

## ECOMORPHOLOGY OF PARASITE ATTACHMENT: EXPERIMENTS WITH FEATHER LICE

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**ABSTRACT:** The host specificity of some parasites can be reinforced by morphological specialization for attachment to mobile hosts. For example, ectoparasites with adaptations for attaching to hosts of a particular size might not be able to remain attached to larger or smaller hosts. This hypothesis is suggested by the positive correlation documented between the body sizes of many parasites and their hosts. We adopted an ecomorphological approach to test the attachment hypothesis. We tested the ability of host-specific feather lice (Phthiraptera: Ischnocera) to attach to 6 novel species of pigeons and doves that vary in size by nearly 2 orders of magnitude. Surprisingly, Rock Pigeon lice (*Columbicola columbae*) remained attached equally well to all 6 novel host species. We tested the relative importance of 3 factors that could facilitate louse attachment: whole-body insertion, tarsal claw use, and mandible use. Insertion, per se, was not necessary for attachment. However, insertion on coarse feathers of large hosts allowed lice to access feather barbules with their mandibles. Mandible use was a key component of attachment regardless of feather size. Attachment constraints do not appear to reinforce host specificity in this system.

Ecomorphological studies examine an organism's morphology with the intent of predicting the organism's ecology or vice versa (Karr and James, 1975; Losos, 1990). Morphology has been shown to successfully predict ecology in several systems. For example, *Anolis* spp. lizards with similar leg lengths and body masses choose similar-sized perches (Pounds, 1988; Losos, 1990), leg morphology is correlated with the foraging posture and feeding ecology of tits (*Parus* spp.; Moreno and Carrassal, 1993), and among herbivorous insects, tarsal morphology is often specialized for use on particular types of plant surfaces (Kennedy, 1986; Betz, 2002). Ectoparasitic insects are ideal organisms with which to test ecomorphological hypotheses because the host represents a considerable proportion of the parasite's environment, making ecological manipulation relatively easy. Furthermore, in the case of ectoparasites that have coevolved with their hosts, coevolution provides a window into the historical ecological context in which the parasite evolved (Page, 2003; Clayton et al., 2004).

Adopting an ectoparasitic lifestyle provides a reliable source of food and habitat but requires the evolution of adaptations for remaining attached to the host's integument (Waage, 1979; Marshall, 1981). Some ectoparasites go to extreme measures to remain attached to the host. Ascodipteron flies and Tungid fleas burrow underneath the host's skin, enclosing virtually all of their body within host tissue (Askew, 1971; Lehane, 1991). However, most ectoparasites use less invasive means of attachment, such as hooks, clamps, suckers, adhesive secretions, or friction (Gorb, 2001).

Another factor that can influence the ability of a parasite to remain attached to its host is relative body size (Kirk, 1991). Parasite size correlates with host size in a wide variety of taxa, including parasitic worms, crustaceans, fleas, flies, lice, and ticks, as well as herbivorous aphids, thrips, beetles, flies, moths, and flower mites (Harvey and Keymer, 1991; Kirk, 1991; Thompson, 1994; Poulin, 1998; Sasal et al., 1999; Tompkins and Clayton, 1999; Morand et al., 2000). Several studies have shown direct correlations in size between particular features of parasite and host morphology. For example, the hook size of monogenean ectoparasites of fish is correlated with gill size (Sasal et al., 1999). The spacing of flea-comb spines that snag

host hair correlates with host hair diameter (Humphries, 1967; Lehane, 1991). Likewise, the size of the rostral head groove that helps gopher lice attach to host hair is correlated with hair diameter (Reed et al., 2000). The tarsal claws of human crab lice (*Phthirus pubis*) are similar in size to coarse pubic hair, but not to the finer hairs of the head (Askew, 1971). These correlative studies suggest that relative size is an important component of attachment. Indeed, if parasites are unable to attach to the "wrong"-sized host, then attachment could be an important determinant of host specificity (Clay, 1949). Unfortunately, the influence of size on host use has seldom been tested experimentally. This was the goal of our study.

We studied the ecomorphology of feather lice (Phthiraptera: Ischnocera) found on pigeons and doves (Columbiformes). Species of *Columbicola* are host specific, with most species found on only 1 genus or even species of host (Price et al., 2003). In this system, host and parasite phylogenies are significantly congruent, indicating that these lice have a long coevolutionary history with their hosts (Clayton et al., 2004). Species of *Columbicola* spend their entire life cycle (egg, 3 nymphal instars, and adult) on the body of the host, where they feed on the fluffy portions of abdominal contour feathers (Nelson and Murray, 1971). These lice are so specialized for life on feathers that they do not even venture onto the host's skin (Clayton, 1991), and individuals dislodged from the host die within a few days. Adult *Columbicola* spend most of their time on feathers of the host's wings, where attachment can be difficult, especially when the bird is flying. It is for this reason that species of *Columbicola* are frequently referred to as "wing lice."

Birds hosting *Columbicola* wing lice vary in size by nearly 2 orders of magnitude, from 30-g Common Ground-doves (*Columbina passerina*) to 2,400-g Victoria Crowned-pigeons (*Goura victoria*; Dunning, 1993; del Hoyo et al., 1997). As in many other parasite systems (listed above), wing louse size is correlated with host size (Johnson et al., 2005). We used the wide range of host body size to test the attachment ability of a medium-sized wing louse (*Columbicola columbae*) that occurs on a medium-sized host, the Rock Pigeon (*Columba livia*).

Wing lice frequently insert their bodies between adjacent feather barbs on the wings and tail (Fig. 1a). Stenram (1956) suggested that lice insert to avoid direct exposure to swiftly moving air on a flying bird, thus aiding attachment. In addition, wing lice use their hooklike tarsal claws to cling to and move along the feather barbs (Fig. 1b) and their clamplike mandibles to clench feather barbules (Stenram, 1956; Fig. 1c). We mea-

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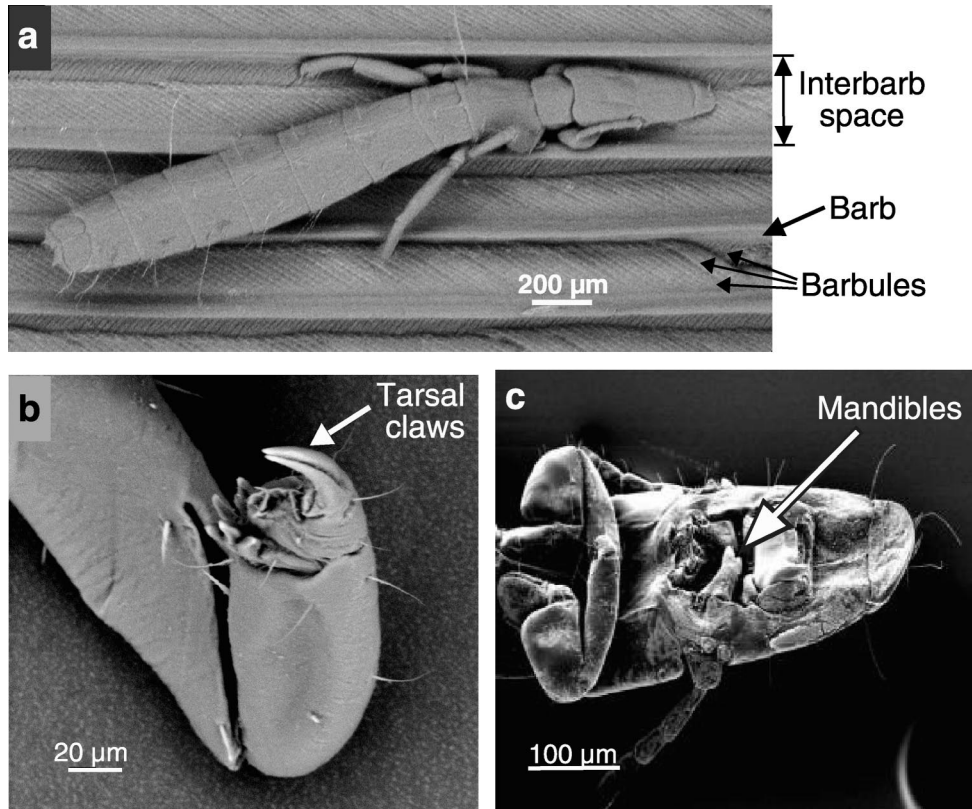


FIGURE 1. Three traits of wing lice (*Columbicola columbae*) that might facilitate attachment to the host: (a) insertion behavior, in which lice wedge themselves between adjacent barbs of a flight feather; (b) tarsal claws; and (c) mandibles (arrow indicates tip of the left mandible overlapping tip of right mandible). SEMs in panels a and b by J. Ichida and E. H. Burt; SEM in panel c from Smith (2000).

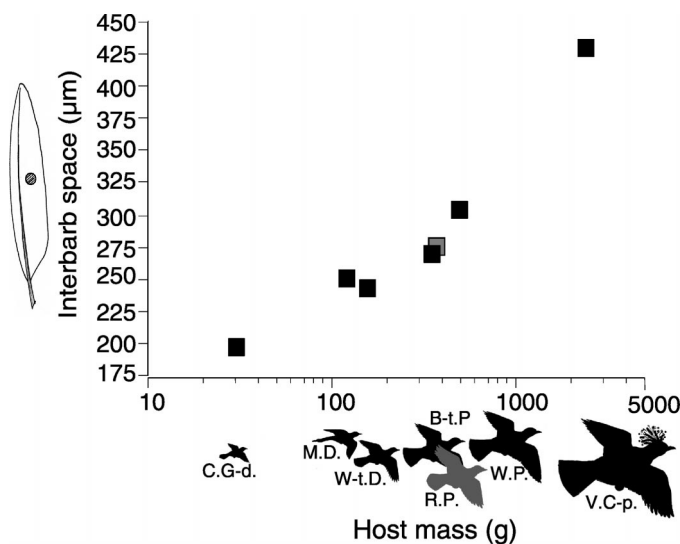


FIGURE 2. Relationship of the mean interbarb space of the fifth primary to the body mass of pigeons and doves (drawn to scale): C.G-d. = Common Ground-dove (*Columbina passerina*); M.D. = Mourning Dove (*Zenaida macroura*); W-t.D. = White-tipped Dove (*Leptotila verreauxi*); B-t.P. = Band-tailed Pigeon (*Patagioenas fasciata*); R.P. = Rock Pigeon (*Columba livia*); W.P. = Wood Pigeon (*Columba palumbus*); V.C-p. = Victoria Crowned-pigeon (*Goura victoria*). The native host of *Columbicola columbae* is indicated in gray.

sured the frequency with which *C. columbae* used each of these 3 means of attachment across 7 species of pigeons and doves. We also examined the relative contribution of tarsal claws and mandibles to attachment by experimentally blocking the mandibles.

## MATERIALS AND METHODS

### Feather size compared with host body size

Wing louse size is highly correlated with overall host size (Johnson et al., 2005), but lice are probably matching a particular host feature. Feathers are the relevant substrate for feather lice, and wing feathers are the most relevant substrate for wing lice. We, therefore, measured the size of wing feather microstructure and compared it to overall body size across 7 species of hosts (Fig. 2). We measured the width of the interbarb space (Fig. 1a) at 5 haphazardly chosen locations in the center of the middle (fifth) primary. Each primary was placed on a microscope stage, and computerized video images were obtained with a Nikon DIC microscope (Nikon Instruments, Melville, New York). Interbarb space measurements were highly repeatable ( $r = 0.88$ ;  $P < 0.0001$ ,  $n = 18$ ; Lessells and Boag, 1987). The mean of 5 measurements was used as an index of wing feather interbarb space for each species. Body masses of birds were taken from Dunning (1993) and del Hoyo et al. (1997).

### Attachment on novel hosts

We tested the ability of *C. columbae* to remain attached to 6 novel host species, relative to the native host, the Rock Pigeon. We tested louse attachment in experimental arenas created by grafting novel host feathers onto Rock Pigeon feathers. We used a scalpel to remove a 1-cm<sup>2</sup> section of feather vane from the fifth primary on each wing of a Rock Pigeon. We then grafted a 1-cm<sup>2</sup> section from the same region of the fifth primary of another species to 1 wing, chosen at random (Fig.

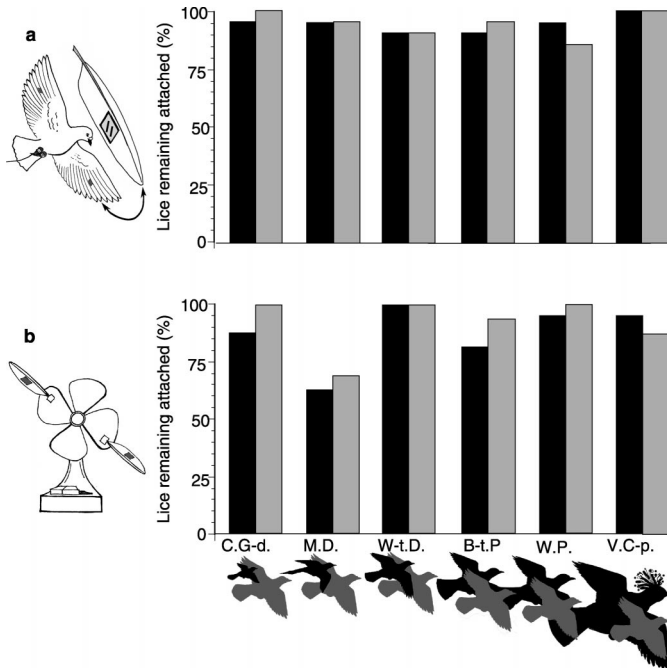


FIGURE 3. Percentage of wing lice (*Columbicola columbae*) remaining attached to feather grafts from 6 novel host species (black) compared with the native host (gray). Host abbreviations as in Figure 2. Attachment did not differ significantly among host species on (a) feather grafts on Rock Pigeons allowed to fly a distance of 50–100 m (Fisher's exact test,  $P \geq 0.61$  in all cases) or (b) feather grafts on feathers taped to a high-speed fan for 20 min (Fisher's exact test,  $P \geq 0.48$  in all cases). Some data are repeated from Clayton et al. (2003) for direct comparison.

3a). To the opposite wing, we grafted a 1-cm<sup>2</sup> section from another (control) Rock Pigeon. All experimental sections and control grafts were outlined with Scribbles® 3-dimensional (3D) paint (Duncan Crafts, Fresno, California), which is harmless to the lice when dry (Clayton et al., 2003). The paint formed a slick ridge that prevented lice from crawling off the experimental section onto adjacent parts of the feather.

Lice were taken from a culture stock bred on wild-caught Rock Pigeons. In each trial, 2 lice were placed on the experimental graft and 2 lice were placed on the control graft. The pigeon, attached to a long tether, was released into the air with its wings open and was retrieved before it could close its wings at the end of a 50–100-m-long flight. Six Rock Pigeons were used, each with an experimental graft from a different novel host species (10 trials per species  $\times$  6 species = 60 trials).

We also tested the ability of lice to remain attached to novel host feathers with the use of a fan. For the fan trials, the experimental and control feathers were removed from the Rock Pigeons in the previous experiment and taped to the blades of a fan set on high speed (Fig. 3b). At the fan's highest setting (1,260 rpm), the lice moved at 85 km/hr, approximating the velocity of racing pigeons in level flight (80–100 km/hr; Johnston and Janiga, 1995). We conducted 8 trials per host species, with each trial lasting 20 min.

#### Insertion on novel hosts

We compared the extent to which wing lice insert on feathers of the 6 novel species relative to the native host. Lice were placed, 1 at a time, in the center of the fifth primary pulled from captive individuals of each of 6 novel host species, as well as on Rock Pigeon controls. Insertion behavior was stimulated by gently blowing on the lice, simulating airflow over feathers during flight. Insertion was quantified by visually examining the lice with a hand-held,  $\times 5$  magnifying glass. The number of lice used on each host species was Common Ground-dove (C.G-d.) = 46, Mourning Dove (M.D.) = 46, White-tipped Dove (W-t.D.) = 46,

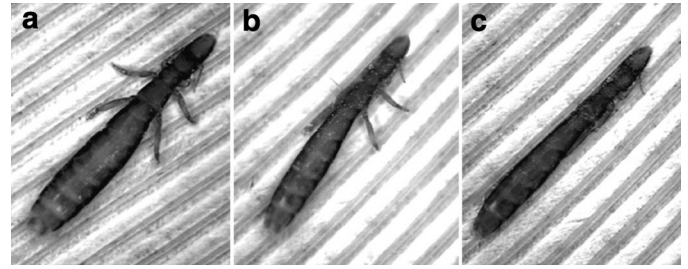


FIGURE 4. Three categories of wing louse (*Columbicola columbae*) insertion and the score assigned to each: (a) not inserted (=0); (b) partially inserted as in Figure 1a (=0.5); (c) fully inserted, with entire body wedged between adjacent feather barbs (=1.0).

Band-tailed Pigeon (B-t.P.) = 41, Rock Pigeon (R.P.) = 126, Wood Pigeon (W.P.) = 26, and Victoria Crowned-pigeon (V.C-p.) = 26. Insertion of each louse was scored as shown in Figure 4.

#### Use of tarsal claws and mandibles on novel hosts

We quantified how often wing lice used their tarsal claws and mandibles to attach to the feathers of 6 novel host species relative to the native host. Individual lice were placed on fifth primaries pulled from 6 novel host species and on feathers from Rock Pigeon controls. The number of lice used on each host species was C.G-d. = 30, M.D. = 30, W-t.D. = 30, B-t.P. = 26, R.P. = 30, W.P. = 10, and V.C-p. = 10. Attachment behavior was stimulated by gently blowing on the lice. The use of tarsal claws and mandibles was determined by gently pulling on lice with forceps under a dissecting scope ( $\times 40$ ).

#### Relative contribution of tarsal claws and mandibles to attachment

We also experimentally tested the relative contribution of tarsal claws compared with mandibles for attachment on flying Rock Pigeons, the native host of *C. columbae*. We blocked mandibular access to the barbules, while preserving the ability of lice to use their tarsal claws to cling to feather barbs. To accomplish this, we blocked the barbules of a 1-cm<sup>2</sup> section in the center of a fifth primary. The barbules were blocked by filling the interbarb space halfway with fingernail polish, which is harmless to the lice when dry (data not shown). The feather was allowed to dry for 1 wk. A 1-cm<sup>2</sup> section in the center of the fifth primary on the opposite wing was designated as a control. The 1-cm<sup>2</sup> feather sections on both wings were cemented around the periphery with Scribbles® 3D paint, which formed a slick ridge that prevented lice from crawling off the experimental feather section onto adjacent parts of the feather.

Two lice were placed on the experimental section and 2 lice were placed on the control section for each of 12 experimental trials. In each trial, the Rock Pigeon, attached to a long tether, was released into the air with its wings open and was retrieved before it could close its wings at the end of a 50–100-m-long flight.

We also tested the relative contribution of tarsal claws compared with mandibles for attachment on feathers taped to the blades of a rotating fan for 30 min. Again, 2 lice were placed on the experimental section and 2 lice were placed on the control section for each of 10 trials.

## RESULTS

#### Feather size compared with host body size

Feather size was highly correlated with overall host body size ( $R = 0.95$ ;  $F = 43.24$ ; 1, 6 df;  $P = 0.0012$ ; Fig. 2).

#### Attachment on novel hosts

Most of the lice (85%) remained attached to feather grafts on Rock Pigeons allowed to fly 50–100 m, regardless of feather size. There was no significant difference in the ability of lice

to remain attached to native compared with novel host feather grafts (Fig. 3a). Similarly, there was no significant difference in the number of lice remaining attached to native compared with novel host feather grafts on feathers taped to the fan (Fig. 3b). Over 60% of lice remained attached to feather grafts during the 20-min fan trials, regardless of feather type.

#### Insertion on novel hosts

Insertion of *C. columbae* differed dramatically across host species (Fig. 5a; Kruskal–Wallis,  $H = 132.04$ , 6 df,  $P < 0.0001$ ). Relative to Rock Pigeon controls, lice inserted much less on feathers of the smallest dove species (Dunnett's post hoc  $P < 0.01$  for both C.G-d. and M.D.) and significantly more on feathers of the largest pigeon species (Dunnett's post hoc  $P < 0.05$  for W.P. and  $P < 0.01$  for V.C-p.). On feathers of Common Ground-doves, the smallest species, none of the lice fully inserted, and only 1 louse (2%) was partially inserted. On feathers from Rock Pigeons, the native host, 111 lice (88%) inserted at least partially, and 26 lice (21%) were fully inserted. On feathers from Victoria Crowned-pigeons, the largest species, all of the lice were inserted at least partially and 20 (77%) were fully inserted.

#### Use of tarsal claws and mandibles on novel hosts

The frequency with which tarsal claws were used was similar across host species (Fig. 5b; Kruskal–Wallis,  $H = 1.33$ , 6 df,  $P = 0.97$ ). Similarly, the frequency with which mandibles were used was similar across host species (Fig. 5c; Kruskal–Wallis,  $H = 4.78$ , 6 df,  $P = 0.57$ ). Nearly every louse used tarsal claws. Of 165 tested, only 3 individuals did not use tarsal claws and these lice were on feathers from the 2 largest host species. Use of tarsal claws did not preclude the use of mandibles. Indeed, in 50–77% of the trials across host treatments, the lice used tarsal claws and mandibles simultaneously.

To reach the barbules with their mandibles, *C. columbae* on large novel host feathers nearly always inserted themselves between the feather barbules. On feathers from White-tipped Doves, 95% of lice that attached with mandibles were also inserted. On feathers from Band-tailed Pigeons, Rock Pigeons, Wood Pigeons, and Victoria Crowned-pigeons, each louse that used its mandibles was also inserted. In contrast, lice on feathers from small hosts were able to reach barbules with their mandibles while remaining on the surface of the wing feathers. On feathers from Common Ground-doves, 15 lice (50%) attached with their mandibles, yet none of these lice was inserted. Similarly, 21 lice (70%) on Mourning Dove feathers attached with mandibles, yet only 24% of these lice were inserted.

#### Relative contribution of tarsal claws and mandibles to attachment

Blocking mandibular access to barbules had a strong affect on the attachment ability of *C. columbae* on Rock Pigeons allowed to fly 50–100 m (Fig. 6a). On control feathers, 95% of lice remained attached during the flights. In contrast, when mandibular access to the feather barbules was blocked, the number of lice that remained attached during the flights dropped nearly 3-fold. Still, 33% of these lice remained attached with only their tarsal claws to cling to feather barbules.

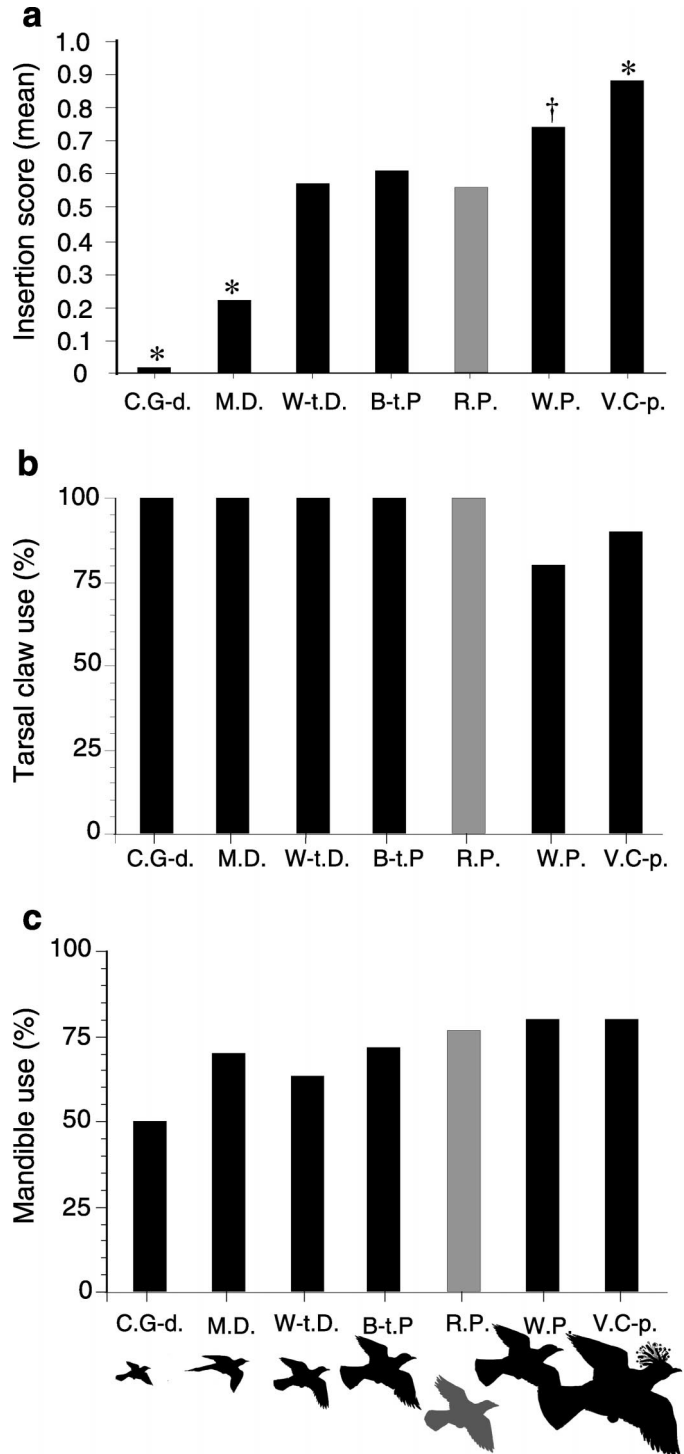


FIGURE 5. Relative (a) insertion, (b) tarsal claw use, and (c) mandible use by wing lice (*Columbicola columbae*) on detached feathers of 6 novel host species (black) compared with the native host (gray); host abbreviations as in Figure 2; \*  $P < 0.01$ , †  $P < 0.05$ .

Attachment was also tested by placing lice on experimental and control feathers that were taped to the blades of a rotating fan. Again, the ability of lice to remain attached to the feathers differed significantly between treatments (Fig. 6b). When lice could use both tarsal claws and mandibles, 60% of the lice

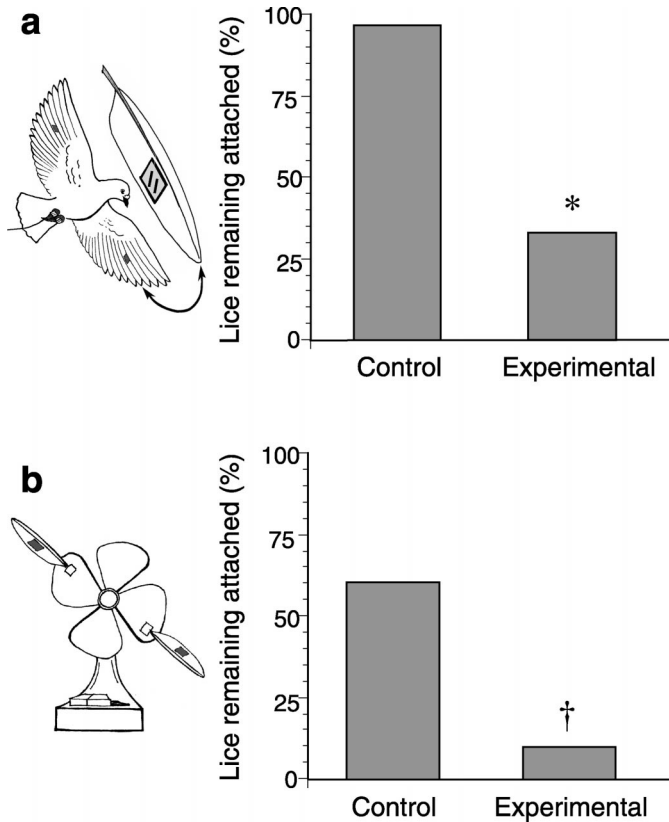


FIGURE 6. Percentage of wing lice (*Columbicola columbae*) remaining attached to native host feathers with normal barbules (control) versus barbules blocked by filling interbarb spaces with fingernail polish (experimental). The number of lice remaining attached to experimental feathers was significantly less both on (a) a Rock Pigeon allowed to fly a distance of 50–100 m (Fisher's exact test, \*  $P < 0.0001$ ) and (b) feathers taped to a fan run at variable speeds for 30 min (Fisher's exact test, †  $P < 0.002$ ).

remained attached. When mandibular access to the feather barbules was blocked, the number of lice that remained attached dropped 6-fold. Only 10% of lice remained attached with just tarsal claws to cling to feather barbules.

## DISCUSSION

Host specificity might be reinforced by adaptations of parasites to remain attached to mobile hosts such as birds. This hypothesis is suggested by the positive correlation documented between the body sizes of different species of host-specific *Columbicola* and their hosts (Clayton et al., 2003; Johnson et al., 2005). The body size correlation might be selectively favored by the need for reliable attachment, assuming that feather size is correlated with overall host body size. This assumption is true for the species in this study (Fig. 2) and also holds in a larger data set analyzed with phylogenetically independent contrasts (Johnson et al., 2005).

We tested the role of relative size in attachment by comparing the ability of host-specific feather lice to remain attached to feathers of very different sizes. Our results indicate that attachment constraints are not, in fact, the basis of host specificity in *Columbicola* spp. feather lice. Lice were able to remain attached to flying Rock Pigeons with feather grafts from hosts of

very different sizes. For example, *C. columbae* remained attached to feather sections from the Common Ground-dove, which is an order of magnitude smaller than the Rock Pigeon, its native host (Fig. 3). Wing lice also remained attached to feather sections from larger novel hosts, including those of the Victoria Crowned-pigeon, which is 7-fold larger than the native host. Attachment was further tested by placing lice on feather grafts attached to a high-speed fan that simulated harsher conditions such as the longer, faster flights of a racing pigeon (Johnston and Janiga, 1995). Over 60% of all lice remained attached to feather grafts during the 20-min trials, regardless of feather type (Fig. 3b). As in the previous experiment, the ability of lice to remain attached to feathers was independent of host size.

How can lice remain attached to feathers that differ so dramatically in size? We quantified 3 potential means of attachment (Fig. 1): (1) lice wedge themselves between the barbules of host feathers (whole-body insertion), (2) lice use tarsal claws (hooks) to cling to feather barbules, and (3) lice used their mandibles (clamps) to clench the barbules. In contrast to attachment ability (Fig. 3), the ability of lice to insert was significantly correlated with host size (Fig. 5a). Lice inserted least on the smallest hosts and most on the largest hosts. *Columbicola* spp. slip sideways into the interbarb space; consequently, this “lock and key” mechanism requires an interbarb space big enough to accommodate the width of the louse. The width of the interbarb space on Common Ground-doves was only 198  $\mu\text{m}$  (Fig. 2), and preliminary measurements indicate that Common Ground-doves have very shallow interbarb spaces, 137  $\mu\text{m}$  deep, which is much less than the width of *C. columbae* (270–330  $\mu\text{m}$ ; Clayton and Price, 1999). Although it is possible for lice to partially insert into this small space (1 of 46 lice placed on C.G.-d. feathers was partially inserted), lice cannot fully insert under these circumstances. The interbarb spaces of Mourning Doves and White-tipped Doves (244–252  $\mu\text{m}$ ) are slightly smaller than the width of *C. columbae*; however, preliminary measurements indicate that the depth of these interbarb spaces is sufficiently large to accommodate the lice (333–340  $\mu\text{m}$ ). At least 1 louse was fully inserted on feathers from each of these host species. The remaining host species (B-t.P., R.P., W.P., and V. C-p.) in the study all had interbarb spaces wide enough (271–431  $\mu\text{m}$ ; Fig. 2) and deep enough (463–540  $\mu\text{m}$ ; preliminary data) to accommodate *C. columbae*. Lice fully inserted on these feathers more readily (35% of lice fully inserted when placed on feathers of the 4 largest hosts). The inability of lice to insert on small novel hosts is strikingly different from their ability to remain attached on these hosts. For example, virtually no lice (1.1%) inserted on feathers of the Common Ground-dove (Fig. 5a), yet nearly all of these lice (95.5%) remained attached to a flying bird (Fig. 3a). Insertion, per se, does not appear to be an important attachment mechanism. However, insertion behavior could have other adaptive functions that influence host specificity and the relationship between host and parasite size. For example, insertion might help these lice escape from preening, a bird's principle means of ectoparasite defense (Clayton, 1991). Lice unable to insert because they are on the “wrong”-sized host could be more susceptible to host defense (Clayton et al., 2003).

We quantified the frequency with which lice use their tarsal claws to cling to feathers by observing louse attachment under

a dissecting scope. There was no significant difference in the use of tarsal claws across host treatments (Fig. 5b). Almost every louse used tarsal claws to aid in attachment. Of the 166 lice observed across all host treatments, only 3 lice did not use their tarsal claws. These 3 lice were inserted in the feathers of the 2 largest host species. The depth of the interbarb space on these 2 hosts ( $>500\ \mu\text{m}$ ) was large enough that some lice could have had difficulty positioning their tarsal claws for attachment.

We quantified the frequency with which lice used their mandibles to grasp feather barbules by observing louse attachment under a dissecting scope. There was no significant difference in the use of mandibles across host treatments (Fig. 5c). Most lice (68%) used their mandibles to attach to host feathers. Lice typically grasped multiple barbules at once with their mandibles. Lice might be able to attach to different-sized feathers by varying the number of barbules they clench in their mandibles. On the 2 smallest host species, the interbarb space is shallow enough that lice can reach feather barbules with their mandibles without inserting their bodies between feather barbs. On Common Ground-doves, 50% of lice attached with their mandibles, yet none of these lice were fully inserted. On Mourning Doves, 70% of the lice attached with their mandibles, even though only 24% inserted. On larger hosts, lice inserted their bodies between feather barbs to gain mandibular access to feather barbules at the base of deep interbarb spaces. Nearly all lice ( $\geq 95\%$ ) that attached with mandibles on the 5 largest hosts were also inserted.

Wing lice that were attached to feathers only with their tarsal claws were easily removed with forceps. In contrast, lice attached with their mandibles were much more tenacious. Occasionally, lice grabbed on so tightly with their mandibles that a quick tug with the forceps caused the body to separate from the head (data not shown). We explored the relative importance of tarsal claws and mandibles experimentally. In the experimental treatment, we allowed lice to attach to feather barbs with their tarsal claws, but blocked the use of mandibles by restricting access to the feather barbules. In the control treatment, lice were able to use both their tarsal claws and mandibles. Lice that could also attach with their mandibles were better able to remain attached to a flying bird (Fig. 6a). In fact, nearly 3 times as many lice remained attached when they could use their mandibles. Similarly, lice that could attach with their mandibles were better able to remain attached to feathers on the blades of a rotating fan (Fig. 6b). Under these more strenuous conditions, the ability to use mandibles improved attachment 6-fold.

Species of *Columbicola* are host specific and have a long coevolutionary history with their hosts (Clayton et al., 2004). Correlated host and parasite body size in this system suggests that *Columbicola* spp. are specializing on size-specific host resources such as feathers. One explanation consistent with these patterns is that a louse is morphologically specialized for attachment to a particular size of feather. We found, however, that *Columbicola* spp. are adept at attaching to feathers from hosts smaller and larger than their native host. Insertion ability was correlated with host size. However, lice remained attached even if they did not insert. Lice effectively used their tarsal claws and, most importantly, their mandibles to attach to different feather surfaces. Attachment ability is not a determinant of host specificity in this system.

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