# Walk or ride? Phoretic behaviour of amblyceran and ischnoceran lice

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A B S T R A C T

Phoresy is a behaviour where one organism hitches a ride on another more mobile organism. This is a common dispersal mechanism amongst relatively immobile species that specialise on patchy resources. Parasites specialise on patchily distributed resources: their hosts. Although host individuals are isolated in space and time, parasites must transmit between hosts or they will die with their hosts. Lice are permanent obligate ectoparasites that complete their entire life cycle on their host. They typically transmit when hosts come into direct contact; however, lice are also capable of transmitting phoretically. Yet, phoresy is rare amongst some groups of lice. Fundamental morphological differences have traditionally been used to explain the phoretic differences amongst different suborders of lice; however, these hypotheses do not fully explain observed patterns. We propose that a more fundamental natural history trait may better explain variation in phoresy. Species able to disperse under their own power should be less likely to engage in phoresy than more immobile species. Here we experimentally tested the relationship between independent louse mobility and phoresy using a system with four species of lice (Phthiraptera: Ischnocera and Amblycera) that all parasitize a single host species, the Rock Pigeon (*Columba livia*). We quantified the relative ability of all four species of lice to move independently off the host, and we quantified their ability to attach to, and remain attached to, hippoboscid flies (*Pseudolynchia canariensis*). Our results show that the most mobile louse species is the least phoretic, and the most phoretic species is quite immobile off the host. Our findings were consistent with the hypothesis that phoretic dispersal should be rare amongst species of lice that are capable of independent dispersal; however other factors such as interspecific competition may also play a role.

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## 1. Introduction

Organisms often specialise on resources that are patchily distributed in space and time (MacArthur and Pianka, 1966). Although patches can be resource-rich, dispersing amongst these spatially isolated and ephemeral patches can be difficult. This is particularly true of free-living and parasitic organisms that are relatively immobile such as wingless insects, mites and worms. Some organisms have solved this dispersal problem by being phoretic. Phoresy is a behaviour where a relatively immobile organism disperses by hitching a ride on another more mobile organism (Farish and Axtell, 1971; Houck and OConnor, 1991).

Phoresy has evolved in several phyla and is relatively common amongst nematodes, mites, lice, beetles and pseudoscorpions, some of which are obligate parasites or mutualists of vertebrate hosts (Treat, 1956; Keirans, 1975a; Roubik and Wheeler, 1982; Houck and OConnor, 1991; Zeh and Zeh, 1992; Athias-Binche and Morand, 1993). Hosts are patchily distributed because each host

individual is, in essence, an island of exploitable resources (Kuris et al., 1980). Moreover, hosts are temporally patchy because all hosts eventually die. Thus, dispersal amongst host individuals (also referred to as transmission) is critical for the persistence of parasite and mutualist lineages.

Lice (Phthiraptera) are permanent, obligate ectoparasites of birds and mammals. Lice most commonly transmit between hosts when individuals come into direct, physical contact, such as contact between mates and contact between parents and offspring (Rothschild and Clay, 1952; Johnson and Clayton, 2003b; Clayton et al., 2016). However, lice also engage in phoretic transmission. In most cases, lice hitch rides on hippoboscid flies, which are blood-feeding parasites of birds and mammals (Keirans, 1975a; Durden, 1990). Rarely, lice also hitch rides on other insects such as fleas, dragonflies, bees and butterflies (Worth and Patterson, 1960; Keirans, 1975b; Durden, 1990; Kirk-Spriggs and Mey, 2014).

There are three major suborders of lice: Anoplura, Amblycera and Ischnocera (Price et al., 2003). Although there are records of phoretic lice from all three suborders (Table 1), phoresy appears to be exceptionally rare amongst amblyceran lice (Table 2). To date, there is only one documented case of phoresy amongst over

**Table 1**
Species of lice that have been found attached to flies, based on a comprehensive survey of literature from 1890 to 2014 (updated from Harbison, C.W., 2008. Ecology and Evolution of Transmission in Feather-Feeding Lice (Phthiraptera: Ischnocera). Ph.D. Thesis, University of Utah, USA). Cases in which the phoretic lice were not identified to genus are not included.

| Suborder | Louse species | Host | References |
|---|---|---|---|
| Amblycera | *Hohorstiella giganteus* [a] | Bird | Hopkins (1946) |
| Anoplura | *Haematopinus eurysternus* | Mammal | Allingham (1987) |
| | *Haematopinus tuberculatus* | Mammal | Mitzmain (1912) |
| | *Linognathus africanus* | Mammal | Braack and Emerson (1986) |
| | *Linognathus breviceps* | Mammal | Pajot and Germain (1971) |
| | *Linognathus vituli* | Mammal | Bedford (1929) |
| | *Linognathus* sp. | Mammal | Worth and Patterson (1960) |
| | *Linognathus* sp. | Mammal | Kirk-Spriggs and Mey (2014) |
| | *Pediculus humanus* | Mammal | Calandruccio (1890), Nutall (1917) |
| Ischnocera | *Ardeicola botauri* | Bird | Peters (1935) |
| | *Bovicola meyeri* | Mammal | Keirans (1975b) |
| | *Brueelia amsel* | Bird | Baum (1968), Walter (1989) |
| | *Brueelia clayae* | Bird | Main and Anderson (1970, 1971) |
| | *Brueelia deficiens* | Bird | Spencer (1928) |
| | *Brueelia glandarii* | Bird | Eichler (1939), Callot (1946), Buttiker (1949) |
| | *Brueelia hectica* | Bird | Harrison (1913) |
| | *Brueelia interposita* | Bird | Ewing (1927), Thompson (1937) |
| | *Brueelia marginata* | Bird | Ash (1952), Harrison (1913), Warburton (1928), Thompson (1933), Blagoveshtchenski (1956) |
| | *Brueelia merulensis* | Bird | Ash (1952), Clay (1949), Clay and Meinertzhagen (1943) Eichler (1939), Walter (1989) |
| | *Brueelia rotundata* | Bird | McAtee (1922) |
| | *Brueelia turdinulae* | Bird | Walter (1989) |
| | *Brueelia unicosa* | Bird | Forsius (1912), Dubinin (1947), Blagoveshtchenski (1956) |
| | *Brueelia varia* | Bird | Baker and Blackie (1963) |
| | *Brueelia zeropunctata* | Bird | Wilson (1964) |
| | *Cervicola meyeri* | Mammal | Overgaard Nielsen (1990) |
| | *Columbicola columbae* | Bird | Martin (1934), Ward (1953), Ansari (1947), Hathaway (1943), Iannacone (1992), Macchioni et al. (2005) |
| | *Columbicola macrourae* | Bird | Couch (1962) |
| | *Damalinia bovis* | Mammal | Matthysse (1946), Bay (1977) |
| | *Damalinia meyeri* | Mammal | Keirans (1975b) |
| | *Damalinia tibialis* | Mammal | Peus (1933) |
| | *Gyropus ovalis* | Mammal | Keirans (1975b) |
| | *Lagopoecus lyrurus* | Bird | Forsius (1912) |
| | *Lipeurus crassus* | Bird | Proctor and Jones (2004) |
| | *Nirmus* sp. | Bird | Keirans (1975b) |
| | *Philopterus coarctatus* | Bird | Eichler (1946) |
| | *Physconelloides zenaidurae* | Bird | Couch (1962) |
| | *Strigiphilus crenulatus* | Bird | Blagoveshtchenski (1956) |
| | *Sturnidoecus pastoris* | Bird | Eichler (1939) |
| | *Sturnidoecus simplex* | Bird | Harrison (1913) |
| | *Sturnidoecus sturni* | Bird | Mjoberg (1910), Harrison (1913), Thompson (1934, 1947), Markov (1938), Eichler (1939), Clay and Meinertzhagen (1943), Corbet (1956) |
| | *Trogoninirmus odontopleuron* | Bird | Guimaraes (1944) |
| | *Trichodectes melis* | Mammal | Keirans (1975b) |

[a] Species formerly known as *Menacanthus giganteus*.

**Table 2**
Relative frequency of phoresy amongst the three major suborders of lice. Data based on published phoretic records (Table 1). The frequency of phoresy differs significantly amongst suborders ($\chi^2$ = 14.06, degrees of freedom = 2, $P < 0.001$). Different letters indicate significant differences (post hoc Fisher's exact tests, $P < 0.001$).

| Suborder | Total species | Phoretic species | % Phoretic species |
|---|---|---|---|
| Ischnocera | 3060 | 33 | 1.08[a] |
| Anoplura | 532 | 8 | 1.50[a] |
| Amblycera | 1334 | 1 | 0.07[b] |

1300 species of amblyceran lice (Hopkins, 1946), whereas at least 33 of the more than 3000 spp. of the suborder Ischnocera are known to engage in phoresy (Table 2). Some species of ischnoceran lice even engage in phoresy quite regularly. Studies by Markov (1938), Edwards (1952), Corbet (1956), Bennett (1961), and Baum (1968) report that 20–43.5% of hippoboscid flies in their field studies carried ischnoceran lice. Moreover, flies frequently carry more than one louse; for example, Peters (1935) found a fly with 31 lice attached.

Keirans (1975a) noted that lice attached to flies with their mandibles, and he hypothesised that the differences in the frequency of phoresy amongst lice is determined by the ability or inability of lice to grab onto flies with their mouthparts. Lice of the suborder Ischnocera have dorso-ventrally aligned, mandibulate mouthparts that are used to bite or scrape the host's integument (Johnson and Clayton, 2003b). Species of the suborder Ischnocera, which use their mandibles to cling tightly to the hair or feathers of their host, also use their mandibles to grasp setae on the body of hippoboscid flies (Keirans, 1975a). In contrast, lice of the suborder Amblycera have chewing mouthparts that are essentially modified to suck blood and lice of the suborder Anoplura have piercing, sucking mouthparts for sucking blood (Johnson and Clayton, 2003b).

Despite these extreme morphological differences, anopluran lice are as phoretic as ischnocerans (Table 2). Instead of using mouthparts, anopluran lice cling to flies with their tarsal claws (Mitzmain, 1912; Allingham, 1987; Durden, 1990). Recent phoretic

records indicate that some ischnocerans also attach to flies using their legs and claws (Harbison et al., 2009). The single published record of phoresy of an amblyceran louse noted that the louse was attached by its mouthparts to one of the fly's legs (Hopkins, 1946). In addition, we recently examined hippoboscids flies (*Pseudolynchia canariensis)* leaving captive Rock Pigeons (*Columba livia*) and found amblyceran lice (*Hohorstiella lata*) attached to several flies (Fig. 1). These lice appeared to be attached using their tarsal claws; these lice may also be attached with their mouthparts but scanning electron microscope images of this point of attachment were inconclusive (Fig. 1).

Regardless of the precise way in which lice attach to flies, it is clear that lice from all three suborders can be phoretic. Given that all lice face similar transmission barriers, why is phoresy so rare amongst some groups of lice? We suggest that a fundamental life-history difference is responsible for these phoretic differences.

Dispersal is risky. However, phoresy may be an especially risky dispersal strategy given that lice typically disperse by moving from one host to another during periods of direct, physical contact between two host individuals (Clayton et al., 2016). Off the vertebrate host, lice can only live a few days (Johnson and Clayton, 2003b). Lice that are not transported to a compatible host during this short time-frame will die. Lice that fall off or are groomed off the fly will also die without reaching a new host. Furthermore, hippoboscid flies are not as host-specific as lice. Flies may transport lice to a novel host species where the lice cannot survive or reproduce. The benefits of phoresy may outweigh the costs of phoretic dispersal for highly immobile species, but species that can move independently between host individuals may not need to engage in such risky behaviour. For example, agile amblyceran lice will crawl away from dead or distressed hosts in search of a new host (Keirans, 1975a; Johnson and Clayton, 2003a; Clayton et al., 2016). It is not clear what cues most lice use to locate new host individuals, but the few studies that have been done indicate that chemosensory and tactile mechanisms are likely involved (Wigglesworth, 1941; Clayton et al., 2016). Regardless of the types of cues used, the probability of crawling to a new host may be high, especially amongst gregarious or colonial host species that roost or nest in close proximity. In contrast, ischnoceran lice are so specialised for life on hair or feathers that they typically remain on the host, even if it is dead (Keirans, 1975a). For these lice, the benefits of phoresy may outweigh the costs.

Here, we investigated the relationship between independent mobility and phoresy amongst four species of lice that are ecological "replicates" in many respects (Johnson and Clayton, 2003b; Johnson et al., 2005). We compared two ischnoceran species: *Columbicola columbae* and *Campanulotes compar*; and two amblyceran species: *H. lata* and *Menacanthus stramineus* (Fig. 2). All four of these species are permanent obligate parasites that are found on Rock Pigeons (*C. livia*; Brown, 1971; Dranzoa et al., 1999; Price et al., 2003; Musa et al., 2011). Rock Pigeons are also parasitized by a hippoboscid fly (*P. canariensis*). These flies feed on blood and crawl throughout the bird's plumage (Harbison, C.W., 2008. Ecology and Evolution of Transmission in Feather-Feeding Lice (Phthiraptera: Ischnocera). Ph.D. Thesis, University of Utah, USA). Flies are found most commonly on the abdomen of the bird (Harbison et al., 2008), a region of the body where all four lice species occur. Thus, all four species have had opportunities to engage in phoresy over macroevolutionary time.

Another aspect of this host–parasite system that makes it especially suitable for testing the relative role of phoretic dispersal versus independent dispersal is that Rock Pigeons nest in flocks. Rock Pigeon nests are often very close together; neighbouring nests are frequently 0.1–1.0 m apart (Johnston and Janiga, 1995). Thus, all four species of lice have had opportunities to disperse to new host individuals by crawling to neighbouring hosts over macroevolutionary time.

Despite these ecological similarities, these four species of lice have very different phoretic records. *Columbicola columbae* has been observed on hippoboscid flies on several occasions (Table 1), and has been shown to be phoretic in experiments (Harbison et al., 2009). The other ischnoceran louse, *Ca. compar*, has not been observed on flies and did not engage in phoresy in experimental settings (Harbison et al., 2009; Harbison and Clayton, 2011). Of the two amblyceran species in this study, neither species has been observed phoretically dispersing. However, one closely related species (*Hohorstiella gigantea*, a parasite of Stock Doves, *Columba oenas*) was found on a hippoboscid fly and is the only known case of phoresy from the suborder Amblycera (Hopkins, 1946, Table 1).

Here, we investigate the relationship between the ability of these four species of lice to move independently off the surface of the host relative to their phoretic ability. Specifically, we quantify how far each species can crawl off the surface of the host in a specified amount of time. We also conduct three assays to determine the relative abilities of these four species of lice to (i) attach to hippoboscid flies; (ii) remain attached to hippoboscid flies while the flies groom, and (iii) remain attached to hippoboscid flies during flight.

## 2. Materials and methods

### 2.1. Relative mobility off the host

We compared the "off-host mobility" of four species of lice (*Co. columbae, Ca. compar, H. lata* and *M. stramineus*) by measuring the distance each species travelled on a filter paper in 2 min. We placed each louse, one at a time, in the center of a filter paper that was 15 cm in diameter. Next, we placed the cover of a glass petri
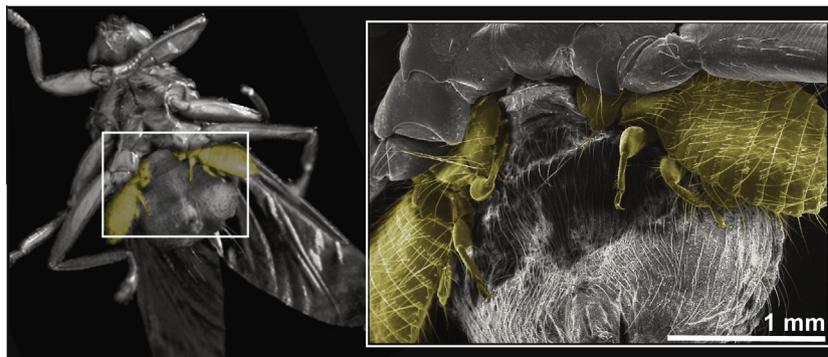


**Fig. 1.** Photo of a hippoboscid fly (*Pseudolynchia canariensis*) captured from a captive Rock Pigeon (*Columba livia*) with two amblyceran lice (*Hohorstiella lata*) attached to the abdomen of the fly. Inset: false-coloured scanning electron microscope image.
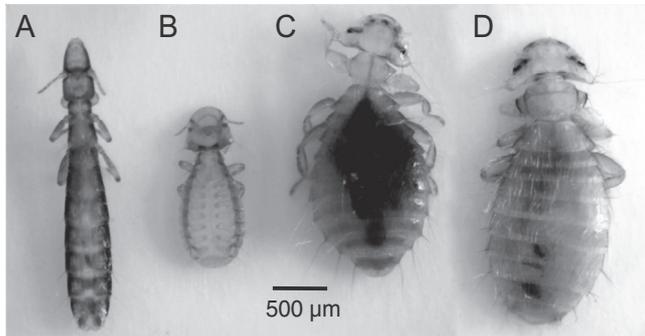
**Fig. 2.** Four species of lice (to scale) from Rock Pigeons (*Columba livia*): (A) *Columbicola columbae* (Ischnocera), (B) *Campanulotes compar* (Ischnocera), (C) *Hohorstiella lata* (Amblycera), and (D) *Menacanthus stramineus* (Amblycera).

dish over the filter paper. To stimulate louse movement, a light (Leica Illuminator, Model 31-35-28) was briefly shone on each louse. Lice are negatively phototactic and they immediately move away from light. As each louse moved, we traced its path on the cover glass with a marker. Each path was photographed and digitally measured using ImageJ software (Rasband W.S., 2015. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland, USA, imagej.nih.gov/ij/). We quantified off-host mobility for 20 lice of each of the four species. Flies and all four species of lice were obtained from culture stocks raised on captive Rock Pigeons kept in an animal facility at the University of Utah, USA, Institutional Animal Care and Use Committee # 11-07018). Our small culture of *M. stramineus* was supplemented with lice from B. Mullens, University of California, Riverside, USA.

### 2.2. Attachment of lice to flies

Three assays were conducted to compare the ability of *Co. columbae*, *Ca. compar*, *H. lata*, and *M. stramineus* to (i) attach to a fly; (ii) remain attached to a grooming fly, and (iii) remain attached to a fly during flight. Flies used in assays all came from a captive culture population that was founded with flies from Salt Lake City, UT, USA.

First, the relative ability of lice to attach to flies was assessed by placing lice, one at a time, in a small (5 mL) glass vial with a single hippoboscid fly. These small vials ensured that each louse came into contact with the fly, and thus had an opportunity to attach. During each "trial" the louse and fly were monitored for 2 min, or until the louse attached, whichever came first. Lice were considered "attached" if they held onto the fly for at least 2 s. We conducted attachment trials for at least 55 lice of each species. Trials were ordered randomly with respect to louse species, and flies were replaced every 20 trials with a new fly, which was a fly that had not previously been used in any assay. Lice that attached during the first assay were immediately placed in the grooming assay (see below).

In the grooming assay, we compared the ability of lice to withstand grooming by flies. Flies with attached lice were placed into a small (10 × 10 × 18 cm) clear plastic observation chamber. Upon entering the chamber, the flies would perch on a wall of the chamber and use their legs to groom their own bodies. This behaviour is easily observable with the naked eye. The length of time that each louse stayed attached to a grooming fly was recorded. The observation period lasted 5 min, or until the louse detached, whichever came first.

Third, we compared the ability of three species of lice to remain attached to flies that flew approximately 3 m. *Menacanthus stramineus* was not used in this assay because very few *M. stramineus*

stayed attached to flies during the previous assays (see Section 3). Flight trials were conducted in a small room (3.5 × 3.0 × 1.5 m) with a large window at the end (as in Harbison et al., 2009). A single fly and a louse were first constrained within a small vial, so that the louse had an opportunity to attach to the fly. Once the louse was attached for 2 s, the fly was released; if a louse did not attach within 2 min, it was discarded. Flies are positively phototactic and flew directly towards the window upon release. Once a fly landed on the window, the cover of a glass petri dish was placed over the fly and the presence or absence of the louse was recorded. A new louse was used for each trial. We conducted flight trials for 55 lice of each species. Trials were ordered randomly with respect to louse species and flies were replaced every 12 trials with a new fly.

## 3. Results

### 3.1. Relative mobility off the host

We compared the relative ability of four species of lice to move off the host by quantifying the distance that each species moved on a filter paper. The four species of lice significantly differed in the distance they travelled in 2 min (Fig. 3A; Kruskal–Wallis, $\chi^2 = 58.3$, degrees of freedom = 3, $P < 0.0001$). Both amblyceran species travelled significantly farther than either species of ischnoceran louse. *Menacanthus stramineus* travelled threefold farther than *H. lata* and over 22-fold farther than either ischnoceran species.

### 3.2. Attachment of lice to flies

We compared the relative ability of four species of lice to attach to hippoboscid flies that were placed in close contact. The four species of lice significantly differed in attachment to flies ($\chi^2 = 119.4$, degrees of freedom (df) = 3, $P < 0.0001$; final sample sizes indicated in Fig. 3B). Nearly all ischnoceran lice attached to flies (100% of *Co. columbae* and 96.9% of *Ca. compar*). The majority of *H. lata* also attached to flies (89.2%), but they did so significantly less than *Co. columbae* (Fisher's Exact test, $P = 0.013$). *Menacanthus stramineus* attached to flies in only 30.9% of trials, which was significantly less than any of the other species (Fisher's Exact test, $P < 0.0001$, in all three cases).

Next, we compared the ability of the four species of lice to withstand fly grooming. Flies did not groom in 5% of trials and these trials were excluded from analyses (final sample sizes are indicated in Fig. 3C). The amount of time that the four species of lice remained attached to grooming flies was significantly different (Kruskal–Wallis, $\chi^2 = 43.3$, df = 3, $P < 0.0001$). A majority of *Co. columbae* (61%) stayed attached for the entire 5 min trial. In contrast, only 4.9% of *Ca. compar*, 18.2% of *H. lata*, and 0% of *M. stramineus* remained attached to the fly for the full 5 min trial.

Lastly, we compared the ability of three species of lice to remain attached to flying flies. Rarely (3%), flies did not fly towards the window; these trials were excluded from analyses. In addition, four (7.5%) *H. lata* did not attach to the fly within the allotted time (2 min), and these trials were also excluded from analyses (Fig. 3D). The percentage of lice that remained attached to flies during flight differed significantly amongst the three species ($\chi^2 = 13.39$, df = 2, $P = 0.001$).

## 4. Discussion

We tested the ability of four species of lice to move, independently, on substrates off the host. We found that the two species of ischnoceran lice, *Co. columbae* and *Ca. compar*, are quite immobile off the host. The mean crawling speed of either ischnoceran spp.
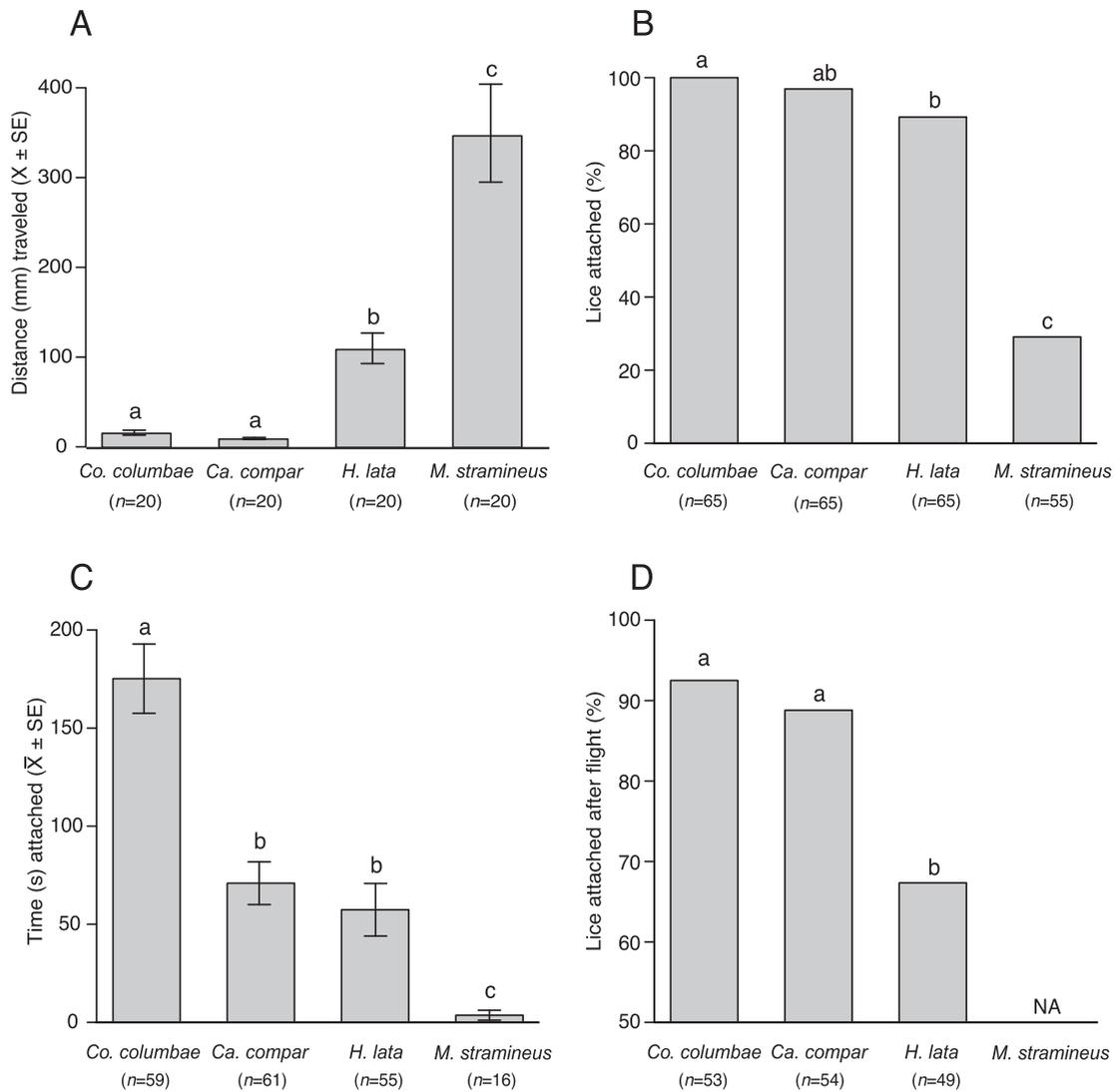
**Fig. 3.** Comparisons of off-host mobility and fly attachment for four species of lice (*Columbicola columbae, Campanulotes compar, Hohorstiella lata, Menacanthus stramineus*) from Rock Pigeons (*Columba livia*). Bars with different letters differ significantly. (A) Distance lice travelled off the host in 2 min. The four species of lice differed significantly in off-host mobility ($P < 0.0001$, see Section 3; Mann–Whitney $U$ post hoc tests, $P < 0.05$). (B) Percentage of lice that attached to pigeon flies (based on post hoc Fisher's Exact tests of raw data, $P < 0.05$). (C) The amount of time that lice stayed attached to grooming flies differed significantly amongst species ($P < 0.0001$, see Section 3; Mann–Whitney $U$ post hoc tests, $P < 0.05$). (D) Percentage of lice remaining attached to a fly during flight (post hoc Fisher's Exact tests of raw data, $P < 0.05$).

did not exceed 8 mm/min off the host. By comparison, *Co. columbae* and *Ca. compar* are much more mobile when they are on feathers. Using the same experimental setup, Bush (Bush, S.E., 2004. Evolutionary Ecology of Host Specificity in Columbiform Feather Lice. Ph.D. Thesis, Department of Biology, University of Utah, USA) placed lice on feathers from their preferred microhabitats on the host and recorded the crawling speed of each species. In this study, *Co. columbae* travelled (mean ± S.E.) 121 ± 8.7 mm/min and *Ca. compar* crawled 161 ± 13.6 mm/min. In short, both species of lice can travel 15-fold faster on feathers than on surfaces off the host.

In contrast, the two amblyceran species in the study were quite mobile off the host. *Hohorstiella lata* crawled at a speed of 55 mm/min, and *M. stramineus*, the most mobile louse species in the study, crawled 174 mm/min, with the fastest individual louse travelling at 401 mm/min. Moreover, both *M. stramineus* and *H. lata* readily crawled off filter paper and on to the glass petri dish, which indicates they could even cross slick surfaces they might encounter in the wild. In contrast, neither species of ischnoceran louse can move on slick surfaces such as glass (personal observation).

At these speeds, amblyceran lice may be able to crawl between nests in the wild. Rock Pigeons frequently nest in close proximity, often less than 1 m apart (Johnston and Janiga, 1995). At the observed speeds, *M. stramineus* could travel between nests 1 m apart in 6 min and *H. lata* could travel between the same nests in 18 min. Given how fast these lice crawl, it seems that crawling between neighbouring nests could be an effective dispersal strategy for these lice. In contrast, it would take *Co. columbae* 2.1 h and *Ca. compar* 3.5 h to cover the same distance, assuming the lice do not encounter any surfaces too slick to cross. Both *Co. columbae* and *Ca. compar* can survive a few days off the body of the host (Johnson and Clayton, 2003b), so it is conceivable that these lice could survive such a journey, however improbable it may be. Whether or not any of the four species of lice actually crawls between hosts in the wild is unknown. Our data indicate that crawling for several hours may prevent ischnoceran lice from successfully dispersing between nests, whereas amblycerans should be able to use this dispersal strategy. A study in the field is needed to test this hypothesis.

We also tested the ability of these lice to move phoretically on hippoboscid flies. The four species of lice in our study differed in their abilities to attach to a fly and remain attached to the fly while it was grooming or flying. Both ischnoceran species and one amblyceran species (*H. lata*) readily attached to flies when they were placed in close contact. All *Co. columbae* attached, and nearly all (>89%) *Ca. compar* and *H. lata* attached to the flies. In contrast, the second amblyceran species (*M. stramineus*) attached to flies only 29% of the time, and the few *M. stramineus* that initially attached to flies quickly detached from grooming flies. On grooming flies, *Co. columbae* stayed attached much longer than any other species. Both *Ca. compar* and *H. lata* remained attached to grooming flies but for less than half as long as *Co. columbae*.

It is difficult to determine how important it is that lice are able to withstand grooming by the fly, because there is no information about the amount of time that hippoboscid flies spend grooming in the wild. The screwworm (*Cochliomyia hominivorax*: Calliphoridae), a distantly related parasitic fly, spends over 19% of its time engaged in grooming behaviour (Thomas, 1991). If the pigeon fly *P. canariensis* also spends a considerable amount of time grooming then this could explain, at a proximal level, why *Ca. compar* does not engage in phoretic dispersal even though it can attach to, and remain attached to, flying flies as well as *Co. columbae* (Harbison et al., 2008). The amblyceran louse *H. lata* detached from grooming flies as frequently as *Ca. compar* and, as with *Ca. compar*, there are no records of *H. lata* being phoretic under natural conditions.

Interestingly, the louse species *M. stramineus* is found on at least eight host species from two different host orders (Brown, 1971; Dranzoa et al., 1999; Price et al., 2003; Musa et al., 2011). By comparison, other lice in this study are restricted to either a single host genus (*Co. columbae*) or a single host species (*Ca. compar* and *H. lata*). *Menacanthus stramineus* is, by far, the least host-specific of any of the species of lice used in this study. One could argue that this species should be the most likely to engage in phoresy because it could potentially survive and reproduce on other host species that the fly is likely to visit (Maa, 1969). Despite the ability of *M. stramineus* to parasitize many host species, however, this louse was the least likely to engage in phoresy. In a comparative study, Harbison (Harbison, C.W., 2008. Ecology and Evolution of Transmission in Feather-Feeding Lice (Phthiraptera: Ischnocera). Ph.D. Thesis, University of Utah, USA) showed that phoretic species are more likely to be found on multiple host species than are closely related species that are not phoretic. Our data examines this relationship from another angle, and shows that species found on multiple host species are not necessarily more phoretic.

We hypothesised that parasites, which are able to move independently off the surface of the host, should be less likely to engage in phoresy than relatively immobile parasites. We found that the species that was best able to crawl off the surface of the host, *M. stramineus*, performed poorly in all assays designed to quantify phoretic ability. In contrast, one of the least mobile species, *Co. columbae*, was able to attach to, and remain attached to, flies more often and for a longer period of time than any other species. *Hohorstiella lata* exhibited intermediate performance in the off-host mobility assay as well as the three assays quantifying phoretic ability. Perplexingly, however, *Ca. compar* is as immobile off the host as *Co. columbae*, yet *Ca. compar* exhibited intermediate performance in the assays quantifying phoretic ability. Moreover, there are no records of *Ca. compar* being phoretic, whereas *Co. columbae* has repeatedly been found on flies (Table 1).

Other ecological factors may be driving the phoretic differences between *Co. columbae* and *Ca. compar*. Bush and Malenke (2008) found that *Co. columbae* is competitively inferior to *Ca. compar*. Harbison et al. (2008) found that phoresy can be an important mechanism for escaping competition with other species of lice on the same host. Our results are also consistent with a competition-colonisation trade-off model between these two species. If by dispersing phoretically, *Co. columbae* are better able to escape from competition with *Ca. compar*, then this benefit may outweigh the potential risks to phoretic dispersal.

Competition is thought to drive phoretic behaviour in other systems. For example, the phoretic behaviour of the pseudoscorpion *Paratemnoides nidificator* seems to be driven, in part, by intraspecific competition (Tizo-Pedroso and Del-Claro, 2007). This species is most likely to attempt phoresy when there are many pseudoscorpions living together in a single colony (Tizo-Pedroso and Del-Claro, 2007). More studies are needed amongst "ecological replicates" to determine whether mobility and/or competition frequently trigger the evolution of phoretic behaviour in other animal systems.

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