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Walk or ride? Phoretic behaviour of amblyceran and ischnoceran lice

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ABSTRACT

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.

1. Introduction

Organisms often specialise on resources that are patchily distributed in space and time (MacAurthur 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

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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