

Ecology of Congruence: Past Meets Present

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Abstract.—Phylogenetic congruence is governed by various macroevolutionary events, including cospeciation, host switching, sorting, duplication, and failure to speciate. The relative frequency of these events may be influenced by factors that govern the distribution and abundance of the interacting groups; i.e., ecological factors. If so, it may be possible to predict the degree of phylogenetic congruence between two groups from information about their ecology. Unfortunately, adequate comparative ecological data are not available for many of the systems that have been subjected to cophylogenetic analysis. An exception is provided by chewing lice (Insecta: Phthiraptera), which parasitize birds and mammals. For a few genera of these lice, enough data have now been published to begin exploring the relationship between ecology and congruence. In general, there is a correspondence between important ecological factors and the degree of phylogenetic congruence. Careful comparison of these genera suggests that dispersal is a more fundamental barrier to host switching among related hosts than is establishment. Transfer experiments show that host-specific lice can survive and reproduce on novel hosts that are similar in size to the native host as long as the lice can disperse to these hosts. To date, studies of parasite dispersal have been mainly inferential. A better understanding of the role of dispersal will require more direct data on dispersal frequency and distances. [Cospeciation; host specificity; host switching; lice; parasite; phoresis; Phthiraptera; phylogeny.]

Congruent phylogenies are produced by parallel speciation in unrelated lineages. If every speciation event in one group were accompanied by a cospeciation event in the other group and if no species were lost from their original associations, then the phylogenies would be completely congruent (although branch lengths might differ). In reality, phylogenies of interacting taxa seldom show perfect congruence. Generally speaking, the degree of congruence is correlated with the ecological intimacy of the groups. Interactions vary from obligate associations to opportunistic encounters. One end of the spectrum is represented by mitochondria, chloroplasts, and other eukaryotic organelles evolved from free-living prokaryotic ancestors. The other end of the spectrum consists of far less intimate interactions, such as those between generalist herbivores and their host plants. Most interactions lie between these two extremes.

Phylogenetic congruence is governed by the macroevolutionary events reviewed by Johnson and Clayton (this issue). The relative frequency of these events is presumably influenced by ecological factors that govern the distribution and abundance of the interacting groups. Thus, it may be possible to predict the degree of phylogenetic congruence between two groups from information about their ecology. Sufficient comparative ecological data are now available for several genera of chewing lice (Insecta: Phthiraptera) that parasitize birds and mammals. In this study, we used ecological data and phylogenies of lice and hosts to explore the relationship between ecology and phylogenetic congruence.

macroevolutionary events that govern the congruence of interacting clades (Johnson and Clayton, this issue). Ecological factors that reflect the distribution and abundance of organisms (Begon et al., 1990), can influence congruence through their impact on the host, the parasite, or both. For example, any factor that causes a parasite to be patchily distributed over the range of its host may increase the probability of parasite duplication. Ecological factors that affect the abundance of the host and/or its parasite can also have an important influence. For example, stochastic extinction is far more likely for a parasite that is typically found only in small numbers on host individuals.

Host specificity, which is an ecological index describing the distribution of a parasite among host species, can be related to phylogenetic congruence. Parasites range from highly host specific, being restricted to a single species or subspecies of host, to generalists found on a wide variety of host taxa. Although specificity is a necessary precondition for congruence, it is by no means a sufficient condition. Just because a parasite is currently host specific does not mean that its ancestors were specific, much less that they underwent cospeciation (Hoberg, 1992; Hoberg et al., 1997). Specificity merely describes a pattern of current association that may or may not reflect macroevolutionary history.

Specificity does not necessarily mean a parasite is adapted to live on a single host species. Parasites can be limited to a single species of host simply because they are incapable of dispersing to other hosts (Tompkins and Clayton, 1999). In other cases, parasites may be adapted to a particular host species and are thus incapable of establishing themselves on a novel host following dispersal. Successful colonization of a novel host (host switching) requires that the parasite disperse to that host and then establish a viable breeding population. Inability to disperse, establish, or both will prevent a host switch

RELATIONSHIP OF ECOLOGICAL FACTORS TO MACROEVOLUTIONARY EVENTS

Ecological factors can have a fundamental impact on the probability of cospeciation, host switching, and other

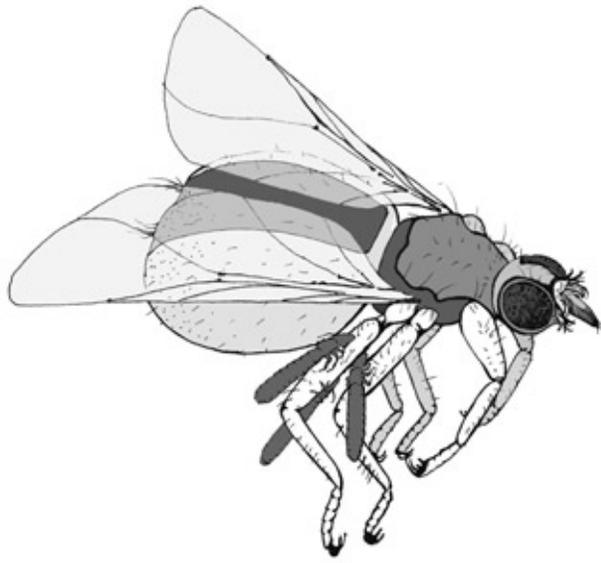


FIGURE 1. Three ischnoceran feather lice (*Columbicola columbae*) hitchhiking phoretically on a parasitic hippoboscid fly (*Pseudolynchia canariensis*). (Illustrated from an actual case by S.E.B.)

from taking place. Dispersal and establishment are influenced by a number of variables.

Variables Influencing Dispersal

Dispersal is constrained by the morphology, physiology, ecology, and behavior of the parasite. Parasites with limited powers of dispersal, such as lice, can disperse only between host species that share both ranges (sympatric) and habitat (syntopic). However, it is not necessary that individuals of different host species be in direct physical contact. Clay (1949) and Timm (1983) postulated four ways in which bird lice can move between species of hosts in the absence of direct host contact: (1) dispersal on detached feathers, (2) shared dust baths, (3) shared nest holes, and (4) phoresis on hippoboscid flies (Fig. 1).

Lice dislodged during host dusting could move onto the next species of bird that uses the same dusting arena (Clay, 1949). For example, Hoyle (1938) provided anecdotal evidence suggesting that lice dislodged from dusting chickens could end up on house sparrows that subsequently dust in the same spots. However, the hypothesis that dusting facilitates dispersal of lice has not been rigorously tested. Likewise, the hypothesis that lice disperse on feathers has not been tested, although anecdotes of lice on molted waterfowl feathers have been reported (Eichler, 1963). Clayton (1990) provided evidence concerning owl lice that is pertinent to the shared nest hole hypothesis. Species of *Strigiphilus* owl lice found on more than one species of host occur on species with overlapping ranges, habitats, and nest habits (Clayton, 1990). Nest holes are a limiting resource that, if used in rapid succession by different species of birds, may provide an ecological opportunity for lice to disperse between species.

The final means of dispersal concerns the ability of lice to hitch rides on other more mobile species, such as hippoboscid flies (Fig. 1). This process, known as phoresis, is surprisingly common. Several hundred records of ischnoceran lice riding on hippoboscid flies have been published (Keirans, 1975). The phenomenon can also be common at a local level. For example, Corbet (1956) documented lice attached to 43.5% of the hippoboscid flies removed from a large sample of freshly netted European starlings (*Sturnus vulgaris*). Because hippoboscids are not as host specific as many lice, they may provide a means of dispersal between host species.

Variables Influencing Establishment

Dispersal is merely the first step in successful colonization of a new host species. Dispersal is of little consequence if successful establishment of a breeding population on the new host does not occur. Like dispersal, establishment may be influenced by many ecological variables, such as the ability of the parasite to remain attached to the host, the ability of the parasite to feed on the host, severity of host defense, and intensity of competition from other parasites already living on the host (Page et al., 1996).

One powerful approach for assessing establishment success is to transfer parasites to a novel host species and then compare the survival and reproductive success of those parasites to those of parasites transferred to new individuals of the native host. Transfer experiments have been reported for gopher lice (Reed and Hafner, 1997), swiftlet lice (Tompkins and Clayton, 1999), and dove lice (Clayton et al., 2003). The results of these experiments are discussed here, along with other data bearing on ecological factors that may explain the variation in congruence seen among genera of lice.

CASE STUDIES

Different genera of lice differ in their degree of historical association with hosts, ranging from extensive congruence (Hafner et al., 1994) to a lack of congruence (Johnson et al., 2002a). These genera of lice also differ in ecological characteristics relevant to congruence. We have reviewed four louse–host associations involving genera of lice for which phylogenies based on DNA sequences have been recently published. Relevant ecological information is also available for all four louse genera (Table 1).

Pocket Gophers and Geomydoecus

Pocket gophers (Rodentia: Geomyidae) and their lice are a textbook example of cospeciation (Hafner et al., 2003). Species in the genus *Geomydoecus* (Ischnocera: Trichodectidae) are extremely host specific. Phylogenetic trees, using many types of data, have been produced for many species of gophers and their *Geomydoecus* lice. In addition, a great deal is known about the ecological details of the interaction between these hosts and parasites (reviewed by Hafner et al., 2003).

TABLE 1. Ecological factors promoting phylogenetic incongruence between lice and their hosts. The value in parentheses under each genus is the percentage of host nodes involved in cospeciation events. Entries are relative assessments among the four genera, with no absolute meaning. Categories are not mutually exclusive. Syntopy refers to populations that are in close physical proximity because they share the same habitat. Prevalence is the percentage of individuals in a host population with parasites; mean intensity is the average number of parasites across parasitized individuals (Bush et al., 1997).

Ecological factors	Relative assessments				Positive result ^a
	<i>Geomydoecus</i> (67%)	<i>Dennyus</i> (60%)	<i>Columbicola</i> (37%)	<i>Brueelia</i> (20%)	
Distributional					
Sympatry of host species	—	—	+	+	F, H
Syntopy of host species	—	+	+	+	F, H
Host populations without lice (patchiness)	—	—	+	+?	D, M
Dispersal to novel hosts	—	—	+	+	F, H
Abundance					
Prevalence usually low	—	—	—	+	M, E
Mean intensity usually low	—	+	—	+	E
Establishment on novel hosts					
Survival	+	+	+	+	F, H
Reproduction	+	?	+	?	F, H

^aPositive relative assessment (+) promotes, failure to speciate (F), host switching (H), duplication (D), missing the boat (M), or extinction (E).

Phylogenies based on mitochondrial cytochrome oxidase I (COI) sequences for 15 taxa of gophers and 15 species of *Geomydoecus* show considerable congruence (Fig. 2). More detailed comparisons of these phylogenies revealed that 8 of the 12 ingroup nodes (67%) show po-

tential cospeciation events (Page and Hafner, 1996). This amount of cospeciation is more than expected by chance alone ($P < 0.01$; reconciliation analysis, as implemented in TreeMap 1; Page, 1995). These comparisons indicate that cospeciation between gophers and lice is extensive.

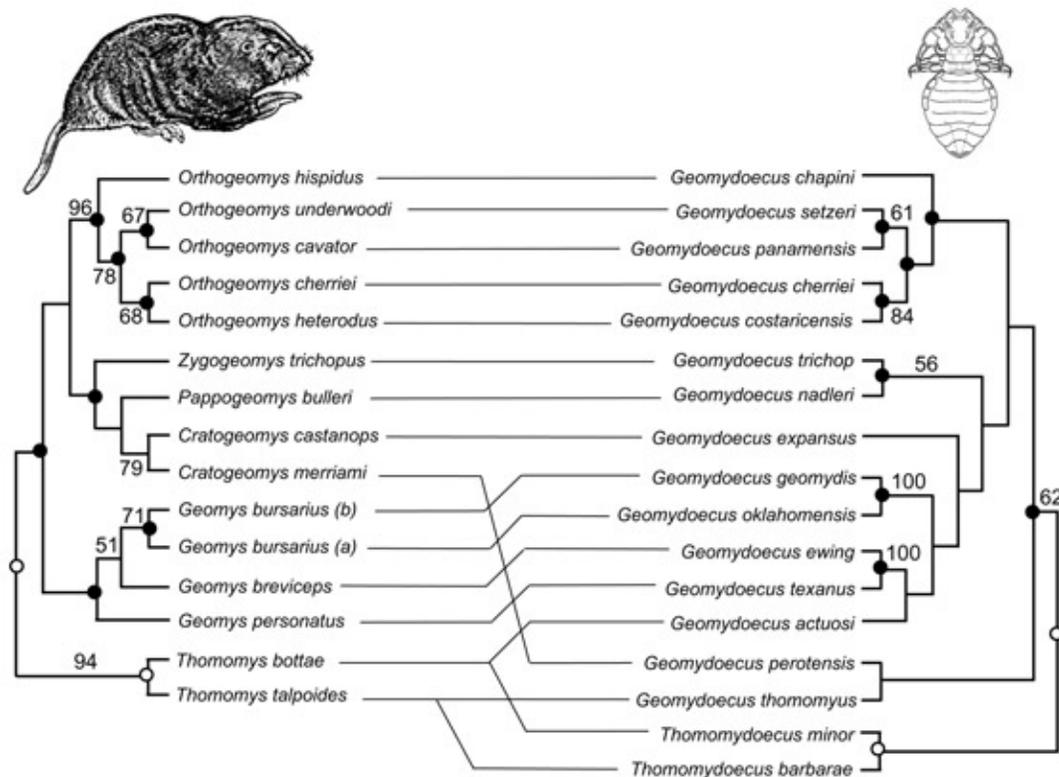


FIGURE 2. Comparison of phylogenies for pocket gophers and their lice. The phylogenies are composite trees based on nucleotide sequence data (Hafner et al., 1994) and multiple methods of analysis detailed by Hafner et al. (2003). Lines connecting gophers and lice show host-parasite associations. Solid circles are cospeciation events involving *Geomydoecus* that were inferred from reconciliation analysis; open circles are cospeciation events involving the outgroup *Thomomydoecus*. Numbers associated with branches are nodes supported in >50% of 1,000 parsimony bootstrap replicates.

Several ecological parameters have undoubtedly contributed to the extensive history of cospeciation between gophers and lice (Table 1). First, the distribution of the hosts themselves plays a major role. Most individual gophers build extensive tunnel systems from which they exclude other individuals except when mating. Sympatry of gopher species is rare, and syntopy is even rarer (Table 1). In addition, gophers have some of the lowest dispersal distances known for mammals. Individuals rarely travel far from their natal homes and populations are very patchily distributed. Together these factors provide little opportunity for dispersal of lice between individuals of the same host species and even less opportunity for dispersal between different host species. Thus, opportunities for host switching are few and far between, promoting congruence of host and parasite phylogenies.

Second, the intrinsic ability of *Geomydoecus* lice to move between hosts is low. These lice are specialized for climbing on the hairs of the host, but they are not very mobile off the body of the host. In addition, dispersal routes other than vertical transmission are not known for gopher lice (although apparently they do exist; Demastes et al., 1998; Hafner et al., 1998). Hippoboscids do not occur on gophers, meaning that gopher lice cannot disperse phoretically. The low dispersal ability of *Geomydoecus* makes both host switching and failure to speciate unlikely events.

In contrast to their low dispersal ability, species of *Geomydoecus* do seem to be able to establish themselves on novel host species, at least in transfer experiments with no competitors present (Reed and Hafner, 1997). However, lice have difficulty surviving on novel hosts that differ in size from the native host. Establishment ability may be related to host defense. Individuals of *Geomydoecus* hang onto host hairs using a rostral groove in addition to their legs and mouthparts. The size of this groove closely matches host hair diameter (Morand et al., 2000; Reed et al., 2000), which may help gopher lice avoid being removed by the host during grooming. Thus, the ability of lice to establish on novel hosts may be constrained by the size of the louse relative to the size of the host. Although establishment may well be possible on hosts of the right size, the inability of gopher lice to disperse is probably a major factor preventing widespread establishment and switching to new hosts.

The probability of duplication and sorting events also appears to be low in *Geomydoecus* because of several underlying ecological factors. Virtually all populations of gophers are infested with lice. Thus, gene flow in gopher lice is likely to correspond to gene flow in gophers, reducing the possibility for parasite duplication. Similarly, nearly all gophers in a population seem to have lice (high prevalence). High prevalence reduces the risk of extinction or missing the boat. Finally, the mean intensity of lice on gophers is often high, numbering several hundred individuals, which greatly reduces the risk of stochastic extinction (mean intensity is the average number of lice among infested hosts; Bush et al., 1997).

Taken together, these ecological factors appear to promote a history of cospeciation between gophers and

Geomydoecus. However, this degree of cospeciation and phylogenetic congruence is not the norm, as seen in other examples.

Apodidae and Dennyus

Another system that has received scrutiny on both the ecological and phylogenetic levels consists of members of the amblyceran louse genus *Dennyus*, which are parasites of swifts and swiftlets (Aves: Apodidae). Species of *Dennyus* are quite host specific but not to the same degree as are *Geomydoecus*. Cophylogenetic analysis of swiftlet and *Dennyus* trees (Clayton et al. 2003; Fig. 3) recovered 13 cospeciation events, a higher number than expected by chance ($P < 0.001$; reconciliation analysis as implemented in TreeMap 1; Page, 1995). Twelve of 20 host nodes (60%) are associated with a cospeciation event. This analysis indicates that *Dennyus* cospeciates extensively with its hosts but less so than in the gopher-*Geomydoecus* system.

Several ecological factors contribute to this intermediate degree of congruence between host and parasite phylogenies (Table 1). Many species of swiftlets are endemic to isolated oceanic islands, which provides their lice with little prospect for moving between host species. However, in some locations up to four species of swiftlets may be sympatric and syntopic, nesting together in clusters in caves. The lice on these species have an opportunity to disperse between hosts, at least at a low rate (Tompkins and Clayton, 1999).

The intrinsic dispersal ability of species of *Dennyus*, although higher than that of species of *Geomydoecus*, is still fairly low. *Dennyus*, like other members of the suborder Amblycera, have some locomotor capabilities when off the body of the host. It may be possible for individuals of *Dennyus* species to crawl between closely positioned nests in caves where several species of hosts co-occur. However, prospects for long-distance dispersal are more limited. Phoresis on hippoboscids has not been recorded for *Dennyus* and is exceedingly rare for amblyceran lice in general (Keirans, 1975).

Although prospects for dispersal in *Dennyus* are limited, there is evidence that *Dennyus* species can establish on novel hosts, provided they can get there. Transfer experiments revealed that when transferred to a novel host with feathers that are similar in size to the native host, species of *Dennyus* can survive on that host (Tompkins and Clayton, 1999). As for *Geomydoecus*, body size for species of *Dennyus* tends to be correlated with host size (Clayton et al., 2003). Swifts and swiftlets are presumably inefficient preeners, so the importance of feather size may relate to the ability of lice to hang onto the host during flight.

Factors promoting duplication and sorting events appear to be minor for *Dennyus* but may still play some role in the reduced phylogenetic congruence between the species of *Dennyus* and their hosts. Most populations of swifts and swiftlets appear to have lice. However, lice are sometimes absent from small host populations on islands. For example, lice have never been found on

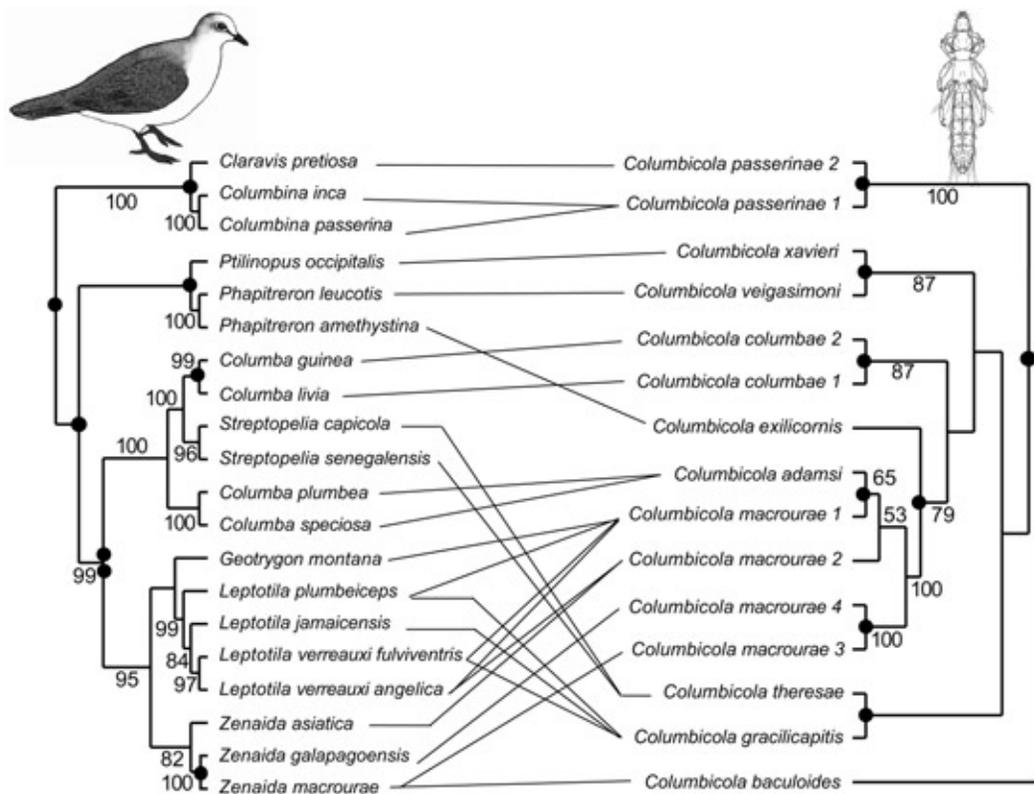


FIGURE 4. Comparison of phylogenies for Columbiformes and their *Columbicola* lice based on maximum likelihood analyses of nuclear and mitochondrial DNA sequences (from Johnson and Clayton, 2003). Numbered terminal taxa indicate cryptic species of lice documented by Johnson et al. (2002b). Numbers associated with branches are nodes supported in >50% of 1,000 parsimony bootstrap replicates. Other conventions as in Figure 2.

1975). Studies of the genetics of populations of *Columbicola* on different host species generally indicate a lack of structure, suggesting continuous capabilities for dispersal between hosts (Johnson et al., 2002b). Following dispersal, *Columbicola* must also be able to establish a breeding population on the novel host. Transfer experiments show that this is indeed possible, at least for lice transferred to novel hosts similar in body size to the native host (Clayton et al., 2003).

The population distribution of *Columbicola* suggests that these populations are prone to duplication and missing the boat events but unlikely to experience an extinction event. Species of *Columbicola* often have patchy distributions, possibly due to climatic factors. For example, several species of *Columbicola* are almost completely absent from doves in arid Arizona, but these same species on the same hosts are abundant in the humid climate of southern Texas (Moyer et al., 2002). These gaps in the geographic distribution of parasites increase the probability of duplication and missing the boat. However, species of *Columbicola* often show high prevalence (80%) and high mean intensity (50–100 lice/host), making extinction unlikely (unpubl. data). Together these factors appear to generate an intermediate level of congruence between host and parasite phylogenies.

Birds and *Brueelia*

The avian ischnoceran louse genus *Brueelia* is known from four orders of birds: Passeriformes (songbirds), Coraciiformes (kingfishers, bee-eaters, and rollers), Piciformes (barbets and woodpeckers), and Trogoniformes (trogons). Based on current taxonomy, species of *Brueelia* appear to be quite host specific. Although ecological interactions between *Brueelia* and their hosts are not as well studied as those in the previous three examples, enough is known to make meaningful comparisons.

Comparisons of the phylogenies of 15 species of *Brueelia* to those of their hosts (Johnson et al., 2002a; Fig. 5) show only seven cospeciation events, well within the number expected by chance alone ($P = 0.25$; reconciliation analysis as implemented in TreeMap 1; Page, 1995). Only 5 of 24 (20%) nodes in the host tree have a cospeciation event associated with them. Thus, there is very little evidence for cospeciation between species of *Brueelia* and their hosts, despite their relatively high host specificity. This lack of phylogenetic congruence may arise from several important features of the ecology of *Brueelia*.

First, opportunities for host-switching and failure to speciate are high. Many species of passerines (often >100) co-occur in the same geographic region, and many of these species co-occur in the same habitat (Table 1). In

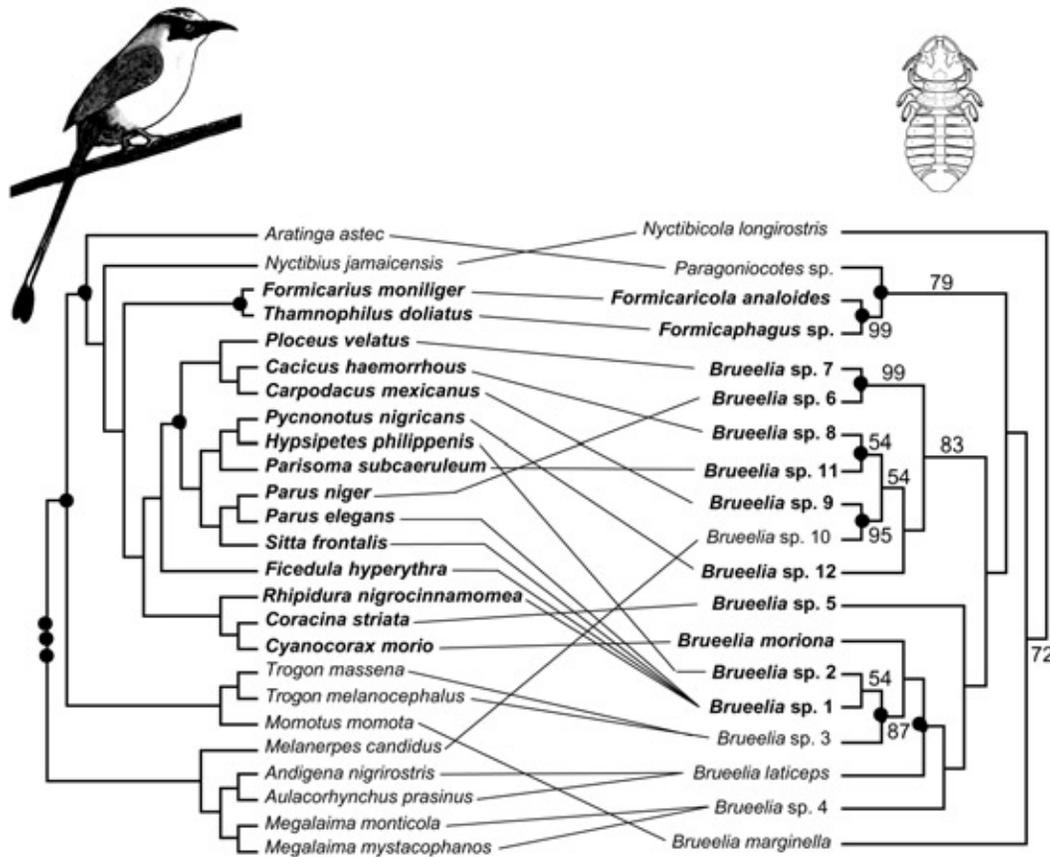


FIGURE 5. Comparison of bird and *Brueelia* louse phylogenies (after Johnson et al., 2002a). Phylogeny of *Brueelia* based on maximum likelihood analysis of nuclear and mitochondrial DNA sequences. Phylogeny of birds compiled from DNA-DNA hybridization data from Sibley and Ahlquist (1990). Bold taxa indicate passeriforms and their associated louse species. Numbers associated with branches in the louse tree are nodes supported in >50% of 100 maximum likelihood bootstrap replicates. No bootstrap analysis of the bird tree is available. Other conventions as in Figure 2.

addition, many species of passerines and nearly all of the nonpasserine hosts of *Brueelia* nest in holes. Competition for holes is high among species of birds, and interspecific takeovers of hole nests often occur (Merilä and Wiggins, 1995). Bird species that nest in holes often share species of *Brueelia* (Johnson et al., 2002a). Nest takeovers provide an opportunity for dispersal to a new host species.

In addition to the sympatry and syntopy of many hosts of *Brueelia*, the lice themselves seem to be excellent dispersers, at least via phoresis on hippoboscids. About 80% of the nearly 350 records of phoresis summarized by Keirans (1975) involve *Brueelia* and the closely related *Sturnidoecus*. Although little is known about the establishment ability of *Brueelia*, some species are found on multiple host families (Johnson et al., 2002a). *Brueelia* is a generalist louse, being found on many regions of the host's body (Clay, 1951). Taken together, these factors suggest high potential for host switching and failure to speciate.

In addition to dispersal opportunities and abilities, several factors promoting duplication and sorting events are also evident in *Brueelia*. The single population-level study of *Brueelia* to date (unpubl. data) revealed localities where *Brueelia* is absent. Such patchiness could lead to

duplication and missing-the-boat events. In addition, the prevalence of species of *Brueelia* tends to be low (<10%) (Clayton et al., 1992; Hahn et al., 2000). Low prevalence increases the chance of missing-the-boat and extinction events. In addition to their low prevalence, the intensity of *Brueelia* is also often rather low (<10 lice) (Clayton et al., 1992; Hahn et al., 2000). These low intensities increase the chance of extinction. In summary, nearly all aspects of the biology of *Brueelia* (Table 1) appear to favor events that reduce congruence between host and parasite phylogenies.

CONCLUSIONS

As outlined in these four case studies, the ecological basis of coevolutionary history is discernable. Genera of lice that show more congruence with host phylogeny tend to have fewer factors that would promote failure to speciate, host switching, duplication, missing the boat, or extinction events (Table 1). As ecological factors increasing the probability of these events become more common across the four louse genera considered here (*Geomydoecus*, *Dennyus*, *Columbicola*, and *Brueelia*), the degree of cospeciation declines. However, the ecological factors

outlined in this chapter do not account for everything that may influence the coevolutionary history of hosts and parasites. Rare events, such as dispersal, can be extremely important over evolutionary time, even though they may be difficult to measure in ecological time.

Rock wallabies and their lice (*Amblycera: Heterodoxus*) are one case in which current ecological factors do not appear to be directly reflected in coevolutionary history. Rock wallabies live in groups on isolated rock outcroppings (Barker, 1991). There is little contact between host species or even between populations of the same host species on different rock outcroppings. In many respects, the lack of opportunity for rock wallaby lice to switch hosts makes them much like gopher lice, and congruent host-parasite phylogenies might be expected. However, cophylogenetic analysis of *Heterodoxus* and their rock wallaby hosts indicates little congruence (Barker, 1991; Barker et al., 1992). This pattern is further illustrated by a mismatch in the geographic distributions between species of *Heterodoxus* and their hosts. Some species of *Heterodoxus* appear to have dispersed across host species, which are often parapatric, such that some species of *Heterodoxus* overlap the geographic distributions of two adjacent species of hosts. This parapatric leakage is presumably the result of rare host dispersal events into the range of a nearby species of host, providing an opportunity for a host switch.

The *Heterodoxus* example shows that caution is needed when drawing conclusions about coevolutionary history from studies of extant species. However, valid generalizations can still be made. The case studies in Table 1 suggest that dispersal is a more fundamental barrier to host switching among related hosts than is establishment. Opportunities for dispersal appear quite limited in some systems, such as pocket gophers and their lice. To date, studies of parasite dispersal have been mainly inferential. A better understanding of the role of dispersal will require more direct data on dispersal frequency and distances.

ACKNOWLEDGMENTS

This work was supported by NSF awards DEB-9703003 and DEB-0107947 to D.H.C., NSF DEB-0107891 to K.P.J., and NSF-PEET DEB-0118794 to D.H.C. and K.P.J. We are grateful to Susan Perkins, David Reed, and Jennifer Wernegreen for comments that improved the manuscript.

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Final acceptance 12 September 2003

Associate Editor: David Reed