CORRELATED EVOLUTION OF HOST AND PARASITE BODY SIZE: TESTS OF HARRISON'S RULE USING BIRDS AND LICE

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Abstract.—Large-bodied species of hosts often harbor large-bodied parasites, a pattern known as Harrison's rule. Harrison's rule has been documented for a variety of animal parasites and herbivorous insects, yet the adaptive basis of the body-size correlation is poorly understood. We used phylogenetically independent methods to test for Harrison's rule across a large assemblage of bird lice (Insecta: Phthiraptera). The analysis revealed a significant relationship between louse and host size, despite considerable variation among taxa. We explored factors underlying this variation by testing Harrison's rule within two groups of feather-specialist lice that share hosts (pigeons and doves). The two groups, wing lice (*Columbicola* spp.) and body lice (Physconelloidinae spp.), have similar life histories, despite spending much of their time on different feather tracts. Wing lice showed strong support for Harrison's rule, whereas body lice showed no significant correlation with host size. Wing louse size was correlated with wing feather size, which was in turn correlated with overall host size. In contrast, body louse size showed no correlation with body feather size, which also was not correlated with overall host size. The reason why body lice did not fit Harrison's rule may be related to the fact that different species of body lice use different microhabitats within body feathers. More detailed measurements of body feathers may be needed to explore the precise relationship of body louse size to relevant components of feather size. Whatever the reason, Harrison's rule does not hold in body lice, possibly because selection on body size is mediated by community-level interactions between body lice.

Key words.—Aves, body size, coevolution, comparative method, parasites, Phthiraptera.

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In general, when a genus is well distributed over a considerable number of nearly related hosts, the size of the parasite is roughly proportional to the size of the hosts. (Harrison 1915, p. 96)

Parasites on large-bodied species of hosts are often bigger than those on small-bodied hosts. Early tests of this correlation, known as Harrison's rule, were descriptive in nature (Harrison 1915; Clay 1949, 1951, 1962; Ward 1957; Kettle 1977). More recently, the relationship has been demonstrated using phylogenetically independent comparisons within a variety of groups, including animal parasites and herbivorous insects (Harvey and Keymer 1991; Kirk 1991; Morand et al. 1996, 2000; Poulin and Hamilton 1997; Sasal et al. 1999). Although Harrison's rule is a common pattern, its adaptive basis remains poorly understood. Three adaptive hypotheses put forth to explain the correlation between parasite and host body size pertain to how size influences the parasite's ability to remain attached to its host (Kennedy 1986; Sasal et al. 1999; Morand et al. 2000), escape host defenses (Clay 1949; Kirk 1991; Clayton et al. 1999), or feed on its host (Clay 1949; Kirk 1991; Thompson 1994).

Recent studies provide support for Harrison's rule within genera of lice (Harvey and Keymer 1991; Kirk 1991; Tompkins and Clayton 1999; Morand et al. 2000; Reed et al. 2000; Clayton et al. 2003a). For example, Harvey and Keymer (1991) showed a significant correlation between the body sizes of gophers and their lice using phylogenetically independent comparisons. They interpreted their results by noting that larger hosts live longer, which gives their lice a longer period of time in which to grow to larger sizes (Morand and

Poulin 2000). As Reed et al. (2000) argued, however, this logic is flawed for parasitic lice because the generation time of gopher lice is an order of magnitude less than that of gophers. Instead, they noted that the size of gopher lice appears to be closely related to the size of the hairs of the host, which are in turn correlated with host body size (Reed et al. 2000). Gopher lice hang onto the host body by means of a rostral groove that attaches to the hair shaft. A mismatch in size between the rostral groove and the host's hair would presumably increase the risks to the louse of falling off the host. This match between host size and parasite size could be a potential mechanism underlying the correlation between louse and gopher body size.

In another study, Tompkins and Clayton (1999) transferred host-specific cave-swiftlet lice (genus *Dennyus*) to novel species of hosts that varied in size. Lice survived just as well as on the native host when transferred to novel hosts that were similar in size to the native host. However, lice transferred to hosts that differed in size from the native host showed a significant reduction in survival compared to control transfers to the native host. Tompkins and Clayton (1999) argued that, as in the case of gopher lice, the match between host and parasite size could be central to the ability of the parasite to remain attached to the host. The match between host and parasite size in *Dennyus* was further demonstrated by Clayton et al. (2003b), who showed with phylogentically independent comparisons that increases in louse body size are associated with increases in overall host size.

In addition to attachment, the match between louse and host size can also be important for efficient escape from host defense (Clayton et al. 2003a). Dove wing lice (*Columbicola*) have a long, slender body shape and escape from host preening by inserting between the barbs of the wing feathers (Fig.
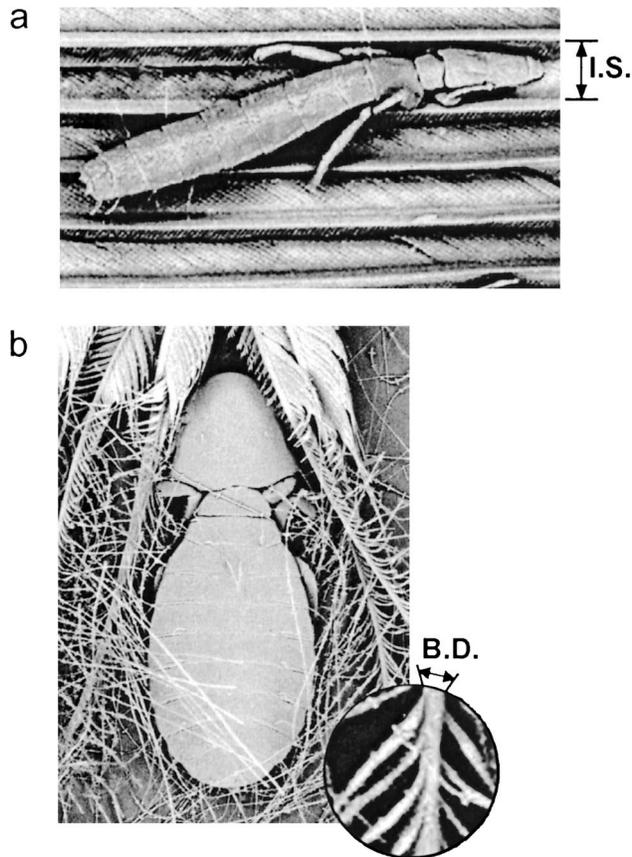

FIG. 1. Scanning electron micrographs of lice escaping from simulated host preening: (a) wing louse (*Columbicola columbae*) partially inserted between the barbs of a wing feather; insertion of the entire body into the interbarb space protects the louse from removal by preening (I.S., interbarb space); (b) body louse (*Campanulotes compar*) burrowing into the downy region of an abdominal contour feather, which helps it avoid preening (B.D., barb diameter). Figure 1 modified with permission from Johnson and Clayton (2003) and the University of Chicago Press.

1; Clayton 1991). Host preening has been shown to exert selection on the size of these lice, improving the fit between host feather barbs (Clayton et al. 1999). In addition, host transfer experiments involving *Columbicola* show that the ability of the lice to avoid host defense is the primary determinant of whether they can survive and reproduce when transferred experimentally to novel species of hosts (Clayton et al. 2003a).

Louse foraging biology may also contribute to the match between parasite and host body size. A correlation between mouthpart size and feather size could drive Harrison's rule in bird lice, assuming larger feathers require more robust mouthparts that, in turn, require larger heads and bodies for adequate support (Clay 1949, 1951; Kirk 1991). For example, foraging-mediated selection could be responsible for the fact that *Philopterus* species tend to increase in size with increasing host size (Kettle 1977). Because these species live mainly on the host's head, which is safe from preening, host defense is unlikely to be the selective force responsible for the fit to Harrison's rule in this case (Clay 1949).

Here we use phylogenetically independent comparisons to

test Harrison's rule across a more diverse set of taxa, including data from 78 species of bird lice representing several dozen genera from both suborders of lice found on birds (Amblycera and Ischnocera). Our results show a significant overall correlation between parasite and host body size, but the fit to Harrison's rule varies among taxa. To explore this variation, we compare two unrelated but ecologically similar, groups of lice that coexist on a single group of hosts, that is, wing and body lice on doves (Columbiformes). All else being equal, these two groups should respond similarly to evolutionary changes in host body size. Dove wing and body lice have similar life histories, and both feed on the downy portions of the host's abdominal contour feathers (Nelson and Murray 1971; Clayton 1991). Hence, the body sizes of both groups should be correlated with abdominal feather size if feeding constraints are responsible for Harrison's rule.

In contrast, wing and body lice use different feather tracts for other aspects of their ecology. Wing lice glue their eggs to underwing covert feathers, whereas body lice glue their eggs to abdominal contour feathers. Wing lice escape from host preening by inserting themselves between the barbs of the wing feathers (Fig. 1a). Body lice escape preening by burrowing into the downy portions of abdominal contour feathers (Fig. 1b). Thus, the body sizes of the two groups should be correlated with feathers from different feather tracts if escape or attachment constraints are the principle source of selection favoring Harrison's rule. Because feathers represent the main phenotypic interface between doves and lice, we collected data on the relative sizes of wing and body feathers, in addition to data on overall host and parasite body size. We examined the correlations between louse size, feather size, and overall host size using phylogenetically independent contrasts for these two groups of dove lice.

MATERIALS AND METHODS
Diverse Genera of Lice

Lice are sexually dimorphic. Because females were more readily available for each species than males, we used female measurements in all analyses. Measurements of female metathoracic width were made for representatives of 78 species of avian Amblycera and Ischnocera (Appendix 1). The metathorax is heavily sclerotized and its width scales strongly with total length and other measurements of size in lice (D.H. Clayton, unpubl. data). In most cases, these measurements were made from slides used as vouchers in a DNA sequence study of the phylogeny of these same taxa (Cruickshank et al. 2001; Johnson et al. 2003a). When possible, we supplemented these measurements from slides of the same species in the Price Institute for Phthirapteran Research collection (Univ. of Utah). Body mass for each host species was obtained from Dunning (1993).

Dove Wing and Body Lice

We also obtained measurements for 19 lineages of wing lice (Appendix 2) and 24 lineages of body lice (Appendix 3). We calculated average values of female metathoracic width from multiple specimens of each lineage of wing and body louse using values from voucher specimens, in conjunction with data from Tendeiro (1965, 1969a,b, 1973,

1976), Clayton and Price (1999), and Price et al. (1999). Host body masses were obtained from Dunning (1993), as well as from del Hoyo et al. (1997) and museum specimens. Single lineages of lice sometimes occur on more than one species of host (Johnson and Clayton 2003). In such cases, we averaged the metathoracic width for female lice across these hosts and we used an across-species average of host body masses.

Dove Feather Measurements

We measured wing and body feathers from each of 28 species of Columbiformes for which feather samples were available. For wing feathers we measured the width of the interbarb space in which wing lice hide from preening (Fig. 1a). Interbarb space was measured at five haphazardly chosen locations in the center of a number 5 primary feather placed on a Nikon (Tokyo) DIC microscope stage; measurements were taken from computerized video images obtained using NIH Image (National Institutes of Health, Bethesda, MD). Interbarb space measurements made a day apart were highly repeatable ($r = 0.88$, $P < 0.0001$, $n = 18$; Lessells and Boag 1987). The mean of the five measurements was used as an index of wing feather interbarb space for each species.

For body feathers we measured barb diameters (Fig. 1b) from a central upper tail covert from each of the 28 species for which we had feather samples. Five haphazardly chosen barbs from the center of each feather were mounted on microscope slides. We measured the diameter of these barbs using an ocular micrometer affixed to the microscope. Body feather barb measurements made more than a year apart were highly repeatable ($r = 0.71$, $P < 0.001$, $n = 10$). The mean of the five measurements was used as an index of body feather barb diameter for each species.

Comparative Analyses

To examine the relationship of parasite size to host body size, we plotted female metathoracic width against the natural log of host body mass for each host and parasite (shown to be linear with louse measurements in previous studies; Clayton et al. 2003a,b). Because species of lice are not phylogenetically independent datapoints, methods that take into account this nonindependence, such as independent contrasts (Felsenstein 1985), are necessary. Various authors (Harvey and Keymer 1991; Morand et al. 2000; Morand and Poulin 2003) have suggested that in comparisons of parasite-host body size it is best to compare congruent regions of parasite-host phylogenies, that is, nodes that have undergone cospeciation. However, we believe that host size can be taken as an independent variable representing the parasite's environment. If host body size has an important influence on the evolution of parasite size, then parasites should respond evolutionarily to changes in host size regardless of whether the parasite and host have a history of cospeciation. A lack of cospeciation is not expected to bias the relationship, although the variance may be higher. For this reason, we used a parasite phylogeny only to perform phylogenetically independent contrasts involving louse size (the dependent variable), as implemented in the CAIC computer program (Purvis and Rambaut 1994).
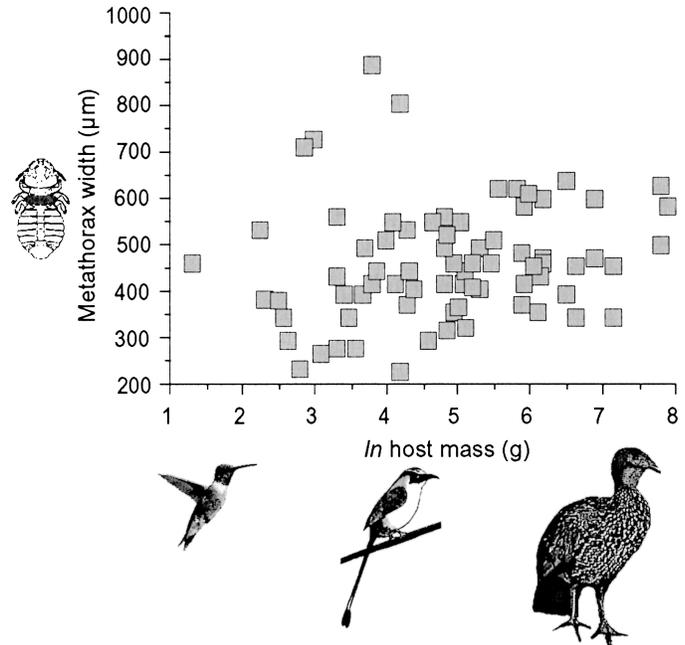

FIG. 2. Plot of female louse metathoracic width (shown in gray), against *ln*(host body mass) for a diverse group of bird louse genera from the suborders Amblycera and Ischnocera, but excluding species of wing and body lice from Columbiformes (see Figs. 3–6).

For the analysis of diverse genera of lice we used a phylogeny derived from elongation factor 1α and cytochrome oxidase I sequences (Cruickshank et al. 2001; Johnson et al. 2003a). We used the phylogenies in Johnson et al. (2001) and Johnson and Clayton (2003a) for *Columbicola* wing lice and Physconelloidinae body lice, respectively, which were based on the same genes used for the other genera of lice. We calculated contrasts under a gradual model of character evolution (Felsenstein 1985), using branch lengths estimated from the molecular data. We regressed through the origin contrasts in louse metathoracic width against those for *ln*(host body mass).

To evaluate the relationship between feather measurements and body mass in Columbiformes, we regressed contrasts in wing feather interbarb space and body feather barb diameter against those for *ln*(body mass). We used the phylogeny of doves with associated branch lengths from Johnson (2004) for this analysis, because dove feather measurements were the dependent variable. In addition, we regressed contrasts in louse metathoracic width against those for interbarb space (for wing lice) and body feather barb diameter (for body lice). We used the relevant louse phylogeny for each of these independent contrast analyses, because louse body size was the dependent variable.

RESULTS

First, we evaluated the relationship between louse size and overall host size (mass) for both a diverse assemblage of bird lice and for the lice of doves. For the 78 species of diverse bird lice and their hosts (Appendix 1), plots of female metathoracic width against *ln*(host body mass) for this group indicated a positive trend (Fig. 2). Independent contrasts anal-
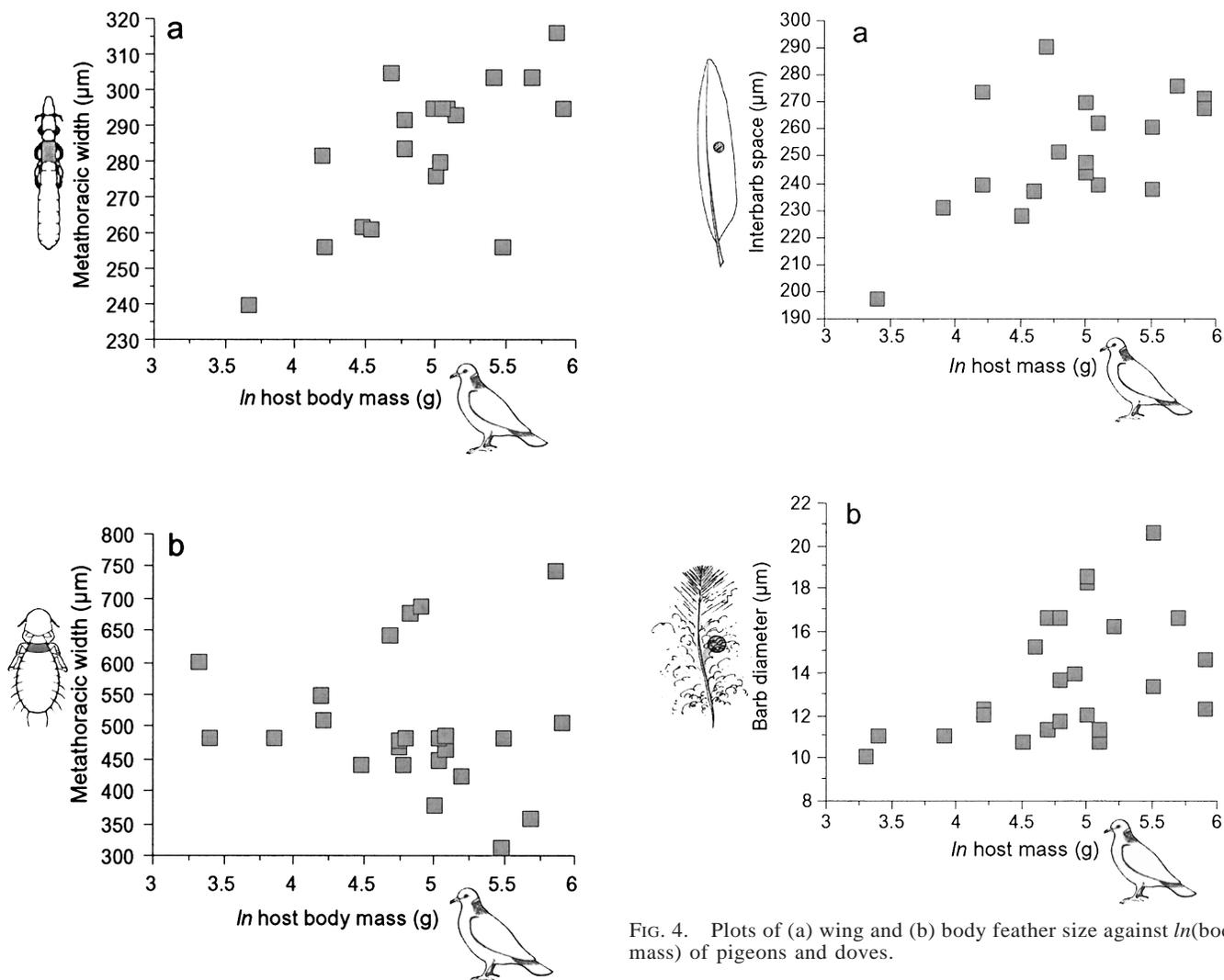
FIG. 3. Plots of female louse metathoracic width (shown in gray) against *ln*(host body mass) for (a) members of the wing louse genus *Columbicola*; (b) members of the four genera of body lice from the subfamily Physconelloidinae. Panel (a) modified with permission from Clayton et al. (2003b) and the University of Chicago Press.

FIG. 4. Plots of (a) wing and (b) body feather size against *ln*(body mass) of pigeons and doves.

ysis of this data set produced 49 positive contrasts and 27 negative contrasts, and regression through the origin of these contrasts revealed a significantly positive association ($P = 0.018$). For 19 lineages of wing lice and 25 species of doves (Appendix 2), a strong relationship exists between wing louse size and host size (Fig. 3a). Independent contrasts analysis produced 12 positive and five negative contrasts, and regression through the origin of these contrasts revealed a significantly positive association ($P = 0.001$). In contrast, for the 24 lineages of body lice and 25 species of doves (Appendix 3), there was no clear trend between body louse size and host size (Fig. 3b). Independent contrasts analysis produced 11 positive and 11 negative contrasts, and regression of these contrasts through the origin was not statistically significant ($P = 0.30$).

Feathers are the substrate on which these lice interact with their hosts most directly, so we evaluated the relationship of

feather structure sizes with host body mass in doves. The interbarb space of wing feathers was positively correlated with host body size (Fig. 4a). Independent contrasts analysis produced 12 positive and five negative contrasts, whose regression through origin was significantly positive ($P = 0.006$). In contrast, the diameter of the barbs of body feathers was weakly correlated with host body mass (Fig. 4b). Independent contrasts analysis produced 12 positive and nine negative contrasts, and regression of these contrasts showed no significant relationship ($P = 0.70$).

Evaluation of louse body size in relation to these feather measurements produced contrasting results for the two groups of dove lice. The body size of wing lice was highly correlated with wing feather interbarb space (Fig. 5a; 13 positive, four negative contrasts; $P = 0.001$). In contrast, the size of body lice did not increase with body feather barb diameter (Fig. 5b; 10 positive, 12 negative contrasts; $P = 0.17$); indeed, the weak relationship showed a negative trend.

DISCUSSION

Our analysis of evolutionary changes in body size in relation to host size across a diversity of avian lice revealed a
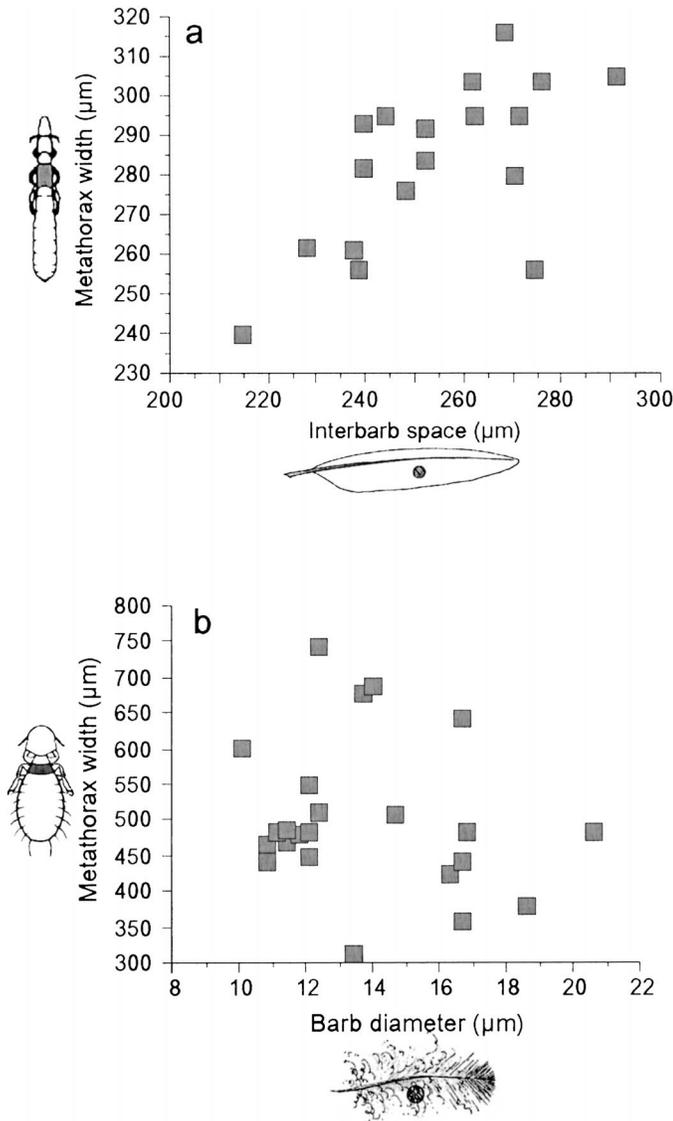
FIG. 5. Plots of (a) female louse metathoracic width against interbarb space for the wing louse genus *Columbicola*; (b) female louse metathoracic width against body feather barb diameter for four genera of body lice (see Table 3).

positive association. This result suggests that Harrison's rule applies not only among closely related species, but across avian lice, in general. No single factor is likely to explain this relationship. While some lice eat mainly feathers, others also feed on blood, so a match between mouthpart size and food size is not necessarily relevant across all lice. Escape from preening is not relevant to all groups of lice either, because certain groups, such as those specializing on the head, are relatively safe from preening. Finally, while the ability to remain attached to the host is certainly important for all groups of lice, different taxa may hang on to the host in different ways. Examination of the ecology of the host-parasite interaction is necessary within particular parasite groups to determine what specific factors might be important in determining the relationship between host and parasite body size.

Our investigation of Harrison's rule in dove wing lice indicates a strong association between parasite size and host size. Curiously, however, Harrison's rule did not hold for body lice on the same group of hosts. Within the single wing louse genus *Columbicola*, escape from host defense plays an important role in the correlated evolution of host and parasite body size (Clayton et al. 2003a). *Columbicola* escapes from host preening by inserting between the barbs of the wing feathers (Fig. 1). Because this interbarb space is strongly correlated with body mass in Columbiformes (Fig. 4a), we would expect a match between the width of species of *Columbicola* and the interbarb space, and indeed this was observed (Fig. 5a). This match is likely driven by selection for escape from host defenses given that experiments with the rock pigeon (*Columba livia*) wing louse, *Columbicola columbae*, show that preening dramatically reduces the fitness of lice transferred to smaller-bodied hosts (Clayton et al. 2003a). Selection for small size to insert between the feather barbs may be opposed by selection for increasing size, because of the correlation between female fecundity and body size in insects (Sibly and Calow 1986). Additional experiments have shown that the other possible factors of attachment and feeding ability are not influenced by host size. *Columbicola columbae* is fully capable of remaining attached to host species of different sizes during real and simulated flight (Clayton et al. 2003a; Bush et al. 2005) and is also capable of feeding on the feathers of hosts that vary substantially in size (Clayton et al. 2003a).

Escape from host preening is also related to host size in body lice. Experiments with the rock pigeon body louse *Campanulotes compar* show that, as in the case of wing lice, preening reduces the fitness of lice transferred to smaller bodied hosts (Bush 2004). Body lice escape from preening by burrowing through the downy regions of body feathers, essentially entangling themselves in the downy matrix. It is possible that a match between body louse and body feather size would optimize burrowing ability, and that this optimal size should increase with increasing host size. However, our results did not confirm this prediction. The size of body lice was not correlated with feather barb size (Fig. 5b), nor was feather barb size correlated with overall host size. It is not surprising, therefore, that body louse size is not dependent on overall host size (Fig. 3b).

One factor that may drive body lice away from some single optimal size is microhabitat partitioning. Species of doves are host to only one, and rarely two, species of wing lice. However, a single dove species is often host to more than one species of body louse. In most cases these species of body lice on the same host are in different genera or species groups, and they use different microhabitats within body feathers. For example, *C. compar* is normally found on the ventral surfaces of body feathers, whereas *Physconelloides eurysema* is found on the dorsal surfaces of body feathers (S. Bush, pers. obs.). Behavioral modification of such microhabitat preferences may allow lice to survive across a range of host species. For example, species of swiftlet lice (*Dennyus*) behaviorally shift their microhabitat when they are transferred to hosts of different size than their native host (Tompkins and Clayton 1999). Such microhabitat shifts may
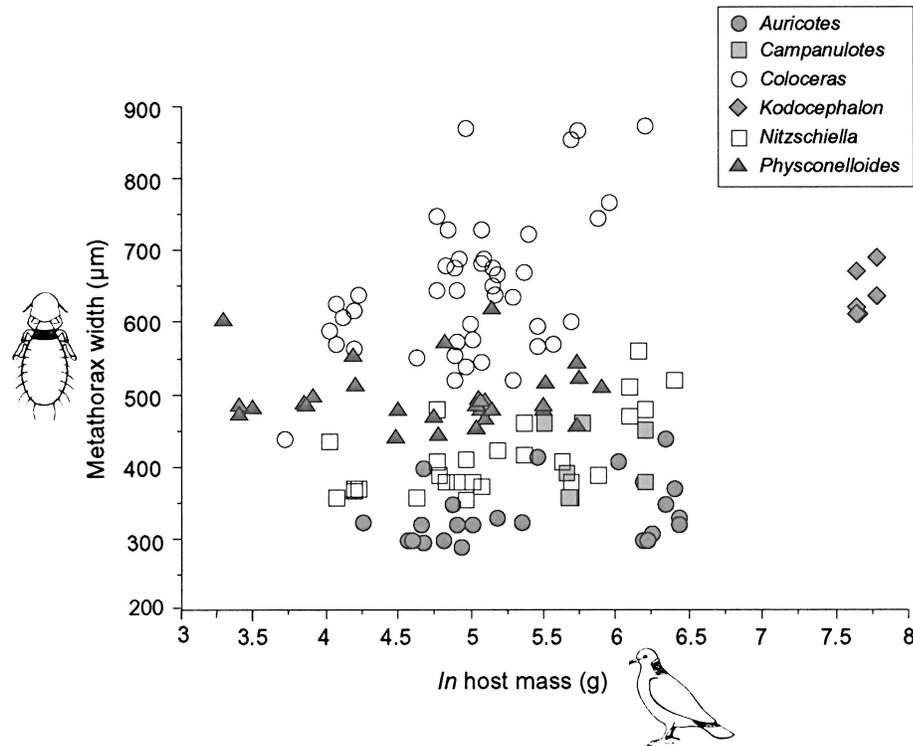
FIG. 6. Plot of female louse metathoracic width against host mass for 141 species of body lice from the subfamily Physconelloidinae.

allow lice to avoid selection for a changing body size over evolutionary time.

However, in cases where potentially competing species already occupy the alternate microhabitat, such a behavioral shift may not be possible, and there may be selection for a size that matches the size of the feathers in the microhabitat where that species of louse occurs. To explore this possibility, we examined the sizes of genera of body lice that tend to coexist with other genera compared to those that occur alone on a host. In cases where several species of body lice coexist, these species often differ dramatically in size and can span the entire range in size observed across Physconelloidinae (Fig. 6). For example, the Australian pigeon *Phaps chalcoptera* is host to four species of body lice in three different genera: *Campanulotes*, *Coloceras*, and *Physconelloides*. These species range from a female metathoracic width of around 350 μm to a metathoracic width greater than 800 μm (Fig. 6).

We plotted louse size against host size in six genera within Physconelloidinae (Fig. 6). Five of these plots indicated a positive trend, and one (*Physconelloides*) indicated a negative trend (overall sign test $P = 0.22$). In our comparative analysis (Fig. 3b), we only had phylogenetic data for a few species within each genus. It is possible that the overall phylogenetically controlled pattern might change if more species within Physconelloidinae were added to this analysis. (The difference in correlation with host body size between wing and body lice was not due to a lack of relative statistical power for body lice, because there were actually more contrasts available for body lice than wing lice). Regression of body louse size against host size without phylogenetic control

indicates a significant positive correlation ($P < 0.01$) for only two of these genera (*Coloceras* and *Nitzschiella*; Fig. 6). Approximately 75% of the species in the two genera coexist with some other species of body louse. In contrast, only about 30% of the species in the remaining four genera coexist with another body louse (Price et al. 2003). These results suggest that body lice may be able to behaviorally alter their microhabitat selection in the absence of competitors, but when competitors are present there is selection for a match between parasite and host size. Because a phylogeny is not currently available for enough of these species, we are not able to test these trends rigorously. Further exploration of host-parasite size relation patterns within Physconelloidinae will need to take into account more species, including an assessment of the number of coexisting species. Both competition and selection for optimal size in relation to the host may be important determinants of the size of dove body lice.

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APPENDIX 1

Measurements of host and parasite size for diverse taxa of bird lice (host families listed as headings).

Host species	Body mass (g)	Louse species	Female metathoracic width (μm)
Tinamidae			
Crypturellus cinnamomeus	419	*Discocorpus mexicanus*	473
Crypturellus cinnamomeus	419	*Heptapsogaster temporalis*	463
Crypturellus cinnamomeus	419	*Megapeostus asymmetricus*	601
Crypturellus cinnamomeus	419	*Pseudoliepeurus similis*	463
Anatidae			
Anas platyrhynchos	1082	*Anaticola crassicornis*	453
Anas platyrhynchos	1082	*Anatoecus* spp.	345
Megapodidae			
Alectura lathami	2330	*Colpocephalum alecturae*	581
Cracidae			
Ortalis vetula	563	*Amyrsidea spicula*	64
Ortalis vetula	563	*Chelopistes texanus*	64
Ortalis vetula	563	*Oxylipeurus chiniri*	394
Penelope purpurascens	2060	*Chelopistes oculari*	63
Penelope purpurascens	2060	*Menacanthus* spp.	502
Phasianidae			
Callipepla californica	173	*Colinicola docophoroides*	404
Callipepla californica	173	*Goniodes* spp.	493
Francolinus africanus	391	*Cuclotogaster* spp.	355
Rallidae			
Aramides cajanea	397	*Rallicola* spp.	433
Fulica americana	642	*Fulicoffula longipila*	345
Fulica americana	642	*Incidifrons transpositus*	453
Heliornithidae			
Heliornis fulica	135	*Fulicoffula heliornis*	414
Heliornis fulica	135	*Pseudomenopon carrikeri*	443
Rostratulidae			
Rostratula benghalensis	121	*Actornithophilus erinaceus*	355
Rostratula benghalensis	121	*Pseudomenopon rostratulae*	463
Recurvirostridae			
Recurvirostra americana	316	*Cirrophthirius testudinarius*	581
Recurvirostra americana	316	*Quadraceps zephyra*	414
Laridae			
Larus cirrocephalus	309	*Quadraceps punctatus*	374
Larus cirrocephalus	309	*Saemundssonia lari*	483
Musophagidae			
Musophaga violacea	360	*Turacoeca subrotunda*	453
Psittacidae			
Amazona albifrons	206	*Psittacobrosus* spp.	512
Columbidae			
Columba livia	293	*Hohorstiella lata*	621
Opisthocomidae			
Opisthocomus hoazin	855	*Hoazineus armiferus*	473
Opisthocomus hoazin	855	*Osculotes curta*	601
Cuculidae			
Centropus senegalensis	156	*Rallicola* spp.	404
Chrysococcyx klaas	24	*Cuculicola* spp.	276
Chrysococcyx klaas	24	*Cuculiphilus* spp.	433
Chrysococcyx klaas	24	*Cuculoecus* spp.	561
Piaya cayana	108	*Cuculicola atopus*	315
Strigidae			
Otus guatemalae	107	*Kurodaia* spp.	493
Otus guatemalae	107	*Strigiphilus crucigerus*	561
Trochilidae			
Archilochus colubris	3.2	*Trochilocetes lineatus*	463
Coliidae			
Colius indicus	56.4	*Colilipeurus colius*	227
Colius indicus	56.4	*Colimenopon urocolius*	808

APPENDIX 1. Continued.

Host species	Body mass (g)	Louse species	Female metathoracic width (μm)
Trogonidae			
Trogon massena	141	*Brueelia* spp.	325
Momotidae			
Momotus momota	133	*Brueelia marginella*	552
Bucconidae			
Nystalus chacuru	62.5	*Philopterus* spp.	532
Nystalus chacuru	62.5	*Picicola* spp.	374
Capitonidae			
Lybius torquatus	51.3	*Menacanthus eurysternus*	552
Lybius dubius	90.7	*Penenirmus guineensis*	552
Megalaima mystacophanos	69.8	*Penenirmus* spp.	404
Ramphastidae			
Aulacorhynhus prasinus	154.5	*Brueelia laticeps*	462
Pteroglossus torquatus	226	*Austrophilopterus* spp.	621
Ramphastos sulfuratus	339	*Austrophilopterus subsimilis*	611
Picidae			
Dendropicos goertae	47.6	*Penenirmus auritus*	512
Piculus flavigula	52.9	*Penenirmus auritus*	414
Melanerpes candidus	130	*Brueelia* spp.	364
Picus mentalis	109	*Penenirmus pici*	522
Dendrocolaptidae			
Dendrocincla anabatina	34.4	*Rallicola fuliginosa*	394
Dendrocolaptes certhia	64.2	*Rallicola columbiana*	443
Formicariidae			
Thamnophilus doliatus	27.9	*Formicaphagus* spp.	345
Tyrannidae			
Attila spadiceus	39.1	*Menacanthus* spp.	414
Attila spadiceus	39.1	*Ricinus* spp.	887
Cotingidae			
Querula purpurata	106	*Cotingacola* spp.	414
Hirundinidae			
Hirundo abyssinica	17	*Machaerilaemus* spp.	73
Pycnonotidae			
Pycnonotus nigricans	30.8	*Brueelia* spp.	276
Turdidae			
Myrmecocichla formicivora	41.6	*Penenirmus* spp.	443
Sylviidae			
Parisoma subcaeruleum	14.3	*Brueelia* spp.	236
Muscicapidae			
Ficedula hypererythria	8.2	*Ricinus* spp.	532
Platysteiridae			
Batis pririt	8.7	*Philopterus* spp.	384
Paridae			
Parus niger	18.8	*Brueelia* spp.	266
Sittidae			
Sitta frontalis	12.2	*Brueelia* spp.	296
Emberizidae			
Cyanocompsa parellina	15	*Ricinus* spp.	709
Habia rubica	35.5	*Myrsidea laciniaesternata*	493
Icteridae			
Cacicus haemorrhous	85	*Brueelia* spp.	296
Fringillidae			
Serinus atrogularis	11.4	*Philopterus* spp.	345
Ploceidae			
Philetarius socius	26.7	*Myrsidea ledgeri*	394
Ploceus velatus	31.1	*Brueelia* spp.	276
Sporopipes squamifrons	10.6	*Myrsidea eisentrauti*	384
Corvidae			
Cyanocorax morio	204	*Brueelia moriona*	463

APPENDIX 2

Measurements of host and parasite size for *Columbicola* wing lice from pigeons and doves. Numbers after louse species names are lineages from Johnson et al. (2003b).

Louse species	Female metathoracic width (μm)	Host species	Host mass (g)	Wing feather interbarb space (μm)
Columbicola adamsi	304	*Patagioenas picazuro*	226	
		Patagioenas plumbea	207	
		Patagioenas speciosa	244	261
Columbicola bacillus	276	*Streptopelia decaocto*	244	248
Columbicola baculoides	292	*Zenaida macroura*	119	252
Columbicola columbae 1	304	*Columba livia*	293	276
Columbicola columbae 2	316	*Columba guinea*	352	268
Columbicola extinctus	295	*Patagioenas fasciata*	367	271
Columbicola gracilicapitis	295	*Leptotila jamaicensis*	160	
		Leptotila plumbeiceps	170	
		Leptotila verreauxi	153	244
Columbicola gymnopeliae	282	*Metriopelia ceciliae*	66	240
Columbicola macrourae 1	295	*Geotrygon montana*	115	
		Leptotila plumbeiceps	170	
		Leptotila verreauxi	153	244
Columbicola macrourae 2	280	*Zenaida asiatica*	153	270
Columbicola macrourae 3	284	*Zenaida macroura*	119	252
Columbicola macrourae 4	262	*Zenaida galapagoensis*	88	228
Columbicola macrourae 5	293	*Patagioenas subvinacea*	172	239
Columbicola passerinae 1	240	*Columbina inca*	48	231
		Columbina passerina	30	198
Columbicola passerinae 2	256	*Claravis pretiosa*	67	274
Columbicola theresae	261	*Oena capensis*	41	
		Streptoepelia senegalensis	101	238
		Streptopelia vinacea	107	
Columbicola timmermanni	295	*Leptotila rufaxilla*	156	262
Columbicola veigasimoni	305	*Phapitreron leucotis*	108	291
Columbicola xavieri	256	*Ptilinopus occipitalis*	238	238

APPENDIX 3

Measurements of host and parasite size for physconelloidinae body lice from pigeons and doves. Numbers after louse species names are lineages from Johnson et al. (2001).

Louse species	Female metathoracic width (μm)	Host species	Host mass (g)	Body feather barb diameter (μm)
Auricotes rotundus	315	*Ptilinopus occipitalis*	238	13.4
Campanulotes compar	358	*Columba livia*	293	16.7
Coloceras clypeatum	690	*Phapitreron amethystina*	136	14.0
Coloceras doryanus	424	*Macropygia tenuirostris*	180	16.3
Coloceras hilli	380	*Streptopelia decaocto*	149	18.6
Coloceras indicum	680	*Chalcophaps indica*	124	13.7
Coloceras laticlypeatus	480	*Turtur brehmeri*	116	11.8
Coloceras savoi	746	*Columba guinea*	352	12.4
Coloceras sp. 1	645	*Phapitreron leucotis*	108	16.7
Coloceras sp. 2	483	*Streptopelia capicola*	142	18.3
		Streptopelia senegalensis	101	15.3
Physconelloides ceratoceps 1	466	*Leptotila jamaicensis*	160	10.8
Physconelloides ceratoceps 2	488	*Leptotila plumbeiceps*	170	11.4
Physconelloides ceratoceps 3	483	*Leptotila verreauxi*	153	12.1
Physconelloides cubanus	469	*Geotrygon montana*	115	11.4
Physconelloides eurysema 1	483	*Columbina passerina*	30	11.1
Physconelloides eurysema 2	483	*Columbina inca*	48	11.1
Physconelloides eurysema 3	512	*Claravis pretiosa*	67	12.4
Physconelloides galapagensis	441	*Zenaida galapagoensis*	88	10.8
Physconelloides robbinsi	551	*Metriopelia ceciliae*	66	12.1
Physconelloides spp.	601	*Uropelia campestris*	28	10.1
Physconelloides spenceri 1	483	*Patagioenas speciosa*	244	20.6
Physconelloides spenceri 2	507	*Patagioenas fasciata*	367	14.7
Physconelloides wisemani	451	*Zenaida asiatica*	153	12.1
Physconelloides zenaidurae	443	*Zenaida macroura*	119	16.7