multiple lice presumably increase the chances of successful colonization.

We observed wing lice clinging to flies on three occasions (of 120 flies examined), but we never observed body lice on flies. These observations are consistent with the fact that all of the published accounts of pigeon lice on flies involve wing lice. Recent work reveals a proximal reason why body lice are seldom, if ever, phoretic. Body lice placed on flies in the laboratory are very poor at remaining attached to flies that are walking, flying, or grooming (Harbison 2008). In contrast, wing lice can easily remain attached during all of these activities. Indeed, they hang onto active flies for more than six hours, which suggests they may be capable of long-distance phoretic transmission between host colonies (Brown and Brown 2004). This difference in attachment ability is not surprising, considering the long "outrigger" legs that wing lice use for locomotion and attachment on the coarse barbs of wing and tail feathers (Bush et al. 2006). The legs of body lice, which are small by comparison, are well suited for burrowing into the downy matrix of abdominal feathers. However, they are probably not good for attachment to flies.

In the year-3 phoresis experiment, we tested whether the presence of body lice triggers phoresis by wing lice, but we found no evidence in support of this hypothesis. In fact, the trend was for phoresis to *increase* in the

absence of body lice (Fig. 3E, F, Table 1). The difference in phoresis between sheds in year 3 was probably related to differences in the number of wing lice on donor birds. Over all years, there was a significant positive correlation between the number of wing lice on donor birds and the number of phoretic wing lice on recipients (Fig. 4). This correlation may simply be due to an increased encounter rate between flies and wing lice when lice are at a higher density. Alternatively, competition among wing lice may trigger phoresis. Clearly, flies are necessary for phoresis, but they may limit phoresis only at low densities. Above a certain threshold, increases in fly number appear to have little impact on the rate of phoresis. Our results suggest that this threshold was surpassed even when flies numbered only one per bird (year 2).

In conclusion, we have demonstrated significant differences in transmission between ecologically similar competitors. The greater vertical and phoretic transmission of wing lice, relative to body lice, provides wing lice with a means to escape competition, facilitating the coexistence of wing and body lice. We believe these findings are important for a number of reasons. Empirical tests of predictions derived from competition–colonization trade-off models are rare in non-plant assemblages. Our results show the applicability of competition–colonization models to host–parasite systems. Furthermore, we show that differences in transmission are mediated by interspecific interactions with unrelated parasites in the community. These results emphasize that transmission between hosts is not necessarily simple, but it can occur via several mechanisms over different spatial scales. Our results underscore the importance of a broad community approach to understanding the complex nature of transmission.

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