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THE ECOLOGICAL BASIS OF COEVOLUTIONARY HISTORY

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Macroevolutionary patterns are difficult to interpret because they are the product of a time scale so vast that deterministic and chance events are hard to distinguish. Although the macroevolutionary history of a group can be reconstructed from extant species, determining the ecological context in which that group evolved is a tall order. Ecology involves interactions between organisms and both the living and nonliving components of their environments. These interactions are important because they influence selection, dispersal, drift, and other microevolutionary processes that govern macroevolution. Short of inventing time travel, the best bet for obtaining data on ecological history has traditionally been to focus on groups that have an unusually good fossil record. A more recent approach, however, is to focus on groups having a history of prolonged coevolution that yields congruent phylogenies.

Congruent phylogenies are produced by repeated bouts of parallel speciation in unrelated lineages. If every speciation event in one group is accompanied by a "cospeciation" event in the other group, and if no species are lost from their original associations, then phylogenies will be completely congruent (although branch lengths may differ). In reality, however, phylogenies seldom show absolute congruence. Generally speaking, the degree of congruence is correlated with the ecological intimacy of the groups, whose interactions vary from obligate association 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.

Inferences about the ecological history of interacting groups are perhaps easiest when the environment of one species is delineated completely by the members of another species, as in the case of "permanent" parasites. For such parasites, which carry out their entire life cycle on the body of the host, the branching pattern of the host phylogeny provides a detailed record of vicariance events that may influence the parasites. The host phylogeny also can be used to draw inferences about the habitat parameters of ancestral parasites. For example, estimating the body size of an ancestral host is tantamount to knowing the size of the resource base available to its parasites. Unfortunately, it is not usually possible, even in cases of extensive congruence, to reconstruct specific ecological processes, such as demographic fluctuations, or competitive interactions. On the other hand, processes generating congruence can be illuminated to some extent by extrapolating backwards from data on modern ecological parameters. In this chapter we adopt such a reverse engineering approach, using information about the ecology of extant species to explain differences in the degree of phylogenetic congruence among related host-parasite systems. Although we have chosen to focus on host-parasite interactions, we make an effort to address issues that are applicable to coevolving systems in general.

The ecological basis of coevolutionary history can be explored by comparing interactions that vary in their degree of phylogenetic congruence. Unfortunately, adequate comparative ecological data are not available for many of the systems that have been subjected to cophylogenetic analysis. A fortunate exception is provided by parasitic lice (Insecta: Phthiraptera), which occur on birds and mammals. For a few genera of lice, enough data are now available to begin exploring the relationship between ecology and congruence. Making comparisons among taxa of lice helps ensure against spurious conclusions drawn from comparisons of distantly related taxa that may have evolved in entirely different environmental contexts.

Phylogenetic congruence is governed by several kinds of macroevolutionary events, which we review below. We then consider the impact of various ecological factors on the relative frequency of these macroevolutionary events. We conclude the chapter by comparing the ecology of four genera of lice that have histories ranging from extensive phylogenetic congruence with their hosts, to a complete lack of congruence.

Macroevolutionary Events governing Phylogenetic Congruence

Phylogenetic congruence is a historical pattern produced by repeated bouts of *cospeciation*. Cospeciation is a process in which speciation in one lineage is accompanied by speciation in an associated, but unrelated lineage (fig. 13.1a). All else being equal, phylogenies containing a high proportion

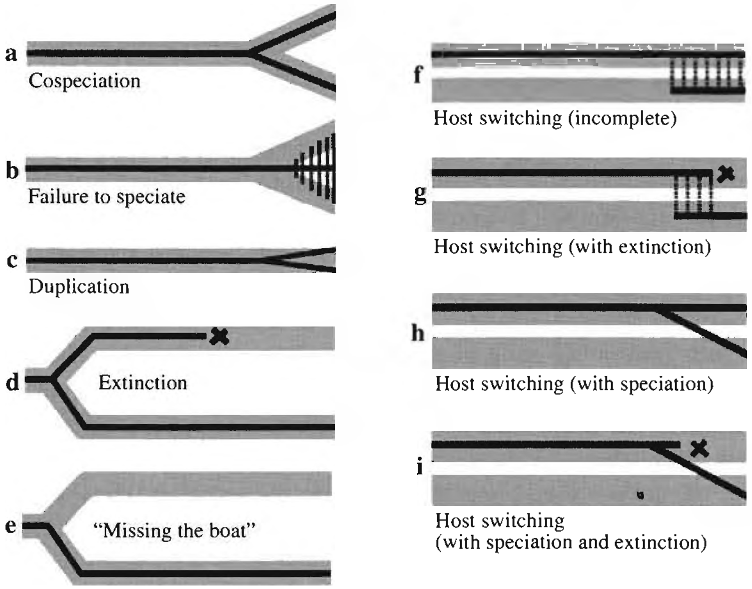

FIGURE 13.1. Macroevolutionary events that influence phylogenetic congruence. Gray lines represent hosts; black lines represent parasites. Black stippling represents gene flow between parasite populations. See text for discussion.

of cospeciated nodes will show more congruence than those containing a low proportion. However, the amount of cospeciation cannot be inferred directly from the amount of congruence between two phylogenies because it is possible for "false" congruence to be generated by processes other than cospeciation, such as extinction. Moreover, incongruence between phylogenies does not necessarily mean that there has been no cospeciation. As outlined below, other macroevolutionary events can reduce congruence between lineages that have undergone a considerable amount of cospeciation.

Aside from cospeciation (fig. 13.1a), all the events depicted in figure 13.1b–i effectively reduce congruence. For example, if a reproductive barrier affects a host lineage, but not its parasite, the parasite will *fail to speciate,* thereby reducing congruence (fig. 13.1b). Conversely, reproductive barriers that affect only the parasite lineage promote parasite *duplication* (fig. 13.1c), which also reduces congruence. Congruence is further reduced when parasites are lost from a host lineage, either through parasite *extinction* (fig. 13.1d), or by *"missing the boat,"* which occurs when parasites fail to disperse onto one of two new host clades (fig. 13.1e).

The final macroevolutionary event governing congruence is *host switching,* in which parasites colonize a "foreign" host species on which they did not previously occur. Host switching involves an initial expansion of the parasite's host range (fig. 13.1f). This expansion is not a host switch, in and of itself, because the parasite persists on the original host. The host switch is completed by extinction of the parasite on the original host (fig. 13.1g), speciation of the parasite on the new host (fig. 13.1h), or by concurrent extinction and speciation (fig. 13.1i). It is not possible, using phylogenies reconstructed from extant species, to distinguish switching with extinction (fig. 13.1g) from switching with speciation and extinction (fig. 13.1i). However, information on the ecology of the descendant species can suggest the relative likelihood of the two types of host switches. A parasite with poor dispersal ability is more likely to speciate after colonizing a new host, since there will be little or no parasite gene flow between the original and new host species. In such cases, the host switch is completed by the speciation event, which may later be followed by extinction (fig. 13.1i). In contrast, when parasite dispersal is common, incomplete host switching may be a frequent event (fig. 13.1f).

Relationship of Ecological Factors to Macroevolutionary Events

Ecological factors can have a fundamental impact on the probability of host switching and other macroevolutionary events governing the congruence of interacting clades (fig. 13.1). Ecological factors, which, by definition, affect the *distribution* and *abundance* of organisms (Begon et al., 1990), 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 (fig. 13.1c). 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 in the case of a parasite that is typically found only in small numbers on host individuals.

Generally speaking, the distributions of host taxa have been reasonably well documented (e.g., Sibley and Monroe, 1990; Nelson, 1994; Nowak, 1999). In contrast, the distributions of most parasite taxa remain poorly known (Brooks and McLennan, 1993; Clayton and Moore, 1997). Parasites with indirect life cycles are especially problematic in this regard, since they involve one or more intermediate host species, in addition to free living stages and the final host. Distributions of parasites with direct life cycles are much simpler to characterize, being tied largely to the distribution of a single host species. Permanent parasites, which complete their entire life cycle on the body of the host, have distributions that are particularly easy to characterize.

Given their close association with the host, the abundance of permanent parasites also can be measured accurately. This is particularly true for permanent *ecto*parasites, such as lice, which can even be observed and counted on live hosts (Clayton and Drown, 2001). These advantages make it possible to track the distribution and abundance of such parasites over the course of longitudinal studies. It is also possible to add or remove the parasites in controlled experiments designed to test the relative importance of the ecological factors thought to influence phylogenetic congruence (see below).

It is difficult to overemphasize the need for rigorous data on parasite abundance. Sampling errors can create the false impression of parasite-free host individuals, populations, or species, leading to erroneous conclusions about extinction or missing the boat (Paterson and Gray, 1997). Parasite ecologists normally measure two main components of parasite abundance: *prevalence* and *intensity* (Bush et al., 1997). Prevalence is the percent of individuals in a host population that actually have parasites. Intensity is the number of parasites on a parasitized individual; mean intensity is the average number of parasites across all parasitized individuals. Accurate measures of parasite prevalence and intensity require sampling methods that have demonstrated efficacy. Such methods have been tested thoroughly for lice (Clayton and Drown, 2001).

Ecological factors relevant to phylogenetic congruence vary in both time and space. Data from long-term studies are often required to document how ecological factors vary over time. In contrast, spatial variation can be relatively easy to document. However, is important to recognize that spatial variation exists on a variety of scales, ranging from variation among the microhabitats on a single host individual, to variation among host individuals, populations, and species (fig. 13.2). In the next section we consider the relevance of each of these four scales to the macroevolutionary events that govern phylogenetic congruence.

Variation among Microhabitats within a Host Individual

Different species of parasites appear to partition microhabitats on individual hosts (Poulin, 1998). For example, species of helminth worms tend to be concentrated in different regions of the host intestinal tract (Stock and Holmes, 1988). This pattern is consistent with competitive displacement owing to interspecific competition for limited resources, such as food. If competitive displacement is pervasive, it could influence the composition of parasite communities, leading to an absence of congeneric species on

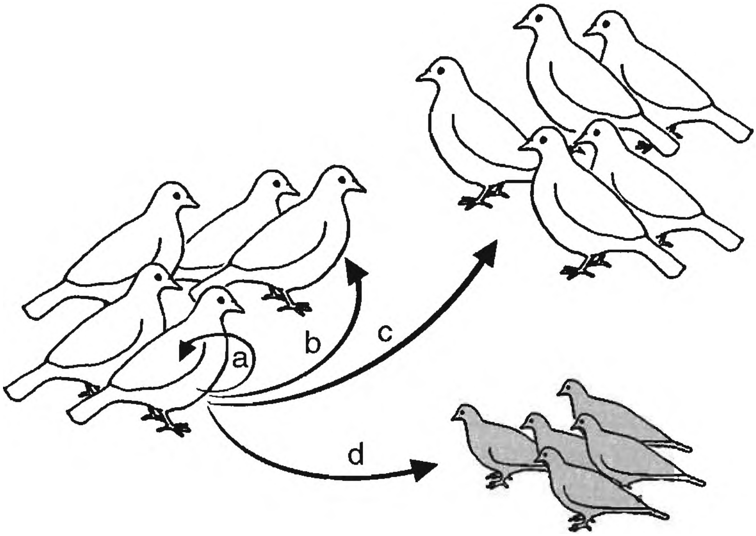

FIGURE 13.2. Ecological factors that influence host-parasite congruence vary among *(a)* microhabitats within a host individual (e.g., body versus wing); *(b)* host individuals; *(c)* host populations; and *(d)* host species.

a single species of host (e.g., Barker and Close, 1990; see also chap. 8). Competitive displacement may also operate between higher taxa. For example, since dispersing to dogs from its original host (a wallaby), the louse *Heterodoxus spiniger* appears to have displaced the louse *Trichodectes canis* from much of its former range (Barker, 1994).

Although intriguing, such patterns do not constitute robust evidence for competition (Simberloff, 1990; Page et al., 1996). Rigorous tests of competition require an experimental approach in which the population response of one or more species to the removal of a potential competitor(s) is carefully monitored (Poulin, 1998). Figure 13.3 summarizes the results of such a test that we recently conducted with wing lice *(Columbicola columbae)* and body lice *(Campanulotes bidentatus compar)* on Feral Pigeons *(Columba livia)*. Wing lice spend most of their time on the host's wing and tail feathers, whereas body lice reside primarily on the abdominal feathers (see chap. 11). Despite these microhabitat differences, both species depend on abdominal contour feathers for food (Nelson and Murray, 1971). Figure 13.3 shows that body lice have a negative impact on the population growth of wing lice. Although the reason for this negative impact is unknown, it may have to do with better foraging ability on the part of body lice, assuming abdominal feathers are a limiting resource.

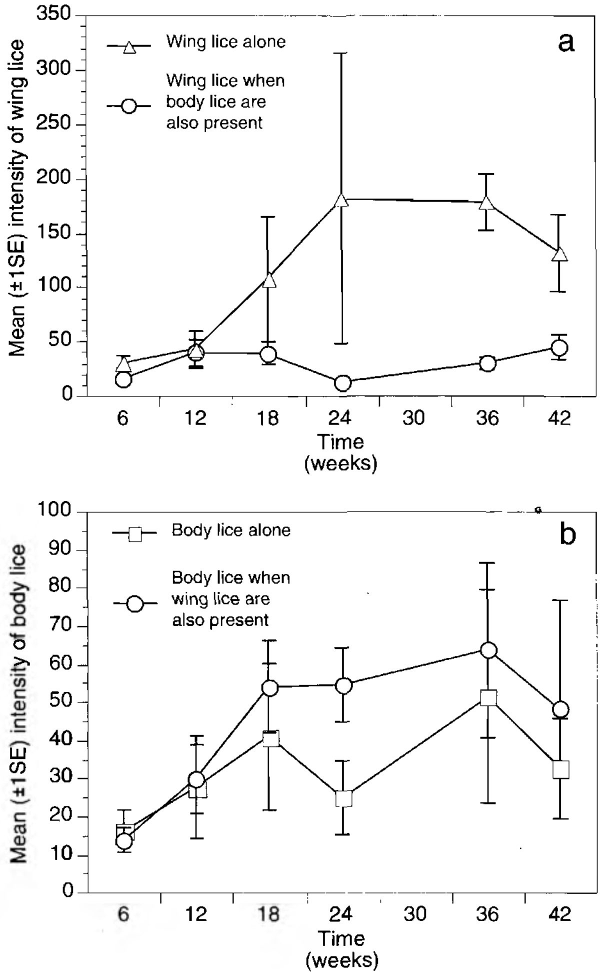

FIGURE 13.3. Competitive interaction between wing lice and body lice on Feral Pigeons. Population growth of wing lice *(a)* was slower on birds also parasitized by body lice, than on birds only parasitized by wing lice (repeated-measures ANOVA, $p = .02$). In contrast, population growth of body lice *(b)* was similar with and without wing lice present ($p = .38$). At the start of the experiment birds were "seeded" with identical numbers of lice, as follows: 16 pigeons were captured in Salt Lake City, Utah, then housed at low relative humidity (<30%) for 10 weeks, to exterminate their natural populations of lice and eggs (Moyer et al., 2002). The birds were then isolated in 16 cages and assigned randomly to three "seeding" treatments: 100 wing lice, 100 body lice, or 50 wing and 50 body lice. The data for mixed species of lice (circles in panels *a* and *b*) are thus from the same individual birds ($n = 6$). The preening behavior of all birds was impaired with harmless plastic bits to facilitate increases in their lice (Clayton et al., 1999). Louse populations were monitored for approximately 10 months

If interspecific competition influences the structure of parasite communities in general, then it is reasonable to predict that it could influence host switching in particular (Barker, 1994). For example, successful host switches should be more likely in the case of parasites dispersing to hosts that have depauperate parasite communities, because such hosts will represent greater ecological opportunity, that is, more untapped resources. This prediction could be tested by comparing the survival and reproductive success of parasites experimentally transferred to foreign hosts with and without other species of parasites already present. If interspecific competition reduces the fitness of parasites transferred to foreign hosts, then it clearly has the potential to influence host switching.

The *direction* of interspecific competition could also influence host switching. Asymmetric competitive effects have been documented in a number of parasite communities (Poulin, 1998). Figure 13.3 provides an example of asymmetric competition in which wing lice do worse in the presence of body lice, while body lice are unaffected by wing lice. These results predict that it would be easier for body lice to switch to foreign hosts already parasitized by wing lice, than for wing lice to switch to hosts with body lice. Body lice are significantly more host specific than wing lice (Johnson et al., 2002), further suggesting that host specific parasites may have a competitive edge over generalists. Data on the underlying causes of asymmetric competition are needed to begin exploring this intriguing possibility.

Microhabitat diversity and resource availability may also influence parasite duplication. A possible example involves the human body louse *(Pediculus humanus),* which is the sister species of the human head louse *(Pediculus capitis)* (Amevigbe et al., 2000). The two species are so similar that they are often classified as subspecies rather than full species (e.g., Durden and Musser, 1994). [Crab lice, which are confined to pubic hair, are members of another genus *(Pthirus pubis)*]. Body lice attach their eggs to clothing, while head lice attach their eggs to hair. Body lice probably diverged from head lice concurrent with the loss of hair and adoption of clothing by hominids (Busvine, 1978). Clothing may therefore have provided a novel microhabitat that facilitated a duplication event, in which the

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FIGURE 13.3 (*continued*) by periodically counting all lice on the underside of one wing, the tail, and lice observed during timed intervals on three additional body regions: back and keel (30 seconds each), and rump (60 seconds). The sum of lice on these five regions significantly predicts the total number of *C. columbae* ($R^2 = .66$) and *C. b. compar* ($R^2 = .79$) on feral pigeons ($p < .0001$ for both species; Clayton and Drown, 2001).

common ancestor of head and body lice diverged through speciation on a single species of host. Alternatively, head and body lice may have speciated allopatrically and subsequently come into secondary contact (Busvine, 1978). Under either scenario of parasite speciation, the probability of duplication may increase with the diversity of microhabitats available on a given host. This hypothesis could be tested by comparing the number of potential microhabitats among different hosts to the number of congeneric parasites they support.

Microhabitat specialization could conceivably also increase the probability of parasite extinction, assuming the abundance of microhabitat specialists is lower than that of microhabitat generalists. For example, chimpanzees *(Pan troglodytes)* have a single species of louse *(Pediculus schaeffi)* (Durden and Musser, 1994) that presumably roams all of the host's body, given its continuous distribution of hair. If so, then one can predict that the mean abundance of this louse will be greater than that of human lice, all three species of which are more restricted in their microhabitat distributions (see above). The chimp louse may therefore be less prone to extinction if it really is more abundant. Of course, this ignores differences in host body size, population size, and other factors that are already known to influence parasite abundance (Poulin, 1998). The impact of microhabitat specialization on risk of extinction could be explored with comparative analyses that control for these and other factors.

Variation among Individuals within a Host Population

Parasite abundance varies within host populations, ranging from heavily parasitized individuals to individuals having no parasites. Low parasite prevalence increases the probability that a parasite will miss the boat, since a dispersing founder population of hosts is more likely to be comprised solely of individuals having no parasites (Paterson et al., 1999). Variation in parasite intensity—the number of parasite individuals on a host (see above)—may also influence the probability that parasites will miss the boat or go extinct (Rózsa, 1993). At the very least, parasites that are rare are more likely to miss the boat or go extinct than those that are abundant. In contrast, parasites that are abundant might increase the probability of host switching, assuming that dispersal is density dependent, that is, attempts at host switching will presumably be higher when parasites are dispersing at a higher rate.

Parasite abundance is usually quite variable even in populations that have a high mean parasite intensity. This is particularly the case for "macroparasites," such as helminths and arthropods (Anderson and May, 1979). Macroparasites tend to concentrate on a minority of heavily infested individuals, forming an aggregated distribution with the property that the variance in parasite intensity exceeds the mean. Proximal reasons for aggregation are unclear, although variation in host susceptibility and the contagious nature of parasite transmission are probably important factors (Hudson and Dobson, 1995).

Aggregation should increase the probability of parasites missing the boat. A founder population dispersing from a parent population containing aggregated parasites is more likely to be parasite free than one dispersing from a parent population containing an even distribution of parasites. Aggregation could also increase the probability of parasite extinction if heavily parasitized individuals die before their parasites are transmitted to new hosts. This is probably not an overly likely scenario, since parasite virulence is generally correlated with the ease of transmission (Ewald, 1994). Parasites that are transmitted vertically from parent to offspring, such as feather lice, are usually fairly benign, since their reproductive fitness is linked closely with that of the host (Clayton and Tompkins, 1994). More virulent parasites tend to be transmitted horizontally, which prevents them from being marooned on a dead or dying host (Herre, 1993).

Variation among Host Populations

Parasites can be rare or absent from some host populations, while abundant on others. For example, feather lice have a patchy distribution in which they are abundant on doves in many areas of the world, yet virtually absent from the same species of doves in arid regions (Moyer et al., 2002). Patchiness can also be generated when host population size falls below the minimum threshold required to support parasites (Rózsa, 1993). Thus, an area of low host density can be a dispersal barrier for parasites, or a sink that limits gene flow between parasite populations in different parts of the host's geographic range.

Patchiness has the potential to influence macroevolutionary events. Nested within their host limits, parasites often show geographic limits to their distribution (see Clay, 1964, 1972). These geographic limits increase the likelihood of parasites missing the boat, since parasites may be absent from hosts involved in founder events (Brown and Wilson, 1975). For example, 18 bird species were historically introduced to New Zealand by humans. The species richness of lice on these birds in New Zealand is significantly lower than that on the same birds in their native environments (Paterson et al., 1999). The founding populations of most of these introduced birds were small—a few individuals to as many as 100 individuals. Although stochastic loss of ectoparasite species has undoubtedly contributed to the lower species richness of lice on these birds, it is conceivable that some of the founder hosts came from native populations that were relatively free from parasites in the first place. Gaps in parasite distribution may also facilitate parasite duplication if little or no parasite gene flow occurs across the gaps (Clay, 1949). In summary, variation in the distribution of parasites among host populations is another potential factor with direct relevance to the macroevolutionary events that govern phylogenetic congruence.

Variation among Host Species

The distribution of parasites among host species is, of course, directly relevant to phylogenetic congruence. Host specificity is essentially an index to a parasite's distribution among host species. Parasites range from highly specific, being restricted to a single species or subspecies of host, to generalists found on a variety of host taxa. Although host specificity is a necessary condition for phylogenetic congruence, it is by no means a sufficient condition. Just because a parasite is currently host specific does not mean that its ancestors were host specific, much less that they underwent cospeciation with their hosts (Hoberg, 1992; Hoberg et al., 1997). Specificity describes a pattern of current association that may or may not reflect macroevolutionary history or even current adaptation to the host. Some parasites may be specific simply because they are incapable of dispersing among host taxa (Tompkins and Clayton, 1999). Other parasites may indeed be adapted to a particular host. In such cases, specificity can be viewed as a phenotypic trait of the parasite that, assuming a heritable component, has the potential to evolve just like any other trait (Secord and Kareiva, 1996).

Host specificity is integral to three macroevolutionary events in addition to cospeciation: failure to speciate, extinction, and host switching. All three of these events can reduce host-parasite congruence. Failure to speciate occurs when gene flow is maintained between populations of parasites on hosts that have already undergone speciation (Johnson et al., in review.b.).

Host specificity is also relevant to extinction, particularly in the case of the coextinction of parasites on hosts that have themselves gone extinct (Brooks and Hoberg, 2000). For example, the louse *Columbicola extinctus* was considered extinct because it was assumed to be a host specific parasite of the extinct Passenger Pigeon *(Ectopistes migratorius)* (Stork and Lyal, 1993). However, Clayton and Price (1999) recently showed that this species is synonymous with extant wing lice on the Band-Tailed Pigeon *(Columbicola fasciata)*, thus resurrecting the species from extinction, so to speak. True coextinction of host specific parasites with their hosts can alter phylogenetic congruence, depending on how deletion of one (or both) of the "missing" clades alters reconstruction of the rest of the phylogenetic tree(s).

Host specificity is, of course, directly relevant to host switching, in which a parasite colonizes a foreign host on which it did not previously occur. Successful colonization of a foreign host requires that the parasite *disperse* to that host, and then *establish* a viable breeding population on it. Inability to disperse, establish, or both will prevent a host switch from taking place. In cases of incomplete host switching (fig. 13.1f), the parasite merely incorporates a new host species, thereby reducing its host specificity. If the parasite switches to a new host while going extinct on the original host (13.1g), host specificity effectively remains the same. Likewise, if the parasite speciates after switching (13.1h), the specificity of each sister species is the same as that of the common ancestor, assuming each daughter species is unable to colonize additional hosts. Finally, if the parasite speciates after switching, then goes extinct on the original host (13.1i), specificity again remains the same as that on the ancestral species.

The distribution of parasites among host species is often documented in a qualitative sense, that is, whether or not a parasite occurs on a given species of host. Qualitative thinking leads to the erroneous assumption that parasites found on foreign hosts are "stragglers" that are of little evolutionary significance. As Rózsa (1993) has argued, however, stragglers may represent the initial (dispersal) stage in host switching. Although most stragglers are presumably doomed, it may take but a single breeding pair—or single inseminated (or asexual) female—to establish a viable population of parasites on a foreign host. 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.

Understanding straggling and host switching requires a more quantitative concept of host specificity that is based on large scale sampling of parasites from many host individuals. Tompkins and Clayton (1999) recently compared the host specificity of six species of *Dennyus* lice on four species of Bornean Cave Swiftlets (Apodiformes: Collocalliini). For each species of host they carefully removed all the lice from hundreds of host individuals. The study documented at least three instances of lice that would normally be labeled as stragglers, since they were present on foreign hosts at very low frequencies (< 3%). The study also revealed species of lice present on foreign hosts at frequencies of 5.3%, 8.6%, and 8.9%. Should these also be deemed stragglers? What really matters is the frequency with which host specific parasites disperse to foreign hosts, and the establishment ability of the parasites following dispersal. Dispersal and establishment are influenced by a number of variables, which we consider below.

Variables influencing Dispersal

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

Lice dislodged during dust bathing could conceivably move onto the next species of bird to use the same dusting arena (Clay, 1949). For example, Hoyle (1938) provided anecdotal evidence suggesting that lice dislodged from dust bathing chickens could end up on house sparrows that subsequently dust bathe 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 do exist (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 invariably 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 well 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. This process, known as phoresis, is suprisingly 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)*. Since hippoboscids are not as host specific as many lice, they may provide a means of dispersal between host species. Like straggling, phoresis has often been considered a red herring of little evolutionary significance. We suspect, however, that it actually plays an important role in the ecology and evolution of lice.

Variables influencing Establishment

As merely the first step in successful colonization of a new host species, dispersal is of little consequence if it is not followed by successful establishment of a breeding population on the new host. Like dispersal, establishment may be influenced by many ecological variables, such as the ability of the parasite to remain attached to the host (tenacity), the nutritive value of the host, severity of host defense, and intensity of competition from other parasites already living on the host.

One powerful approach for assessing establishment ability is to transfer parasites to a "foreign" host species, then compare the survival and reproductive success of those parasites to that of parasites transferred to new individuals of the usual host. Transfer experiments have recently been published for gopher lice (Reed and Hafner, 1997) and swiftlet lice (Tompkins and Clayton, 1999). The results of these experiments show that lice are able to survive and breed on reasonably closely related foreign hosts, both in captivity and in the field, at least over the course of short term experiments. Tompkins and Clayton (1999) showed that relative fitness on a foreign host is highly correlated with feather barb size. Transfers of lice to swiftlet hosts that had feathers >2 microns different from the original host resulted in greatly reduced survival. When transferred to hosts that differed only slightly in size, swiftlet lice shifted their microhabitat to prefer feathers closer in size to those of their original host. These results suggest that lice on feathers too dissimilar in size may simply have trouble hanging on to the host.

Another factor that could conceivably block host switching is competition from resident lice. No test of this hypothesis has been carried out, although we do know that pigeon wing and body lice compete (fig. 13.3). To our knowledge, these are the only rigorous data relevant to interspecific competition in lice. Furthermore, we are unaware of tests in any other host-parasite system designed to measure the impact of competition on host switching or other macroevolutionary events relevant to phylogenetic congruence.

A final variable that appears to contribute substantially to host specificity is host defense (see below). Wing and body lice transferred among species of pigeons and doves have much higher fitnesses on foreign hosts having impaired preening ability, the main defense against lice (unpub. data). Experiments we are currently conducting will shed additional light on the importance of host defense and interspecific competition in host switching and other macroevolutionary events.

Case Studies

As discussed earlier, lice are an excellent group for exploring the relationship of ecology to coevolutionary history. Different genera of lice vary considerably in their degree of congruence with their hosts, ranging from extensive congruence (Hafner et al., 1994) to a lack of congruence (Johnson et al., in review.a.). In addition, different genera of lice differ in ecological characteristics relevant to processes affecting the degree of congruence between host and parasite phylogenies. Below we review four case studies involving genera of lice with recently published phylogenies based on DNA sequences. Relevant ecological information is also available for all four genera (table 13.1).

Pocket Gophers and *Geomydoecus*

Pocket gophers (Rodentia: Geomyidae) and their lice are a textbook example of cophylogenetic congruence. Species in the genus *Geomydoecus* (Ischnocera: Trichodectidae) are extremely host specific, and often different subspecies of gophers harbor different species of lice. Phylogenetic

TABLE 13.1 Ecological factors promoting phylogenetic *incongruence* between lice and their hosts. Entries are relative assessments among the four genera, with no absolute meaning. Categories are not mutually exclusive; see text for discussion. "Syntopy" refers to populations that are in close physical proximity because they share the same habitat (Lincoln et al., 1982).

	Geomydoecus	*Dennyus*	*Columbicola*	*Brueelia*
Distributional factors				
Sympatry of host species[1,2]	-	-	+	+
Syntopy of host species[1,2]	-	+	+	+
Host populations without lice[3,4] (patchiness)	-	-	+	+?
Dispersal to foreign hosts[1,2]	-	-	+	+
Abundance factors				
Prevalence usually low[4,5]	-	-	-	+
Mean intensity usually low[5]	-	+	-	+
Establishment on foreign hosts[1,2]				
Survival	+	+	+	+
Reproduction	+	?	+	?

Increase in factor (+) promotes

[1] Failure to speciate

[2] Host switching

[3] Duplication

[4] Missing the boat

[5] Extinction

trees, using many types of data, have been produced for many species of gophers and for their respective parasitic lice in the genus *Geomydoecus*. In addition, a great deal is known about the ecological details of the interaction between these hosts and parasites (reviewed by Hafner et al., chap. 8).

Phylogenies based on mitochondrial cytochrome oxidase I (COI) sequences for 15 taxa of gophers and 15 species of *Geomydoecus* show considerable congruence (Hafner et al., 1994). More detailed comparisons of these phylogenies reveal 8 out of 12 nodes (67%) in the in group with potential cospeciation events (Page and Hafner, 1996). This amount of cospeciation is considerably more than expected by chance alone ($p < .01$). These comparisons indicate that cospeciation between gophers and lice is widespread.

Several ecological parameters have undoubtedly contributed to the extensive history of cospeciation between gophers and lice (table 13.1). First, the distribution of the hosts themselves plays a major role. Most individual gophers build extensive tunnel systems from which they exclude other individuals over most of their life cycle. Sympatry of gopher species is rare and syntopy is even rarer (table 13.1). 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). Hippoboscid flies do not occur on gophers, meaning that gopher lice cannot disperse phoretically. The low dispersal ability of *Geomydoecus* thus makes host switching and failure to speciate unlikely events.

In contrast with low dispersal ability, species of *Geomydoecus* do seem to be able to establish themselves on foreign host species, at least in transfer experiments in which no competitors were present (Reed and Hafner, 1997). However, lice have difficulty surviving on hosts that are only distantly related to their own. Establishment ability may be related to host defense. Individuals of *Geomydoecus* hang on to host hairs using a rostral groove, in addition to their legs and mouth parts. Studies of the size of this groove indicate a close match between louse groove size and host hair diameter (Morand et al., 2000; Reed et al., 2000). This close match may help gopher lice avoid being removed by the host during grooming. Thus, the ability of lice to establish on foreign hosts may be dictated by the match between the size of the louse and the size of the host. Although establishment may well be possible when the match is close enough, 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 gophers is likely to correspond to gene flow in lice, reducing the possibility for parasite duplication. Similarly, nearly all gophers in a population seem to have lice (high prevalence), thereby reducing the risk of extinction or missing the boat. Finally, the mean intensity of lice on gophers is quite high, often numbering several hundred individuals, which greatly reduces the risk of extinction.

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 will become evident in the additional case studies below.

Apodidae and *Dennyus*

Another system that has received scrutiny at both the ecological and phylogenetic scales are 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 *Geomydoecus*. Page et al. (1998) conducted a preliminary analysis of cytochrome *b* (cyt *b*) sequences for both hosts and parasites. Here we present expanded results for more taxa and additional sequences. Our cophylogenetic analysis (fig. 13.4) recovered 13 cospeciation events, which are more than expected by chance ($p < .001$). A total of 12 out of 20 host nodes (60%) were associated with a cospeciation event. This analysis indicates that *Dennyus* cospeciates extensively with its hosts, but a smaller fraction of host nodes showed cospeciation than for the gopher-*Geomydoecus* system.

Several ecological factors can be identified that contribute to this intermediate degree of congruence between host and parasite phylogenies (table 13.1). Many species of swiftlets are endemic to isolated oceanic islands, a situation which obviously provides their lice with little prospect

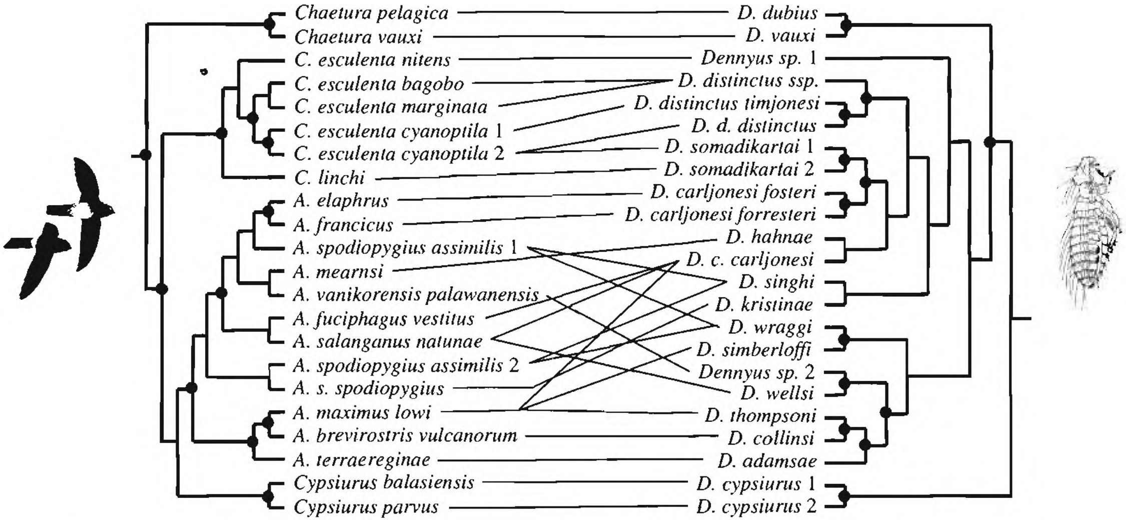

FIGURE 13.4. Comparison of swift(let) (Apodidae) phylogenetic tree to louse tree (*Dennyus* spp). The phylogenies are derived from neighbor joining (Kimura two-parameter distances) of combined mitochondrial cyt *b* and COI sequences (unpub.) for both groups. Bulleted nodes are cospeciation events inferred from reconciliation analysis (Page, 1990) in TREEMAP (Page, 1994). Numbered terminal taxa are those distinguished by molecular differences. Lines connecting birds and lice indicate host-parasite associations. *C.* = *Collocalia*, *A.* = *Aerodramus*, *D.* = *Dennyus*.

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 ample opportunity for dispersal between hosts, at least at a low rate. Collections of *Dennyus* lice from syntopic species show that some species of lice occur on multiple hosts in the same location, albeit at low intensity (Tompkins and Clayton, 1999).

The intrinsic dispersal ability of species of *Dennyus,* while higher than species of *Geomydoecus,* is still fairly low. *Dennyus,* like other members of the suborder Amblycera, have some locomotory capabilities when off the body of the host. It is probably possible for individual *Dennyus* species to crawl between closely positioned nests in caves where several species of hosts co-occur. However, prospects for long distance dispersal are far more limited. Phoresis on hippoboscid flies has never been observed for *Dennyus,* nor for other species of louse in the suborder Amblycera (Keirans, 1975).

While prospects for dispersal in *Dennyus* are limited, there is evidence for the ability of species to establish on foreign hosts provided they can get there. Transfer experiments by Tompkins and Clayton (1999) showed that, when transferred to a foreign host having feathers that are not too different in size from the usual host, species of *Dennyus* can survive on the foreign host. Since swifts and swiftlets have few defenses against lice, being inefficient preeners, the importance of size probably relates to tenacity, the ability to hang on to the host during flight. Like *Geomydoecus,* species of *Dennyus* tend to match the size of their hosts (fig. 13.5). However, the match isn't perfect, and different subgroups of *Dennyus* appear to have different louse-to-host body size ratios. The ability of species of *Dennyus* to alter their microhabitat preferences when on different sized hosts (Tompkins and Clayton, 1999) may be a factor in their ability to survive on hosts over a relatively wide size range.

Prevalence of species of *Dennyus* is usually high (Lee and Clayton, 1995; unpub. data), which should make extinction and "missing the boat" events relatively infrequent. In general, most populations of swifts and swiftlets appear to have lice. However, there may be some absences of lice from small populations on islands. For example, lice have not been found on *Aerodramus bartshii* (Hawaii) or *A. sawtelli* (Cook Islands), despite concerted sampling of both species (unpub. data). Small body size may also be a factor: no lice have been recovered from the Philippine endemic species *Collocalia troglodytes* (unpub. data), which, although abundant, is the smallest bodied species of swiftlet. One factor promoting extinction of louse populations—low mean intensity—does seem to be the rule in

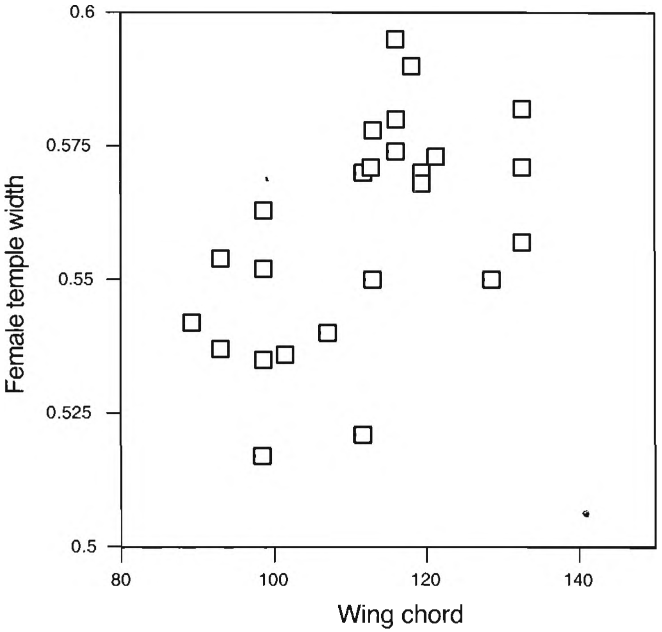

FIGURE 13.5. Plot of average temple width of female *Dennyus* species (in millimeters) against wing chord length of host species (in millimeters). Independent contrasts analysis (Felsenstein, 1985) over the *Dennyus* phylogeny produces a significant association between changes in host body size and louse body size ($p < .01$).

Dennyus. Most parasitized host individuals harbor less than 10 individual lice, owing to the small body size of swifts and swiftlets.

In sum, opportunities and ability to disperse between host species are limited for species of *Dennyus*, but do occur on measurable ecological time scales. Species of *Dennyus* have the ability to establish on a foreign host, provided that host is not too different in size from the usual one. These lice also exhibit a relatively high prevalence and low intensity. Taking these factors together, we would predict some degree of incongruence between host and parasite phylogenies. Moreover, it should be possible to predict from the ecological details which clades are the most likely ones to be incongruent.

Columbiformes and *Columbicola*

A third well studied system consists of species of the ischnoceran louse genus *Columbicola*, which are parasites of pigeons and doves (Aves: Columbiformes). Studies of many aspects of the biology of *Columbicola* have been conducted. Indeed, the species *Columbicola columbae* is considered the "white rat" of bird lice (Eichler, 1963; Nelson and Murray, 1971). Species of *Columbicola* range from those that are completely host specific, to those that are parasitic on many species of hosts over a wide geographic area (Johnson et al., 2002).

A phylogeny for *Columbicola* has been reconstructed on the basis of both mitochondrial (12S and COI) and nuclear (EF1-α) DNA sequences. Comparisons of the *Columbicola* phylogeny to that of its pigeon and dove hosts indicated eight cospeciation events (see chap. 11), which is more cospeciation than expected by chance ($p < .01$). Of 19 nodes in the host phylogeny, 7 of these (37%) had an associated cospeciation event. While cospeciation occurs in *Columbicola,* several factors appear to break down congruence with the host phylogeny in this genus.

First, many species of pigeons and doves are sympatric and syntopic (table 13.1), which provides an opportunity for dispersal between host species. In addition, widespread host species often overlap with the ranges of host species that have more restricted distributions. This pattern provides an opportunity for lice to disperse between allopatric species via dispersal on more widespread host species, which may have contributed to failure of the lice to speciate. For example, the species *Columbicola theresae* occurs on two widespread species of hosts, *Oena capensis* and *Streptopelia senegalensis*. In addition, this louse occurs on two allopatric sister taxa having more restricted distributions: *Streptopelia capicola* (South and East Africa) and *S. vinacea* (sub-Saharan North Africa). Populations of nonspecific lice on widespread host species may keep that louse species from diverging on other allopatric hosts.

In addition to proximity of hosts, species of *Columbicola* appear to be able to take advantage of dispersal opportunities. There are records of phoresis by species of *Columbicola* on hippoboscid flies (Couch, 1962; Keirans, 1975). Studies of the genetics of populations of *Columbicola* on different host species generally indicate a lack of structure, suggesting high continuous capabilities for dispersal between hosts (Johnson et al., 2002).

Although *Columbicola* lice can disperse between host species, they still must be able to establish breeding populations on those hosts. Preliminary transfer experiments to birds whose preening ability is impaired show that pigeon wing lice *(Columbicola columbae)* may be able to establish on foreign hosts. Several hundred *C. columbae* have been recovered from Mourning Doves and Common Ground Doves four months after being "seeded" with 50 lice (unpub. data). These results are noteworthy, particularly given that Common Ground Doves are an order of magnitude smaller

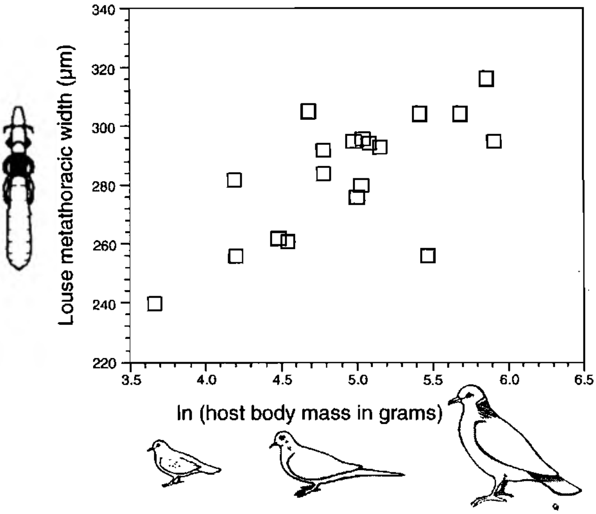

FIGURE 13.6. Plot of average metathoracic width of female *Columbicola* species (in micrometers) against ln body mass (in grams) of Columbiform host species (body mass is significantly correlated with feather barb size; unpub. data). Independent contrasts analysis (Felsenstein, 1985) of these data over the *Columbicola* phylogeny produces a significant association between changes in louse body size and host body size ($p = 0.001$).

than Feral Pigeons. With host defense in place, however, *Columbicola* may not be able to establish over such a broad range of host body size.

Evidence consistent with some limitation to acceptable host body size comes from comparisons of parasite to host body sizes (fig. 13.6), which show a somewhat tighter relationship than in *Dennyus*. This match between parasite and host body size may be related to the mechanism *Columbicola* uses to escape from host preening defense. When exposed to preening, individuals of *Columbicola* insert themselves between the barbs of the wing feathers for protection (fig. 13.7). The size of individual *Columbicola* must therefore approximate the size of the interbarb space in order to prevent being removed by preening. *Columbicola* can probably establish on foreign hosts provided those hosts are not too different in body size from the usual host. This establishment ability, combined with the dispersal ability of *Columbicola,* makes it possible for the members of this genus to move between host species, thereby increasing the probability of host switching and failure to speciate events.

In addition to the ability to move between host species, the population structure of *Columbicola* makes them somewhat prone to duplication

FIGURE 13.7. SEM of *Columbicola* inserting between feather barbs. IS = interbarb space (see text).

and missing the boat events, but makes them unlikely to experience an extinction event. Species of *Columbicola* can often have patchy distributions, possibly resulting from climatic factors. For example, several species of *Columbicola* are almost completely absent from doves in arid Arizona, while 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. On the other hand, species of *Columbicola* can often have a high prevalence (80%) and high intensity (50–100 lice per host), making extinction unlikely. Together these factors appear to generate an intermediate level of congruence between host and parasite phylogenies (chap. 11).

Birds and *Brueelia*

As a final case study, we consider the avian ischnoceran louse genus *Brueelia,* which 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. While ecological interactions between *Brueelia* and their hosts are not as well studied as in the previous three examples, enough is known to make meaningful comparisons.

The phylogeny of 15 species in the louse genus *Brueelia* was reconstructed by Johnson et al. (in review.a.) on the basis of nuclear EF1-α and mitochondrial COI DNA sequences. The phylogeny of *Brueelia,* when compared with that of their avian hosts (fig. 13.8), indicates only seven cospeciation events, well within the number expected by chance alone ($p = .25$). Only 5 of 24 (20%) nodes in the host tree have a cospeciation event associated with them. Thus, despite fairly high host specificity, there is very little evidence of cospeciation between species of *Brueelia* and their hosts. Several aspects of the ecology of *Brueelia* suggest a basis for the lack of phylogenetic congruence between this genus of lice and their hosts.

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 co-occur in the same habitat. In addition, many species of passerines and nearly all 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). Johnson et al. (unpub.) found that species that nest in holes often share species of *Brueelia*. The possibilities for short-term survival of *Brueelia* off the host are high (Dumbacher. 1999), and takeovers of nests 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 hippoboscid flies. In fact, about 80% of the nearly 350 records of phoresis summarized by Keirans (1975) involve passerine lice. Of these, the majority are *Brueelia* and the closely related *Sturnidoecus,* with most of the remaining records involving *Philopterus* (the other major genus of passerine ischnoceran louse). While little is known about the establishment ability of *Brueelia,* some species are found on multiple host families (Johnson et al., unpub.). In addition, Clay (1951) describes *Brueelia* as a generalist louse in relation to its habitat on the host's body. Taken together these factors suggest high potential for host switching and failure to speciate, which would break down congruence between host and parasite phylogenies.

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 (Clayton, Price, and Peterson, in prep.) reveals localities where *Brueelia* is absent. Such patchiness could lead to duplication and missing the boat events. While the extent of distributional patchiness in most species of *Brueelia* is unclear, patterns in prevalence and intensity are well documented. 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

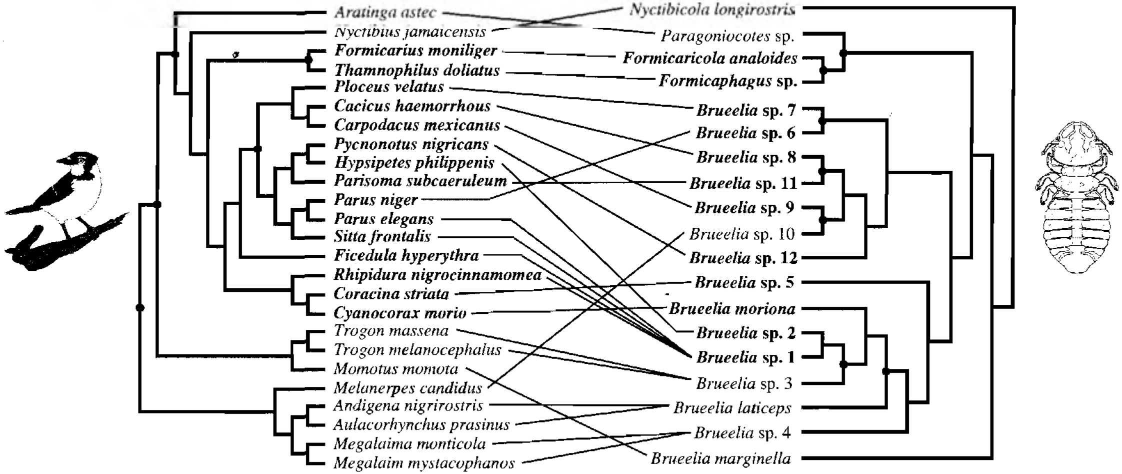

FIGURE 13.8. Comparison of bird phylogenetic tree to louse tree (*Brueelia* spp) (Johnson et al., in review.b). The host phylogeny is derived from Sibley and Ahlquist (1990). Bold taxa indicate Passeriformes and associated louse species. The louse phylogeny is derived from maximum likelihood analysis of mitochondrial COI and nuclear EF1-α sequences. Bulleted nodes are cospeciation events inferred from reconciliation analysis (Page, 1990). Lines between birds and lice show host-parasite associations.

low intensities increase the chance of extinction. In summary, nearly all aspects of the biology of *Brueelia* (table 13.1) appear to favor events that reduce congruence between host and parasite phylogenies.

Conclusions

The ecological basis of coevolutionary history is discernible, as illustrated by the four case studies compared above. Lice having phylogenies that are more congruent with their host phylogeny tend to have fewer factors that promote failure to speciate, host switching, duplication, missing the boat, and/or extinction. As factors responsible for these events become more common, congruence declines. This is not to say, however, that the factors set out in table 13.1 are sufficient to explain all patterns of host-parasite coevolutionary history. For example, rare events, such as dispersal, can be extremely important over long periods of evolutionary time, even though they may be difficult or impossible to measure in ecological time.

A case in point is rock wallabies (Marsupialia: Macropodidae) and their lice (Amblycera: *Heterodoxus*). Several allopatric species of rock wallabies are found along the east coast of Australia. One might expect to find a different species of *Heterodoxus* on each of these species of wallabies. However, this is not the case. A single species of wallaby often harbors more than one species of *Heterodoxus,* even though individual wallabies seldom have more than one species of louse (Barker, 1991). The geographic distribution of a single species of *Heterodoxus* often spans the boundary between host species, although it seldom spans the entire range of both hosts. Not surprisingly, the phylogenies of rock wallabies and their lice show little congruence (Barker, 1991; Barker et al., 1992). These geographic patterns suggest that the lice are capable of dispersing between host species, but that they are not necessarily capable of dispersing among all the populations within a given host species. What's going on? The probable explanation is suggested by the fact that rock wallabies live in small groups on rock outcrops that are often separated by many miles of unsuitable habitat. Thus, wallaby populations are effectively patchier within species than between species. In addition to representing uneven dispersal opportunities for lice, such distributions favor parasite duplication, which further reduces the extent of host-parasite congruence. As additional case studies accumulate, more ecological factors will undoubtedly be found to have an influence on coevolutionary history.

Although caution is advised when drawing conclusions about coevolutionary history from studies of extant species, valid generalizations can still be made. For example, the case studies outlined above suggest that dispersal is a more fundamental barrier to host switching among related hosts than is establishment. Transfer experiments show that host-specific parasites can survive on foreign hosts that are phenotypically similar to the usual host, so long as the parasites can get to these hosts. However, 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.

Although limitations to dispersal are clearly important in maintaining the specificity of parasites among *related* hosts, limitations to establishment appear to be important in maintaining the specificity of parasites among *unrelated* hosts. Data regarding the lice on brood parasitic birds are informative in this regard, since they represent a kind of "natural" dispersal experiment. Brood parasites lay their eggs in the nests of other species, which are then tricked into rearing the young of the brood parasites. Recent studies of lice on brood parasitic cuckoos and cowbirds show that lice disperse from foster species to nestling brood parasites. Although these foster species of lice survive on the brood parasites in the short term, there is little evidence for long term establishment (de L. Brooke and Nakamura, 1998; Lindholm et al., 1998; Hahn et al., 2000). Among other things, these results suggest a major shortcoming of transfer experiments—they may not be of sufficient duration to simulate what actually happens under natural conditions. For example, Hahn et al. (2000) recovered nearly as many species of lice from cowbird fledglings ($n = 11$) as they did from all 30 foster species combined at their study site. However, they recovered only 5 species of lice from adult cowbirds, which is about the number expected for a bird of this size and sampling effort (Clayton and Johnson, 2001).

Although Hahn et al. (2000) concluded that limitations to dispersal are the fundamental factor maintaining the host specificity of lice, their results actually indicate the opposite: limitations to establishment have been the most important factor. If dispersal governed specificity, then adult brood parasites should have thriving populations of most of the lice that are found on juvenile brood parasites (the same ones found on the foster species). Like most birds, however, brood parasites appear to have their own host specific lice, despite continually being exposed to lice from other species. In this case, limitations to establishment must be the reason.

Indeed, limitations to establishment are the basis for the phenomenon known as "resource tracking," in which parasites occur on hosts that share some critical resource, such as feather size, rather than being confined to hosts that have descended from a common ancestor, which we will call "phyletic tracking." If the distribution of the resource being tracked is independent of host phylogeny, and if parasites are able to disperse broadly among hosts, then there will be little congruence between host and parasite phylogenies (Kethley and Johnston, 1975). On the other hand, if dispersal opportunities are severely limited, and/or the resource being tracked is correlated with host phylogeny, then congruence is expected. Thus, resource tracking and phyletic tracking make opposing predictions only when the resource being tracked is *not* correlated with the host phylogeny. However, the similarity of many resources on related hosts means that resource tracking may often *increase* congruence. In other words, phyletic tracking and resource tracking are both processes that can contribute to phylogenetic congruence.

To conclude, this chapter has merely scratched the surface of the potential for synergy between ecological and cophylogenetic studies. As additional data sets become available (e.g., Paterson et al., 2000) we will be able to conduct these analyses in a more comprehensive way. The phylogenies and ecological interface for most coevolving species remain largely a mystery. It is our hope that this chapter has served to convince the reader of the potential for improving our understanding of coevolutionary history by continuing to extrapolate backwards from data on the ecology of extant species.

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