

POINTS IN QUESTION

Lice and cospeciation: A response to Barker

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INTRODUCTION

Although historically lice (Insecta: Phthiraptera) and the scientists who have studied them have played a prominent role in the development of ideas on cospeciation and coevolution (Paterson, Gray & Wallis, 1995), in recent texts on coevolution (e.g., Brooks & McLennan, 1991, 1993; Thompson, 1994) lice have been largely ignored (or have suffered the indignity of being called “mites”). This is despite the fact that lice provide the clearest evidence of host-parasite cospeciation (Hafner & Nadler, 1988; Paterson et al., 1993; Hafner *et al.*, 1994). Barker's (1994) review of the phylogeny and evolution of host associations of lice is therefore welcome and timely. He presents a good overview of higher level louse systematics, and the conditions under which we might expect cospeciation or host-switching to predominate. However, in assessing the available evidence on host-lice cospeciation we believe Barker has overlooked some important studies, and comes to an unjustified conclusion based on the studies he does cite. Furthermore, his review fails to grasp the complexity of the possible phylogenetic and ecological relationships between hosts and parasites.

TESTING THE HYPOTHESIS OF COSPECIATION

Is cospeciation typical?

Barker (1994: 1288) concludes that “Cospeciation, and subsequent coevolution, undoubtedly occur but are less common than previously thought; certainly they are not the prevailing patterns in the Phthiraptera.” Barker cites three studies in support of this claim: Lyal's (1987) study of 351 trichodectid lice for which he estimated that 20.7% of the speciation events involved host switches; Hafner & Nadler (1988), whose data require at most two host switches out of nine speciation events (Page, 1990); and his own studies (Barker, 1991) of 11 species of rock-

wallaby lice for which he found little evidence for cospeciation. It is hard to see how Barker arrived at his conclusion based on these three studies, two of which show a prevalence of cospeciation! Barker (p. 1288) is right to bemoan the ready acceptance of cospeciation as an axiom, but at that same time his conclusion that cospeciation is not the prevailing pattern contradicts the very evidence he cites.

Furthermore, Barker overlooks two major studies of louse-host relationships; Kim's (1988) study of mammalian Anoplura, and Paterson, Gray & Wallis' (1993) study of lice found on penguins, petrels and albatrosses. Kim (1988: 106) concluded that Anoplura have a complicated history of association with mammals which was initiated by a series of "erratic" colonisations occurring at different times, followed by close coevolution with sporadic host changes.

Paterson et al. (1993, 1995) examined the coevolutionary history of seabirds and their lice. Component analysis of phylogenies constructed for seabirds and lice revealed little evidence for host switching in the evolutionary history of this host-parasite system. The pattern found was one of multiple louse lineages present on the ancestral seabird species with occasional episodes of cospeciation and extinction. Subsequent research using 12S mitochondrial DNA sequence data for both seabird and louse species has confirmed that the proposed cospeciation events occurred relatively concurrently and that the rate of molecular evolution, unlike morphological evolution, has been greater in the lice (Paterson & Gray, in press).

WHAT IS EVIDENCE FOR COSPECIATION?

Fahrenholz's Fallacy

Fahrenholz's rule, that host and parasite phylogenies should mirror each other, is often viewed as a cornerstone of cospeciation research. Conversely, failure to find identical host and parasite phylogenies is seen as *prima facie* evidence for host

switching. While strict adherence to Fahrenholz's rule encourages the dismissal of unexpected host records as due to "stragglers" (Ròzsa, 1993) and hence may lead to underestimates of host switching, such adherence can also lead to the naïve equation of incongruent host-parasite phylogenies with host switching. However, incongruence between host and parasite phylogenies can arise from a number of causes, such as the presence of multiple lineages of parasites coupled with parasite extinction, or failure of parasites to colonise both descendants of a host speciation event ("missing the boat" — Paterson, 1994; Paterson & Gray, in press), or collection failure (Page, 1993a). Failure to recognise these factors may lead to overestimates of host switching. For example, the ancestral host seabird lineage splits into penguins and petrels (Paterson et al., 1993). The louse genus *Saemundssonina* is patchily distributed over extant seabird species. One non-host switching explanation for this distribution is that a *Saemundssonina* species was present but was unevenly geographically distributed on the ancestral seabird host. By chance, the founding population for petrels inherited the louse but penguins did not, i.e., *Saemundssonina* "missed the boat." If there is a subsequent history of uneven geographic distribution within a host species and of missing the boat then *Saemundssonina* would become patchily distributed among petrels.

Interestingly, louse taxonomists have long been aware of the potential problem of multiple lineages (e.g., Hopkins, 1948; Clay, 1949; Kim, 1985). Discussing secondary absence of lice, Hopkins (1948:38) wrote: "Let us suppose that two different sets of descendants of the hyrax with eight lice were each to lose six of their lice, but a different six, and it becomes obvious that any deductions from the lack of relationship between the two pairs of survivors of the original set of eight lice would be extremely misleading." Clay (1949:296) was even more explicit. She constructed a hypothetical case where "three related hosts, x, y, z, may have been parasitized by three pairs of sympatric species, a^1 and b^1 on host x, a^2 and b^2 on host y, and a^3 and b^3 on host z [Fig. 1a]...If some of these species become extinct (or have not been collected) so that host species x appears to have only parasite species a^1 , and

y to have only b^2 and z only a^3 ; then, from a consideration of the parasites, host species x and z will appear to be more closely related to each other than either is to y [Fig. 1c] because the parasite species a^1 and a^3 are in fact more closely related to each other than to b^2 .” Both Hopkins and Clay were aware that the relationship between host and louse phylogeny may be complex, and that host switching is not the only process that may cause this complexity.

Wallaby Lice

Based on his extensive studies of lice found on rock-wallabies (*Petrogale*) Barker (1994: 1288) concluded that the lice “have not coevolved absolutely or even closely with their hosts.” Taken at face value this conclusion seems reasonable: the phylogenies for wallabies and their lice do indeed show poor correspondence. Much of this incongruence reflects disagreements between louse and host distribution: lice found predominantly on one host may also be found on adjacent populations of neighbouring hosts (e.g., Barker, 1991: fig. 3).

Petrogale species are often parapatric, and appear to have undergone numerous episodes of introgression. This is reflected in the distribution of mitochondrial DNA (mtDNA) morphs (Bee & Close, 1993), which may transgress species boundaries delimited by chromosome rearrangements. In some cases the distribution of mtDNA morphs hints at parallels with louse distribution. For example, the louse *Heterodoxus orarius* is found on *P. godmani* and southern populations of the “Cape York” species. Southern Cape York populations also contain the W mtDNA morph found nowhere else in *Petrogale*. This morph is most closely related to the V morph found in one population of *P. godmani* which is not closely related to the Cape York species.

Discordant histories of different genes from the same species may arise for a number of reasons, such as lineage sorting of polymorphisms (see e.g., Avise, 1994). Such discordances do not lead us to abandon the hypothesis that genes have “coevolved” with the organisms to which they belong, rather they indicate that the

relationship between organismal and gene phylogenies may be complex. Indeed the kind of complexity reported by Barker (1991) is just what one would expect in a system where hosts are undergoing repeated episodes of hybridisation / secondary contact, as Barker (1994: 1290) himself notes. In this sense, the wallaby lice may indeed closely reflect the history of their hosts.

HOST-SWITCHING AND COMPETITIVE EXCLUSION

The prevalence of cospeciation is an empirical question that requires considerably more studies than are available today. Such studies could then be used to address hypotheses concerning the processes involved in structuring host-parasite assemblages. Barker (1994: 1289) suggests that the relative roles of cospeciation and host-switching **are** a function of opportunities for host switching: the greater the opportunity the greater the preponderance of host-switching. Consistent with this assertion are data showing that host sharing by *Strigiphilus* owl lice occurs exclusively between owls that are sympatric and syntopic (sharing habitat) (Clayton, 1990). *Strigiphilus* species are not shared by allopatric hosts, even closely related ones. Many of the syntopic owls which share lice nest in cavities, which might serve as arenas facilitating secondary transfers of lice between species nesting in rapid succession. Similar patterns of host-sharing are known for lice on sympatric, syntopic parrots (Price and Clayton, 1983).

However, lice clearly do not switch hosts at every opportunity. Furness & Palma (1992) report that different seabird species breeding in high densities in the same habitat (often sharing burrows) on Gough Island show a remarkable lack of shared lice. Paterson (1994) also collected lice off seabirds from seven mixed-species colonies and found no "stragglers." One of the most puzzling "missed opportunities" for host-switching is between brood parasites and their hosts. Despite ample opportunity for transmission of lice to cuckoos (*Cuculus canorus*) from a variety of passerine host species, the former are only parasitized by three genera of lice that are

restricted to members of the cuckoo family (Rothschild and Clay, 1952).

Transmission of cuckoo lice between cuckoos apparently takes place during bouts of mating between older and younger birds (Marshall, 1981). A recent experiment verifies that louse transmission can occur during the lightning fast copulation typical of birds (Hillgarth, 1995).

Barker suggests (1994: 1290) that "competition among lice appears to be an important, though little considered, factor in the success of host-switches." This claim is premature. In perhaps the only thorough study to date, Choe and Kim (1988) found no evidence for competition between lice coexisting on several species of seabirds. They argued that lice may be so narrowly adapted to microhabitats on the host that they do not readily expand their distributions in the absence of a potential competitor. Furthermore, as Choe and Kim (1988) and other authors (e.g. Hastings, 1987) point out, species co-occurrence data are not robust for making inferences about competition. Rigorous tests of competition require an experimental approach, in which the population response of a particular species to the experimental removal of its potential competitor(s) is monitored (e.g. Pertain et al., 1993). Ironically, since lice pass their entire life cycle on the host, they are unusually tractable candidates for competition experiments, as well as for ecological studies in general (Lee and Clayton, 1995). Incidentally, bats infested with fleas seldom have lice, not because of competition, as Barker (1994: 1289) suggests, but because lice do not occur on the order Chiroptera (Marshall, 1981).

It is also misleading for Barker (1994: 1289) to claim that "...an insect that feeds on a certain type of plant will coevolve with that plant if there are no other similar species... available." Actually, there is a sizeable body of literature to the contrary (Strong et al., 1984; Rausher, 1992; Thompson, 1994).

DESIGNING A TEST OF COSPECIATION

We suggest that many apparent absences of lice may reflect “sorting events” due to louse extinction or patchy distribution on ancestral hosts leading to failure of lice to colonise both descendants of the ancestor. Answering these questions requires a methodology for determining the extent of cospeciation in a given host-lice assemblage, hence we think it is useful to outline what we consider to be the basic requirements for a rigorous study of cospeciation.

1. *Adequate alpha-taxonomy of both hosts and parasites.*

An obvious requirement, but its importance cannot be over-emphasised, especially as closely related louse species are often very hard to distinguish morphologically. Multivariate morphometrics offers the potential to resolve suites of closely related taxa, and to permit rigorous identification of lice independent of host information. The lice of pocket gophers provide a salutary example: Price & Emerson’s (1971) revision listed 42 species; two decades of further collecting and morphometric analysis has expanded this total to 122 species (Hellenthal & Price, 1991).

2. *Accurate phylogenies of host and parasites*

Again an obvious requirement. Given that rigorous testing of hypotheses of cospeciation requires phylogenies, we need to be aware of the limitations of both our data and our methods of inferring phylogenies from those data. Accuracy can be best tested by comparing phylogenies obtained from different, independent data sets (Penny, Foulds & Hendy, 1982).

3. *Exhaustive sampling of clades of lice*

Clay's (1949) hypothetical example discussed above (Fig. 1) shows the importance of sampling. The strongest tests of hypotheses of host-lice cospeciation will come from exhaustively sampled clades of lice. Thus, given a choice it is better to sample all representatives of a single clade of lice (e.g. a genus) than to sample the same number of species from a range of different clades. Note that this requirement may conflict with a taxonomist's instinct to try to capture the broad outline of the parasite phylogeny by sampling a range of disparate taxa.

4. *Molecular phylogenies based on comparable genes*

Molecular phylogenies are desirable not because molecular data is inherently better than morphological data, which we do not believe is the case (see Patterson, Williams & Humphries, 1993), rather molecular data offer the prospect of being able to compare host and parasite divergence using comparable units (Page, 1993b; Hafner and Page, in press), especially if homologous genes are studied in both host and parasite (e.g., Hafner *et al.*, 1994).

Molecular divergence may also permit us to decide between the two primary explanations of incongruent host-parasite phylogenies; host switching and multiple lineages. Figure 2a depicts a pair of incongruent host and parasite phylogenies. The incongruence may be due to host switching or the presence of multiple lineages. By themselves the cladograms do not allow us to decide between these explanations although the relative likelihood of either host switching or multiple lineages and extinction scenarios may be assessed. A host switching explanation for Fig. 2a suggests that the ancestor of P2 colonised H1 from H2 and displaced the parasite species (P4) already present on H1 (Fig. 2b). This scenario requires two evolutionary events, one host switching event and the extinction of P4. A multiple lineage explanation suggests that two lineages were present on the ancestral hosts and three

sorting events occurred (Fig. 2c). Which scenario is supported may be determined by the biology of the host-parasite system, i.e. how common are host switching events relative to sorting events?

If we have information on relative time of divergence between the host and parasite species then we may be able to choose between these explanations. In Fig. 2d this information supports host switching (evolutionarily recent parasites colonising new hosts) whereas Fig. 2e supports multiple lineages (the persistence of relict parasites on their original hosts). Such information on timing may come from molecular clocks.

A disadvantage of molecular data is that it is expensive to collect, which places constraints on sampling taxa, conflicting with the previous requirement of exhaustive samples. Pocket gopher lice provide a good illustration; while a complete morphology-based phylogeny for all 122 known taxa is available (Page, Price & Hellenthal, in press), to date only 17 lice have been sequenced (Hafner *et al.*, 1994).

5. *Quantitative comparison of host and parasite phylogenies*

Quantifying the similarity between host and parasite phylogenies makes possible explicit statistical tests of cospeciation, rather than relying on qualitative assessments. Given a measure of fit between the two trees, i.e. how similar the trees are, the distribution of that measure can be obtained using randomisation methods (e.g., Page, 1995). This method is used to test the hypothesis of cospeciation, i.e. if host and parasite trees are more similar than expected by chance then this supports cospeciation. The two main methods for comparing host and parasite phylogenies are Brooks Parsimony Analysis (BPA; e.g., Brooks and McLennan, 1991; Hoberg, Brooks & Seigal-Causey, in press) and component analysis (e.g., Page, 1995; Paterson & Gray, in press).

6. *Host transfer experiments*

Controlled transfer experiments have the potential to shed light on the parameters governing host-switching. By comparing the survival of lice moved to foreign host taxa (experimentals), to that of lice moved to new individuals of the normal host (controls), it should be possible to identify constraints on natural host-switching. A nested two-factor experimental design can be used to test the relative roles of host phylogenetic distance and ecological similarity. Do lice do better on foreign hosts that are closely related to the normal host, or on hosts that are similar in body size, or some combination of the two? Preferably, such experiments would be conducted under field conditions using sympatric host species that vary in ecological traits of potential importance to host-specific lice.

SUMMARY

“The student who intends working on the Mallophaga should take warning that he will be tried almost beyond endurance by the paradoxes and complexities which beset his subject but he will also find, in the dual and inter-related aspect of insect and bird, an infinite fascination.” (Rothschild & Clay, 1952: 156-157)

The study of host-louse coevolution will benefit greatly from the phylogenetic perspective offered by recent advances in molecular systematics. However, in order to make best use of phylogenies we need to appreciate the complexities of the possible relations between host and parasite phylogeny. At the same time, the very complexity of louse-host systems has a potentially useful consequence; the presence of multiple lineages of lice on the same hosts allows for replicated tests of coevolutionary hypotheses. For example, if a number of louse clades infest the same host clade but some lice show more cospeciation than others, we might ask whether there are

features of louse biology that correlate with this difference in host tracking fidelity. It may further be possible to ascertain the relative importance of these features in ecological time through controlled transfer experiments. By beginning to appreciate “the paradoxes and complexities” of host-louse evolution, lice may offer us not only “infinite fascination” but also a chance to address important questions in coevolution.

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Figure captions

FIG. 1. (a) Clay's (1949) scenario where three hosts, x, y, z, are parasitised by three pairs of sympatric lice, a¹⁻³, b¹⁻³. Lice in parentheses are now extinct or unknown (after Clay, 1949: Fig. 4). (b) Cladistic representation of the relationship between the six louse taxa shown in (a). (c) Cladogram for the three extant species of lice. Note that these three species imply that hosts x and z are sister taxa, whereas if we had the cladogram for all six lice (b) we would conclude that x and y are sister taxa (see text).

FIG. 2. (a) Incongruent cladograms for hosts and parasites with (b) host switching and (c) multiple lineage and extinction scenarios to explain the incongruence. Given the two alternative possible molecular phylogenies consistent with those cladograms; (d) is consistent with host switching, whereas (e) is consistent with multiple lineages (see text).

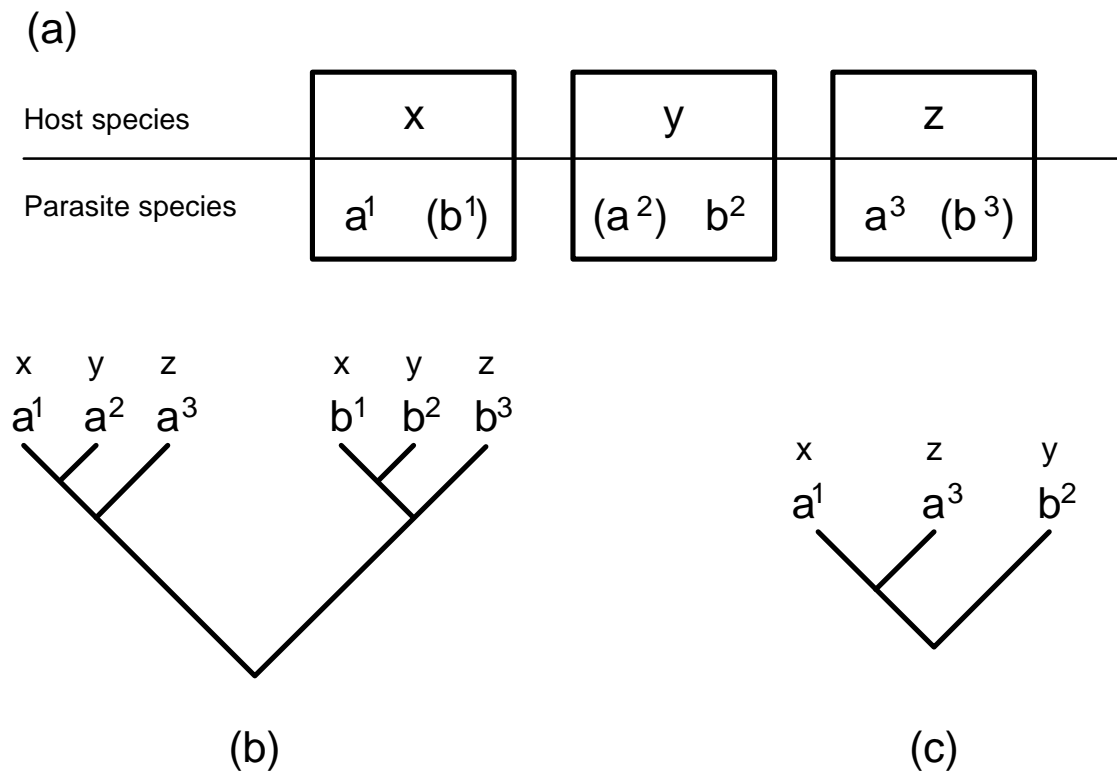


Fig. 1

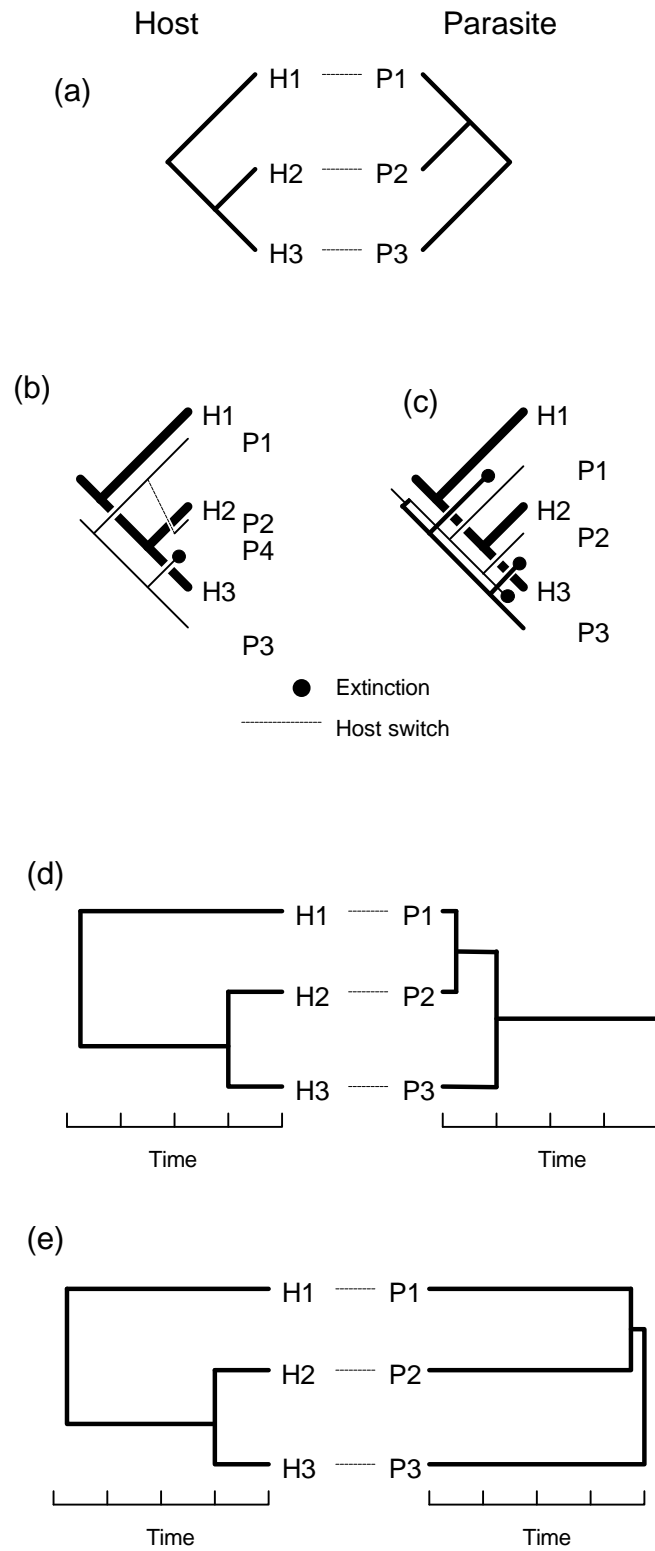


Fig. 2