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International Journal for Parasitology 34 (2004) 1113–1119
www.parasitology-online.com

Differences in straggling rates between two genera of dove lice (Insecta: Phthiraptera) reinforce population genetic and cophylogenetic patterns☆

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Received 19 April 2004; received in revised form 15 June 2004; accepted 15 June 2004

Abstract

Differences in dispersal abilities have been implicated for causing disparate evolutionary patterns between *Columbicola* and *Physconelloides* lice (Insecta: Phthiraptera). However, no study has documented straggling (when lice are found on atypical hosts) rates within these lineages. We used the fact that the Galapagos Hawk, *Buteo galapagoensis* (Gould) (Falconiformes) feeds on the Galapagos Dove *Zenaida galapagoensis* Gould (Columbiformes) within an ecologically simplified setting. The Galapagos Dove is the only typical host of *Columbicola macrourae* (Wilson) and *Physconelloides galapagensis* (Kellogg and Huwana) in Galapagos. We quantitatively sampled and found these lice on both bird species. A DNA barcoding approach confirmed that stragglers were derived from Galapagos doves. We also collected a *Bovicola* sp. louse, likely originating from a goat (*Capra hircus*). On hawks, *C. macrourae* was significantly more prevalent than *P. galapagensis*. On doves, the two lice were equally prevalent and abundant. Differences in prevalence on hawks was a function of differences in straggling rate between lice, and not a reflection of their relative representation within the dove population. This provides further evidence that differences in dispersal abilities may drive differences in the degree of cospeciation in *Columbicola* and *Phyconelloides* lice, which have become model systems in evolutionary biology.
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Keywords: Cospeciation; DNA barcoding; Dove; Galapagos; Lice; Straggling

1. Introduction

Since lice are the most species-rich lineage of ectoparasite, understanding the ecological processes driving their evolution is of general interest to evolutionary biologists (Marshall, 1981; Clayton et al., 2003a,b). The dispersal (and by some, establishment) of a louse species from the typical host species to an atypical one has variably been referred to as host transfer (Kethley and Johnston, 1975), host switching (Clayton et al., 2003a), 'straggling' (Rózsa, 1993) and secondary interspecific infestation (Clay, 1949). Straggling and subsequent host-switching is accepted as a powerful force in phthirapteran evolution (Clay, 1949; Rózsa, 1993; Tompkins and Clayton, 1999; Johnson et al., 2002a,b,c; Clayton and Johnson, 2003). Natural straggling and host-switching are not synonyms (Rózsa, 1993; Clayton et al., 2003a). Straggling is the antecedent of host-switching (Rózsa, 1993). The interpretation of straggling as a window into the development of host-switching merits further study.

Differing interspecific rates of louse straggling between hosts may influence long-term evolutionary outcomes (Johnson et al., 2002a; Clayton and Johnson, 2003). Those louse species that tend to have fidelity to a particular host species over ecological time should have a higher probability of cospeciation, whereas those taxa prone to straggling should show less evidence of cospeciation. "Thus straggling may be of considerable significance, particularly given the expanse of evolutionary time over which repeated dispersal events can eventually yield a successful host switch" (Clayton et al., 2003a). However, little information

☆ Novel nucleotide sequence data reported in this paper are available in the GenBank™ database under the accession numbers AY594662, AY594663, AY594666, AY594667.

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doi:10.1016/j.ijpara.2004.06.003

is currently available on the ecological processes underpinning phthirapteran evolution (Johnson et al., 2002a).

Parasite life-history characteristics must be considered when examining coevolutionary and ecological interactions between lice and their hosts (Johnson et al., 2002a,b; Clayton and Johnson, 2003; Whiteman and Parker, 2004). For example, a spectacular coevolutionary similarity has been revealed between the phylogenies of *Physconelloides* (Ischnocera: Philopteridae) lice and their New World dove hosts (Aves: Columbiformes: Columbidae). In contrast, no significant cospeciation was found between less host-specific *Columbicola* (Ischnocera: Philopteridae) lice on the same hosts (Clayton and Johnson, 2003). *Columbicola* lice are probably more dispersive than *Physconelloides* lice, which has driven the differing degrees of host-specificity and, eventually, cospeciation in these lineages. This assertion was based on a suite of evidence, including experimental (Dumbacher, 1999), observational (Keirans, 1975), and population genetic (Johnson et al., 2002a) data on louse biology. The population genetic data showed that *Columbicola* populations harbored significantly less population genetic structure than *Physconelloides* populations. However, no quantitative behavioral or ecological study has unequivocally shown that *Columbicola* lice have a higher straggling rate than *Physconelloides* lice between two populations of hosts in nature. If such ecological data were available, they would have bearing on the macro- and micro-evolutionary evidence that louse dispersal ability is a key influence on the evolutionary trajectories of these particular lineages, which have emerged as a model system in evolutionary biology (Johnson et al., 2002a,b; Clayton and Johnson, 2003; Clayton et al., 2003a,b).

A prey-predator host system is a good candidate system in which to evaluate the relative rates of straggling between these louse genera. Clay (1949) postulated that prey to predator straggling and subsequent host-switching has been important in the evolutionary history of lice, followed by allopatric speciation between lineages on old and new hosts. Johnson et al. (2002b) have given molecular evidence supporting this notion. Louse species within the *Degeeriella* complex found on the Falconiformes are, in general, more closely related to lice found on non-falconiform birds than they are to each other (Johnson et al., 2002b).

One potential avenue for exploring dispersal rate differences within a predator-prey system is to use an ecologically simplified natural setting. The low α diversity and high population densities of many species of the Galapagos avifauna renders it a good natural laboratory for studies examining the ecology of host-parasite dynamics. We used the fact that Galapagos hawks, *Buteo galapagoensis* (Gould) (Falconiformes) prey on Galapagos doves, *Zenaida galapagoensis* Gould (Columbiformes) (de Vries, 1975; Donaghy Cannon, 2001. Breeding ecology of cooperatively polyandrous Galapagos hawks (*Buteo galapagoensis*) on Santiago Island, Galapagos. M.S. Thesis, Arkansas State University, Jonesboro, Arkansas) within the Galapagos.

In this study, we found that the rate of prey-predator straggling of *Columbicola* and *Physconelloides* lice from doves to hawks was observable and predictable in nature. Moreover, the Galapagos Dove is the only typical host of *Columbicola macrourae* (Wilson) and *Physconelloides galapagensis* (Kellogg and Huwana) in the archipelago. Rock doves (*Columba livia*) occur on islands other than those used in this study; but are not typically host to either of these louse species. Thus, straggling to the predator via a host other than the Galapagos Dove, the only native resident columbiform on these islands is unlikely. Similar studies within more diverse communities are likely confounded by the presence of multiple suitable host species.

2. Materials and methods

2.1. Sampling

From 14 May to 29 June 2002 and 12 to 23 June 2003 Galapagos hawks (*B. galapagoensis*) were live captured on Santiago and Pinta islands, respectively, in the Galapagos National Park, Ecuador, using either a pole-noose, baited balchatri-trap (Berger and Mueller, 1959), or by hand from the nest as is described elsewhere (Bollmer et al., 2003; Whiteman and Parker, 2004). From 15 May to 29 June 2002, Galapagos doves (*Z. galapagoensis*) were captured on Santiago using hand or mist nets as is described in detail elsewhere (Santiago-Alarcon, D., unpublished M.S. thesis, 2003, University of Missouri, St Louis, St Louis, Missouri). Sampling of lice was not carried out on doves from Pinta, due to logistical constraints. Dove and hawk sampling on Santiago was conducted in two general areas: James (Espumilla) Bay, along the western coastline (~00°20′S, 090°82′W), and Sullivan Bay, along the eastern shore (~00°30′S, 090°58′W). Sampling of hawks on Pinta was conducted near a base camp on the southern shore (~00°33′N, 090°44′W). Ectoparasites were quantitatively sampled from the birds via dust-ruffling (Walther and Clayton, 1997) with pyrethroid insecticide (Zema® Flea and Tick Powder for Dogs, St John Laboratories, Harbor City, CA, USA). The particular quantitative sampling procedure used by us is described in detail elsewhere (Whiteman and Parker, 2004). To avoid human-caused transfer of lice, doves and hawks were handled on separate days and sampling for each involved separate equipment.

2.2. DNA barcoding

Some individuals of *C. macrourae* and *P. galapagensis* are morphologically indistinguishable from some mainland congeners (Clayton and Price, 1999; Price et al., 1999), and *C. macrourae* from Galapagos doves is indistinguishable from conspecifics collected from Mourning doves

(*Zenaida macroura*) (Clayton and Price, 1999). Thus, to assure our species identifications were correct, we used a DNA barcoding approach (Besansky et al., 2003; Hebert et al., 2003a,b) to diagnose these louse species and geographical origin (Galapagos vs. mainland). Specifically, mitochondrial DNA from two *C. macrourae* representatives (one each from Galapagos hawk hosts on islas Santiago and Pinta, GenBank accession numbers AY594662, AY594663), one *P. galapagensis* individual (from a Galapagos Hawk host on Isla Pinta, GenBank accession number AY594666) and the *Bovicola* sp. individual (from a Galapagos Hawk host on Isla Santiago, GenBank accession number AY594667) was extracted and a 379-bp portion of subunit I of the cytochrome *c* oxidase gene (COI) amplified and sequenced using primers L6625 and H7005, following Johnson et al. (2002a). For the dove lice, two sequence alignments were created, one each for sequences from *Columbicola* and *Physconelloides*. Specifically, alignments were comprised of straggling louse sequences from Galapagos hawks (using sequences from this study), and of conspecific or congeneric sequences of lice collected from Galapagos doves (using sequences from GenBank and Johnson and Clayton, 2003) and their closest relatives (using sequences from Johnson et al., 2002a), Mourning doves and White-winged doves (*Zenaida asiatica*). In both phylogenies, louse sequences from White-winged dove hosts were used as outgroups (Clayton and Johnson, 2003). These alignments were subjected to phylogenetic parsimony analysis using Paup* version 4.0b10 (Swofford, D., 2002. Paup* version 4.0b10. Sinauer Associates, Inc., Publishers, Sunderland, MA) (Fig. 1).

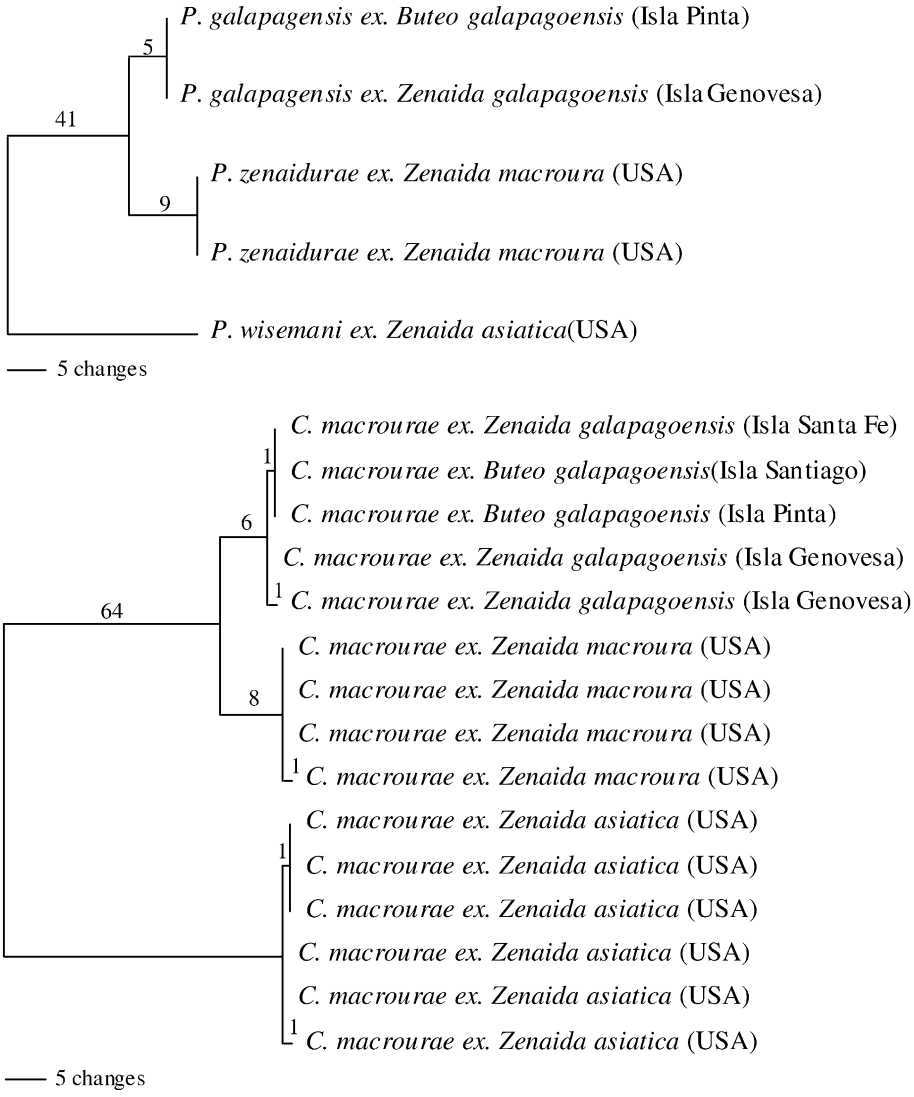

Fig. 1. Most parsimonious phylogenetic tree generated in Paup* version 4.0b10 (Swofford, D., 2002. Paup* version 4.0b10. Sinauer Associates, Inc. Publishers, Sunderland, MA) based on 379 bp of the mitochondrial cytochrome *c* oxidase subunit I gene for *Physconelloides* (*P.*) and *Columbicola* (*C.*) lice from doves in the genus *Zenaida*. Trees include sequences for 'stragglers' of these genera on Galapagos hawks (*B. galapagoensis*). Each louse sequence was derived from a different host individual; each terminus represents one louse sequence from (*ex.*) a unique host individual, followed by the collection locality (USA or islands within the Galapagos). Branch lengths appear as numerals along branches and are proportional to reconstructed changes using maximum parsimony; the branch length scale is indicated below each tree.

The sequences from the nymphal *Bovicola* sp. were compared to those from other trichodectid lice previously sequenced (Johnson et al., 2003).

2.3. Statistical analyses

Prevalence, mean and median intensity, and mean abundances (Margolis et al., 1982; Bush et al., 1997) of the two louse species within each host species were compared using the program Quantitative Parasitology 2.0 (Rózsa et al., 2000; Reiczigel, J., Rózsa, L., 2001. Quantitative Parasitology 2.0. Budapest, Hungary: distributed by the authors). Fisher's exact tests were used to compare prevalences of each parasite species (*C. macrourae* vs. *P. galapagensis*) within each host species. Distribution-free two-sample bootstrap *t*-tests were used to compare mean intensities and abundances (each with 2000 replicates). Mood's median tests were used to compare median (typical) intensities. We report 95% bootstrap confidence intervals (2000 replications each) for mean abundance and intensity (Rózsa et al., 2000). Since only one *P. galapagensis* individual was collected from the 91 Galapagos Hawk hosts sampled, only prevalence and mean abundance were calculated. We also calculated the moment '*k*' of the negative binomial distribution, which is inversely related to the degree of aggregation of parasite abundances among members of the host population (Crofton, 1971), and the index of discrepancy '*D*,' which is directly related to the degree of aggregation of parasite abundances among members of the host population (Poulin, 1993). The index of discrepancy is the degree to which the observed distribution of parasites among the host population differs from a hypothetical one in which each host harbors the same number of parasites (Poulin, 1993).

3. Results

A total of 60 individuals of the Galapagos Hawk, including two nestlings, were live captured on Isla Santiago, and a total of 31 individuals were captured on Isla Pinta. On Santiago, a total of 1602 lice were collected from the 60 hawks, of which 10 lice on six hawks represented stragglers for which hawks are atypical hosts (Table 1). On Pinta, a total of 3306 lice were collected from the 31 hawks, of which four lice on four hawks represented stragglers for which hawks are atypical hosts (Table 1). In total, straggling lice were collected from 10 different Galapagos Hawk host individuals out of the 91 sampled (Table 1). Eight Galapagos hawks harbored 12 individuals of *C. macrourae*. Notably, two hosts from different hawk social groups on Santiago harbored individuals of both sexes (Table 1). In two cases, two hawks from the same social group each harbored a *C. macrourae* individual (from one territory on Santiago and one on Pinta) (Table 1). Only one *P. galapagensis* individual was collected from a single hawk host on Pinta (Table 1). For both islands combined, prevalence of *C. macrourae* on hawks was significantly higher than that of *P. galapagensis* (Table 2). Only one nymphal *Bovicola* sp. was collected from a hawk on Santiago, where its prevalence was 1.67% (1/60 hosts infected) (Table 1). Thus, for both islands combined, its prevalence on hawks was 1.1% (1/91 hosts infected). All stragglers were deposited in the Phthiraptera collection of the Illinois Natural History Survey, Champaign, IL.

Table 1
All straggling lice (Insecta: Phthiraptera) collected after sampling from 91 Galapagos hawk (*B. galapagoensis*) (Aves: Falconiformes) hosts captured on Santiago and Pinta islands, Galapagos (during 2002 and 2003, respectively)

Straggler species	Island	*B. galapagoensis* data (band, age, sex, territorial status)	Straggler data (abundance, age, sex)
I. *C. macrourae*	Santiago	Red 24, AMT	3 AF, 1 AM
	Santiago	Red 26, AMT	1 AF, 1 AM
	Santiago	Blue 2M, JM (nestling)	1 AM
	Santiago	Green 2R, AMT	1 AM
	Santiago	Black 35, AMT (in same territory as Green 2R)	1 AF
	Pinta	Black 49, AMT	1 AM
	Pinta	Red OX, AFT	1 AF
	Pinta	Black 36, AMT (in same territory as Red OX)	1 AF
II. *P. galapagensis*	Pinta	Black 41, JML	1 AF
III. *Bovicola* sp.	Santiago	Blue 4P, JFL	1 N

Abbreviations are: A, adult, M, male, F, female, T, territorial, L, non-territorial, N, nymph.

A total of 28 individuals of the Galapagos Dove were live captured on Isla Santiago. A total of 851 *C. macrourae* and 863 *P. galapagensis* were collected from these hosts. Most hosts (>90%) harbored *C. macrourae* and *P. galapagensis* (Table 2). Prevalence, mean abundance, intensity and median (typical) intensity of the two louse species were not significantly different within the Santiago dove population. The populations of *C. macrourae* and *P. galapagensis* were similarly aggregated among members of the dove population (Table 2).

The two *C. macrourae* COI sequences obtained from Galapagos hawks were identical to each other and identical to a sequence from an individual collected from a Galapagos Dove on Isla Santa Fe, Galapagos (Fig. 1). These sequences differed by about 0.5% from two sequences from *C. macrourae* from Galapagos doves on Isla Genovesa (Fig. 1). In contrast, the difference between sequences of *C. macrourae* from Galapagos doves and Mourning doves (Johnson et al., 2002a) is about 3.3%, indicating that the COI gene provides a 'barcode' to identify the host of origin. *C. macrourae* from White-winged doves (Johnson et al., 2002a) is even more divergent, about 19% from the populations on the Galapagos doves and Mourning doves.

Table 2
Prevalences, mean infection abundances, and degree of aggregation (*k* of the negative binomial and *D*, the index of discrepancy) of 12 *Columbicola macrourae* lice (Insecta: Phthiraptera) collected from 91 Galapagos hawks (*Buteo galapagoensis* (Aves: Falconiformes) host individuals from Santiago (in 2002) and Pinta (in 2003) islands (values are in first row in each category), and 851 *C. macrourae* and 863 *Physconelloides galapagensis* lice collected from 28 Galapagos Dove (*Zenaida galapagoensis*) (Aves: Columbiformes) host individuals from Santiago Island, Galapagos, Ecuador in 2002 (values are in second row in each category)

Louse species	*C. macrourae*	*P. galapagensis*	*t*	*P*
Prevalence	8.8% (3.87–16.59)	1.1% (0.02–5.0)	N/A	0.034
	96.4% (81.65–99.91)	92.9% (76.49–99.13)	N/A	1.000
Mean abundance	0.132 (0.02–0.22)	0.011 (0.00–0.02)	2.170	0.0990
	30.393 (22.43–38.39)	30.821 (20.75–41.57)	−0.062	0.9485
Mean intensity	1.5 (1–2)	N/A	N/A	N/A
	31.519 (23.07–39.63)	33.192 (23.00–44.31)	−0.237	0.8030
Median intensity	1.0 (1–2)	N/A	N/A	N/A
	30.0 (19–41)	24.5 (10–36)	N/A	0.414
k	0.13	N/A		
	1.34	0.93		
D	0.926	N/A		
	0.384	0.477		

Fisher's exact tests were used to compare prevalences of each parasite species (*C. macrourae* vs. *P. galapagensis*) within each host species and the associated *P* values are reported below. Distribution-free two-sample bootstrap *t*-tests were used to compare mean intensities and abundances (each with 2000 replicates) of each parasite species within each host species; the *t* values and associated *P* values of which are reported below. Similarly, mood's median tests were used to compare median (typical) intensities; the *P* values of which are reported below. Because only one *P. galapagensis* individual was collected from the 91 Galapagos Hawk hosts sampled, only prevalence and mean abundance were calculated for this louse species. Numbers in parentheses are 95% bootstrap (2000 replications) confidence intervals. N/A not applicable.

The single *P. galapagensis* COI sequence from a Galapagos Hawk was identical to one *P. galapagensis* sequence collected from Galapagos Dove from Isla Genovesa, Galapagos (Johnson and Clayton, 2003) (Fig. 1).

Since the *Bovicola* individual was a nymph, identification to species based on morphology is not possible. Neighbor joining analysis using Paup* version 4.0b10 (Swofford, D., 2002. Paup* version 4.0b10. Sinauer Associates, Inc., Publishers, Sunderland, MA) involving 380 species of lice (Johnson et al., 2003; unpublished data) indicated the *Bovicola* sp. individual from a Galapagos Hawk was most genetically similar to *Bovicola bovis* from a domestic cow (*Bos taurus*), but differing by 21.8%, clearly indicating it is a different species. Although, COI sequences from *Bovicola* from goats were not available for comparison, this was likely the original host based on possible hosts for *Bovicola* on Isla Santiago.

4. Discussion

We found three straggling louse species on 10 different Galapagos Hawk hosts. These stragglers are species normally associated with Galapagos doves and goats. Given that some lice from Galapagos doves cannot be morphologically distinguished from lice on other hosts (e.g. Mourning doves), a DNA barcoding approach was necessary to clearly identify the host of origin (Besansky et al., 2003; Hebert et al., 2003a,b). We were able to do this in the case of *C. macrourae* and *P. galapagensis*. The ability to determine the source host for the straggling parasites demonstrates the utility of using ecologically simplified settings in which to examine host-parasite ecology. We found that *C. macrourae* were significantly more prevalent than *P. galapagensis* among Galapagos hawks, though our sample sizes were small. In contrast, the prevalence, average abundance, intensity and typical intensity of these species did not differ within the sympatric dove prey population sampled simultaneously. Thus, the difference in prevalence on hawks was likely a function of louse biology (straggling ability), and not an artifact of differences in louse population ecology within the source host's population.

To our knowledge, this is the first report of the straggling rate of *Columbicola* or *Physconelloides*, and the first report of a trichodectid louse straggling to a falconiform host. Previously, two *Buteo b. buteo* specimens were found to be host to one specimen each of *Columbicola columbae columbae* (L.) (Pérez et al., 1988; *C. columbae*, Price et al., 2003). However, the hosts were captive specimens, thus human contamination or the artificial conditions of captivity may have facilitated transfer. Other reports from the Old World include *C. columbae* from *Falco aesalon* Tunstall (Séguy, 1944), *Aviceda l. leuphotes* Dumont, and *Haliastur i. indus* Boddaert (Tendeiro, 1965), and *Columbicola columbae bacillus* (*Columbicola bacillus*, Price et al., 2003) from *Milvus milvus* (Mocci Demartis and Restivo de Miranda, 1978). Our study, which included New World louse species studied in population genetic and phylogenetic studies, is germane to the finding that *Columbicola* species have less population genetic structure within species, and less evidence for cospeciation with their hosts than *Physconelloides* species (Johnson et al., 2002a; Clayton and Johnson, 2003).

Galapagos hawks routinely feed on and provision their young with Galapagos doves and goats, which they have killed or scavenged in the case of goats (de Vries, 1975; Donaghy Cannon, 2001. Breeding ecology of cooperatively polyandrous Galapagos hawks (*Buteo galapagoensis*) on Santiago Island, Galapagos. M.S. Thesis. Arkansas State University, Jonesboro, Arkansas). For example, on Santiago in 2000, a total of 69 Galapagos Dove individuals were brought to 11 nests where prey deliveries were observed (nests were monitored from 36.0 to 64.2 h each; Donaghy Cannon, 2001. Breeding ecology of cooperatively polyandrous Galapagos hawks (*Buteo galapagoensis*) on Santiago Island, Galapagos. M.S. Thesis. Arkansas State University, Jonesboro, Arkansas). Thus, the presence of *C. macrourae* and *P. galapagensis* on Galapagos hawks is most parsimoniously explained by horizontal transfer of these lice from Galapagos doves to hawks after hawks captured them as prey. However, horizontal transfer of straggling lice within hawk social groups cannot be excluded as a factor. That a *C. macrourae* individual was collected from a nestling hawk was probably the result of transfer at the nest from a dove killed by one of its parents. Similarly, two territorial adult female hawks successfully killed newborn goats and goat parts were brought to nests on Santiago in three instances each in 1999 and 2000 (Donaghy Cannon, 2001. Breeding ecology of cooperatively polyandrous Galapagos hawks (*Buteo galapagoensis*) on Santiago Island, Galapagos. M.S. Thesis. Arkansas State University, Jonesboro, Arkansas). Horizontal transfer also most parsimoniously explains the presence of a *Bovicola* individual on a hawk host from a goat host after hawk depredation.

Galapagos hawks are not known to share nests or dust baths with doves, which were two other mechanisms proposed for straggling (Clay, 1949; Timm, 1983; Clayton et al., 2003a). However, another reasonable dispersal avenue for these lice is horizontal transfer of *C. macrourae* and *P. galapagensis* via hippoboscid flies from doves to hawks (Keirans, 1975). The hippoboscid fly *Microlynchia pusilla* (Speiser), typically found on columbiforms, was collected from a Galapagos Hawk host on Española Island, Galapagos in 1929 (Bequaert, 1933). Thus, transient *M. pusilla* with phoretic *C. macrourae* or *P. galapagensis* individuals attached, could have contacted a Galapagos Hawk host followed by subsequent dispersal of the louse or lice.

Straggling is a combination of 'variables influencing dispersal' and 'variables influencing establishment' (Clayton et al., 2003a). In this case, prevalence of both *C. macrourae* and *P. galapagensis* on their typical Galapagos dove hosts is high (>90%). Our finding that ~9% of hawk hosts harbored at least one *C. macrourae* individual may indicate that these hawks are not as effective as doves are in killing *Columbicola* lice by preening. Galapagos hawks do not harbor their own 'wing' lice such as *Falcolipeurus* species, which normally take refuge between feather barbs. It is reasonable to assume that efficiency of wing feather preening is relaxed in the absence of such parasites and that straggling wing lice may be able to survive on these hosts. *Columbicola* lice can establish populations on doves that are an order of magnitude different in body size, but only when host defenses are impaired (Clayton et al., 2003a,b). Thus, the greater dispersal abilities of *Columbicola* lice combined with the absence of a typical hawk 'wing' louse and host defenses, may account for its surprisingly high rate of straggling. The low rate of straggling in *P. galapagensis* is unsurprising given that it does not take refuge between feather barbs, and it is less likely to disperse than *Columbicola*. Experimental transfers of these lice would clarify the importance of these and other variables in determining success of straggling (Tompkins and Clayton, 1999), but are not especially feasible considering the threatened status of *B. galapagoensis*.

In conclusion, predictable differences in straggling rates between two louse lineages were observed in a sympatric avian prey-predator system within a simplified ecosystem. This study adds to the accumulating evidence indicating the importance of basic differences in life history in creating evolutionary patterns between these louse lineages, which are quickly becoming a model system in ecology and evolutionary biology. It is also notable that dove lice have the potential to transmit other parasites to hawks (Harmon et al., 1987; Hong et al., 1989; McQuistion, 1991; Padilla et al., 2004).

Acknowledgements

NKW and PGP were supported by an International Dissertation Enhancement Grant from the US National Science Foundation (INT-030759), grants from the Field Research for Conservation Program of the Saint Louis Zoo, International Center for Tropical Ecology, Sigma Xi, and funds from the E. Desmond Lee and Family Fund's Collaborative Vision in Zoological Studies from UM-St Louis and the Saint Louis Zoo. DSA was supported by a grant from the International Center for Tropical Ecology. KPJ was supported by National Science Foundation grants DEB 0107891 and DEB PEET 0118794. We gratefully acknowledge the logistical support and research permits provided by the Servicio Parqué Nacional de Galápagos and the Estación Científica Charles Darwin, Isla Santa Cruz, Galápagos, Ecuador, with special thanks to Poly Robayo, Howard Snell, Hernan Vargas and David Wiedenfeld. Jennifer Bollmer, Tjitte de Vries, Ken Levenstein, and Pablo Sánchez were steadfast field companions during fieldwork. TAME provided discounted roundtrip air-travel within Ecuador. Two anonymous reviewers provided helpful comments on a previous version of this manuscript.

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