



POINTS IN QUESTION

Lice and Cospeciation: A Response to Barker

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) they 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. It 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

Cospeciation typical?

Barker (1994: p. 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 3 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 2 host switches out of 9 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 3 studies, 2 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 2 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: p. 106) concluded that Anoplura have a complicated history of association with mammals which was initiated by a series of "erratic" colonizations 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?

Farenholz's fallacy

Farenholz'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 Farenholz's rule encourages the dismissal of unexpected host records as due to "stragglers" (Rózsa, 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 colonize both descendants of a host speciation event ("missing the boat"—Paterson, 1994; Paterson & Gray, in press), or collection failure (Page, 1993a). Failure to recognize 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 *Saemundsson* is patchily distributed over extant seabird species. One non-host-switching explanation for this distribution is that a *Saemundsson* species was present but in an uneven geographic distribution on the ancestral seabird host. By the louse but petrels (Paterson *et al.*, 1993) inherited "missed the boat". If there is a subsequent history of uneven geographic distribution within a host species and of missing the boat then *Saemundsson* 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: p. 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: p. 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: p. 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 & Clayton, 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 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 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 hybridization and secondary contact, as Barker (1994: p. 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: p. 1289) suggests that the relative roles of cospeciation and host-switching are a function of opportunities for host-switching and 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 & Clayton, 1993).

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 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 cuckoo lice to cuckoos (*Cuculus canorus*) from a variety of passerine host species, the former are only parasitized by a few genera of lice that are restricted to members of the cuckoo family (Rothschild & 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 (Jalilgarth, 1995).

Barker suggests (1994: p. 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 & Kim (1988) found 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 & 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., Petren *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 & Clayton, 1995). Incidentally, bats infested with fleas seldom have lice, not because of competition, as Barker (1994: p. 1289) suggests, but because lice do not occur on the order Chiroptera (Marshall, 1981).

It is also misleading for Barker (1994: p. 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-louse assemblage, hence we think it is useful to outline what we consider to be the basic requirements for a rigorous study of cospeciation.

Adequate alpha-taxonomy of both hosts and parasites. An obvious requirement, but its importance cannot be overemphasised, 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; 2 decades of further collecting and morphometric analysis has expanded this total to 122 species (Hellenthal & Price, 1991).

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 tested best by comparing phylogenies obtained from different, independent data sets (Penny, Foulds & Hendy, 1982).

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-louse 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.

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 2 primary explanations of incongruence

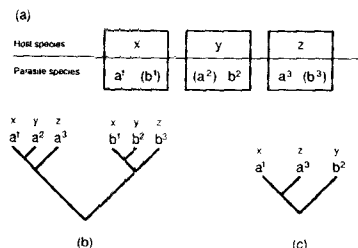


Fig. 1. (a) Clay's (1949) scenario where 3 hosts, x, y, z , are parasitized by 3 pairs of sympatric lice, $a1-3, b1-3$. Lice in parentheses are now extinct or unknown (after Clay, 1949; Fig. 4). (b) Cladistic representation of the relationship between the 6 louse taxa shown in (a). (c) Cladogram for the 3 extant species of lice. Note that these 3 species imply that hosts x and z are sister taxa, whereas if we had the cladogram for all 6 lice (b) we would conclude that x and y are sister taxa (see text).

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 colonized H1 from H2 and displaced the parasite species (P4) already present on H1 (Fig. 2b). This scenario requires 2 evolutionary events, one host-switching event and the extinction of P4. A multiple lineage explanation suggests that 2 lineages were present on the ancestral hosts and 3 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 colonizing 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 they are expensive to collect, which places constraints on sampling taxa, conflicting with the previous requirement of exhaustive samples. Pocket gopher lice

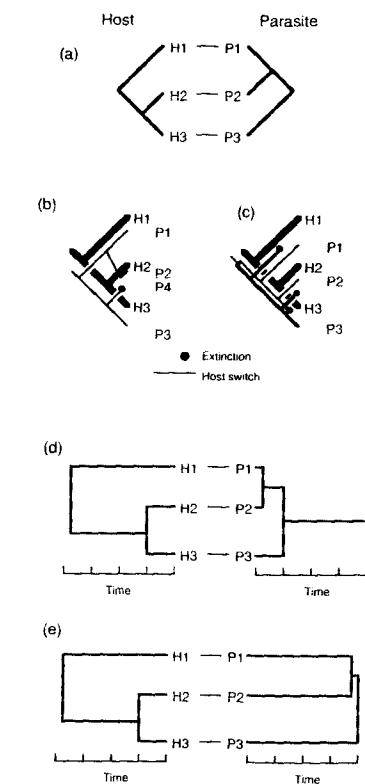


Fig. 2. (a) Incongruent cladograms for hosts and parasites with (b) host-switching and (c) multiple lineage and extinction scenarios to explain the incongruence. Given the 2 alternative possible molecular phylogenies consistent with those cladograms; (d) is consistent with host-switching, whereas (e)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

provide a good illustration; while a complete morphology-based phylogeny for all 122 known taxa is available (Page, Price & Hellenthal, 1995), only 17 lice have been sequenced (Hafner *et al.*, 1994).

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 2 trees, i.e. how similar the trees are, the

distribution of that measure can be obtained using randomization 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 2 main methods for comparing host and parasite phylogenies are Brooks Parsimony Analysis (BPA; Brooks & McLennan, 1991; Hoberg, Brooks & Sall-Causey, in press) and component analysis (Page, 1995; Paterson & Gray, in press).

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 2-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 should be conducted under field conditions using sympatric host species that vary in ecological traits of potential importance to host-specificity.

SUMMARY

The student who intends working on the Malpanga should take warning that he will be tried to last 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 host, an infinite fascination." (Rothschild & Clay, 1952: pp. 156-157).

The study of host-lice 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 allow 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-lice evolution, lice may offer us not only "infinite fascination" but also a

chance to address important questions in coevolution.

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REFERENCES

- Avise J. C. 1994. *Molecular Markers, Natural History and Evolution*. Chapman and Hall, New York.
- Barker S. C. 1991. Evolution of host-parasite associations among species of lice and rock-wallabies: Coevolution? (J. F. A. Spreti Prize Lecture, August 1990). *International Journal of Parasitology* 21: 497-501.
- Barker S. C. 1994. Phylogeny and classification, origins, and evolution of host associations of lice. *International Journal for Parasitology* 24: 1285-1291.
- Bee C. A. & Close R. L. 1993. Mitochondrial DNA analysis of introgression between adjacent taxa of rock-wallabies, *Petrogale* species (Marsupialia: Macropodidae). *Genetical Research* 61: 21-37.
- Brooks D. R. & McLennan D. A. 1991. *Phylogeny, Ecology, and Behavior*. University of Chicago Press, Chicago.
- Brooks D. R. & McLennan D. A. 1993. *Parascript: Parasites and the Language of Evolution*. Smithsonian Institution Press, Washington.
- Choe J. C. & Kim K. C. 1988. Microhabitat preference and coexistence of ectoparasitic arthropods on Alaskan seabirds. *Canadian Journal of Zoology* 66: 987-997.
- Clay T. 1949. Some problems in the evolution of a group of ectoparasites. *Evolution* 3: 279-299.
- Clayton D. H. 1990. Host specificity of *Strigiphilus* owl lice (Ischnocera: Philopteridae), with the description of new species and host associations. *Journal of Medical Entomology* 27: 257-265.
- Furness R. W. & Palma R. L. 1992. Phthiraptera of petrels and skuas from Gough Island, South Atlantic Ocean. *Seabird* 14: 33-42.

- Hafner M. S. & Nadler S. A. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* **332**: 258-259.
- Hafner M. S., Sudman P. D., Villablanca F. X., Spradling T. A., Demastes J. W. & Nadler S. A. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science* **265**: 1087-1090.
- Hafner M. S. & Page R. D. M. 1995. Molecular phylogenies and host-parasite cospeciation: gophers and lice as a model system. *Philosophical Transactions of the Royal Society, London, Series B*, **349**: 77-83.
- Hellenthal R. A. & Price R. D. 1991. Biosystematics of the chewing lice of pocket gophers. *Annual Review of Entomology* **36**: 185-203.
- Hillgarth N. 1995. Ectoparasite transfer during mating in Ring-necked Pheasants (*Phasianus colchicus*). *Journal of Avian Biology*, in press.
- Hoberg E., Brooks D. R. & Siegal-Causey D. Host-parasite cospeciation: history, principles and prospects. In: *Host-parasite Evolution: General Principles and Avian Models*. (Edited by Clayton D. H. & Moore J.). Oxford University Press, Oxford, in press.
- Hopkins G. H. E. 1948. Some factors which have modified the phylogenetic relationship between parasite and host in the Mallophaga. *Proceedings of the Linnean Society, London* **161**: 37-39.
- Kim K. C. 1985. Parasitism and coevolution. In: *Coevolution of Parasitic Arthropods and Mammals*, (Edited by Kim K. C.), pp. 661-682. John Wiley & Sons, New York.
- Kim K. C. 1988. Evolutionary parallelism in Anoplura and eutherian mammals. In: *Biosystematics of Haematophagous Insects* (Systematics Association Special Volume 37), (Edited by Service M. W.), pp. 91-114. Clarendon Press, Oxford.
- Lee P. L. M. & Clayton D. H. 1995. Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology* **20**: 43-50.
- Lyal C. H. C. 1987. Co-evolution of trichodectid lice (Insecta: Phthiraptera) and their mammalian hosts. *Journal of Natural History* **21**: 1-28.
- Marshall A. G. 1981. *The Ecology of Ectoparasitic Insects*. Academic Press, London.
- Page R. D. M. 1990. Temporal congruence and cladistic analysis of biogeography and cospeciation. *Systematic Zoology* **39**: 205-226.
- Page R. D. M. 1993a. Genes, organisms, and area: the problem of multiple lineages. *Systematic Biology* **42**: 77-84.
- Page R. D. M. 1993b. Parasites, phylogeny and cospeciation. *International Journal for Parasitology* **23**: 499-506.
- Page R. D. M. 1995. Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics* **10**: 155-173.
- Page R. D. M., Price R. D. P. & Hellenthal R. A. 1995. Phylogeny of Geomydoecus and Thomomydoecus pocket gopher lice (Phthiraptera: Trichodectidae) inferred from cladistic analysis of adult and first instar morphology. *Systematic Entomology*, **20**: 129-143.
- Paterson A. M. 1994. Coevolution of seabirds and feather lice: a phylogenetic analysis of cospeciation using behavioural, molecular and morphological characters. Ph.D. thesis, University of Otago.
- Paterson A. M., Gray R. D. & Wallis G. P. 1993. Parasites and penguins: does louse presence reflect seal phylogeny? *International Journal for Parasitology* **23**: 515-526.
- Paterson A. M., Gray R. D. & Wallis G. P. 1995. Of lice and men: the return of the 'Comparative parasitology' debate. *Parasitology Today* **11**: 158-160.
- Paterson A. M. & Gray R. D. Host-parasite cospeciation: host-switching and missing the boat. In: *Host-parasite evolution: General Principles and Avian Models*, (Edited by Clayton D. H. & Moore J.) Oxford University Press, Oxford, in press.
- Patterson C., Williams D. M. & Humphries C. J. P. Congruence between molecular and morphological phylogenies. *Annual Review of Ecology and Systematics* **24**: 153-188.
- Penny D., Foulds L. R. & Hendy M. D. 1982. Testing the theory of evolution by comparing the phylogenetic trees constructed from five different protein sequences. *Nature* **297**: 197-200.
- Petren K., Bolger D. T. & Case T. J. 1993. Mechanism of the competitive success of an invading sexual gecko over an asexual native. *Science* **259**: 354-358.
- Price R. D. & Emerson K. C. 1971. A revision of the genus *Geomydoecus* (Mallophaga: Trichodectidae) of the New World pocket gophers (Rodentia: Geomyidae). *Journal of Medical Entomology* **8**: 228-257.
- Price R. D. & Clayton D. H. 1983. A review of the genus *Psittacornimus* (Mallophaga: Philopteridae) from South Pacific parrots. *International Journal of Entomology* **5**: 56-70.
- Rauscher M. D. 1992. Natural selection and the evolution of plant-insect interactions. In: *Insect Chemical Ecology: An Evolutionary Approach*, (Edited by Roitberg B. D. & Isman M. B.). Chapman & Hall, New York.
- Rothschild M. & Clay T. 1952. *Fleas, Flukes and Cuckoo: A Study of Bird Parasites*. Collins, London.
- Rózsa L. 1993. Speciation patterns of ectoparasites and "straggling" lice. *International Journal of Parasitology* **23**: 859-864.
- Strong D. H., Lawton J. H. & Southwood T. R. E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Harvard University Press, Cambridge.
- Thompson J. N. 1994. *The Coevolutionary Process*. University of Chicago Press, Chicago.



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POINTS IN QUESTION

Lice, Cospeciation and Parasitism

The debate about the evolution of lice (Barker, 1994; Page Paterson & Clayton, 1995) centres around 2 questions: what proportion of extant and ancestral lice speciated with their hosts (cospeciated)? and, is the phylogeny of lice a reliable indicator of the phylogeny of their hosts? There are 2 main schools of thought on the ways associations among lice and their hosts have evolved. The first school proposes that cospeciation is typical for extant and ancestral lice and that host-switching is uncommon. They argue also that host-switching can be identified by empirical tests (e.g., Page, 1990, 1994) and that the phylogeny of lice then may be used to infer the phylogeny of their hosts, hence the name "comparative parasitologists" (Paterson, Gray & Wallis, 1995). This application of louse phylogenies to the systematics of their hosts has been advocated and attempted for over 150 years, for example Jardine (1841, cited in Hopkins, 1951), and papers cited by Paterson, Gray & Wallis (1993).

People in the second school, like myself, Lyal (1986) and Rózsa (1993) consider that host-switching has been more and cospeciation less common than is generally accepted. We deduce, therefore, that host-switching has had a profound effect on louse-host associations since lice evolved from free-living insects, possibly in the Cretaceous (Lyal, 1985). It is often difficult, however, to distinguish with confidence between host-switching and other events that lead to incongruence of parasite and host phylogenies, for example where there are multiple evolutionary lineages of parasites and some species of parasites become extinct, despite the existence of elegant tests to probe these events (Page, 1994). Thus, the inference of host phylogeny from the phylogenies of their parasites is likely to be unreliable; therefore, it is better to apply molecular phylogenetic approaches and cladistic analyses of morphological and anatomical features directly to infer the phylogeny of animals. Nevertheless, techniques which estimate and apportion cospeciation, host-switching and parasite extinction, and that identify multiple lineages of parasites (e.g., Page,

1994) will continue to be used to untangle the often (invariably in my experience) complicated histories of associations of parasites and hosts.

I concluded that cospeciation is not the prevailing pattern for lice and their hosts and that the axiom that host and lice coevolve should be abandoned (Barker, 1994). The key to understanding this conclusion is: what is and what is not a prevailing pattern? There are 2 parts to the answer. First, the maximum cospeciation reported in the studies of Lyal (1987), Hafner & Nadler (1988) and Barker (1991) is about 76% [157 of 198 (79%) speciation events reported in Lyal (1987), 6 of 9 (66%) events in Hafner & Nadler (1988) and 3 of 10 (30%) in Barker (1991); the 3 possible but unlikely cospeciation events in Barker (1991) are the louse *Heterodoxus octoseriatus* with the rock-wallaby *Petrogale p. herberti* (now *P. herberti*, Eldridge & Close, 1992), *H. maynesi* with *P. inornata*, and *H. orarius* with *P. godmani*]. Second, the estimates of cospeciation are overestimates, at least for the study of Lyal (1987) as identified by himself, because of the myth of stragglers and pseudo-cospeciation. The myth of stragglers is well established (e.g., Lyal, 1986); early taxonomists often dismissed as "stragglers" lice from the "wrong" host because collectors frequently placed different species of birds and mammals in a single bag and because of an overzealous adherence to Fahrenholz's rule—each species of host was thought to be infested by only 1 species from each evolutionary group (e.g., each genus) of lice. Now we are well aware that lice do move from 1 species of host to another given the chance. Pseudo-cospeciation (Hafner & Nadler, 1988) is where a species of louse switches to a closely related species of host such as a sister-species. Host-switching of this kind is very difficult to detect and can easily lead to errors when the phylogeny of hosts is inferred from that of their lice.

Some studies on relationships between lice and hosts were not used in my review (Barker, 1994). Kim (1988) on sucking lice (Anoplura) presents problems which include: (i) lack of argument for the

polarity of characters states—the author simply stated that “polarity was determined by examination of the pattern of character development and by comparison to an out-group” the Ischnocera (p. 95), which incidentally may not have been the best out-group since the Rhyncophthirina is probably the sister-group of the sucking lice (Lyal, 1985); (ii) the phylogenies were not supported by tests for robustness, like bootstrap resampling; and (iii) no clear directions were given to produce the phylogenetic trees or complete “re-analyses”. In any case, Kim (1988) does not contain strong evidence for cospeciation of extant and ancestral sucking lice; he stated that “no direct cladistic concordance was observed between the family cladogram of Anoplura and their mammalian host cladogram” (p. 105). Kim (1988) did claim, however, that when “further resolutions were made for specific family clades, a close phylogenetic parallelism was evident between Anoplura taxa and their mammalian hosts”.

Paterson *et al.* (1993) on lice from seabirds, neither described the 23 characters used to infer their phylogeny of the lice, nor identified the different characters states ascribed to each louse taxon. They state simply that the louse phylogeny “was generated from morphological and life history characters, and represents preliminary results from an ongoing study” and that “characters were drawn from information contained in Clay & Moreby (1967) and Marshall (1981)” (p. 517). Paterson *et al.* (1993) describe the phylogenetic trees they generated from the lice as “non-robust” (p. 523) and stated that they lacked “confidence in the parasite phylogeny” (p. 524) presumably because all but 1 of the bootstrap values was below 90%. The methods used by Paterson *et al.* (1993) are interesting, however, and the phylogenies of the hosts generated using the presence and absence of species and genera of lice as characters were more like the host tree than would be expected by chance. This indicates some cospeciation, provided the taxonomists responsible for the descriptions of the lice did not either consciously or unconsciously use the identity and phylogeny of hosts when placing species of lice in genera. The papers by Paterson *et al.* (1995) and Paterson & Gray (in press) were not available to me in 1994.

Page *et al.* (1995) list 3 established scenarios which can result in host and parasite phylogenies that are incongruent and yet cospeciation may still have occurred. It is one thing, however, to postulate multiple evolutionary lineages coupled with extinction of some species of parasites, and parasites failing to colonize descendants as the host speciates (“missing the boat”, Paterson & Gray, in press), and failure of people to collect species of parasites, and quite

another thing to demonstrate that these events took place! Moreover, the outcome of some of these postulates is like the outcome of host-switching: the intrinsic inability to predict accurately the phylogeny of hosts using their parasites as characters. It is simpler and more accurate to infer the phylogeny of the hosts directly.

Three of 11 species of lice, *H. octoseriatus* on the rock-wallaby *P. herberti*, *H. maynesi* on *P. inornatus* and *H. orarius* on *P. godmani*, infest a single species of rock-wallaby predominantly and are found on adjacent populations of other species of rock wallabies (see Figure 3 in Barker, 1991; Barker & Close, 1990). It is far more complicated, however, for the other species of lice. At the extreme of this complexity there are 6 species found in different parts of the geographic range of *P. (a) assimilis* (no *P. assimilis*, Eldridge & Close, 1992); here it is unclear which species was or were associated originally with *P. assimilis*. My favoured explanation for the evolution of host associations of the 11 species of the *H. octoseriatus* group of lice and rock-wallabies involves at least 9 host-switches where, in each case the colonizing louse apparently excluded the original louse (Barker, Briscoe & Close, 1992).

Concordance between mitochondrial morphs of rock-wallabies and the presence of species of lice is limited almost entirely to 2 species of lice and the hosts, the louse *H. octoseriatus* and rock-wallaby *P. herberti*, and to *H. maynesi* and *P. inornatus*. Nevertheless, I agree with Page *et al.* (1995) that lineages of the *H. octoseriatus* group reflect the complicated history of their hosts. My view, however, is that the louse-host associations show a zoogeographic rather than a phylogenetic history of their hosts and that contact between the different species of hosts is identified by lice that have switched hosts.

Where 1 or more species of lice switch hosts this indicates to me that other extant and extinct species in that species group may have done the same. Host-switching by ancestral species will contribute incongruence to the phylogenies of hosts and parasites because the descendants of the louse that switched hosts are thereafter on the “wrong” hosts. Consequently, errors may occur when the phylogeny of these hosts is inferred from the phylogeny of their lice. Comparative parasitologists, on the other hand, do not seem as troubled by host-switching and assume, apparently, that the switches are isolated incidents and therefore that the remaining lice and host they infest have cospeciated (e.g., Page, 1990).

The frequency of host-switching in nature relates to the availability of suitable, alternative hosts and where lice do not encounter such hosts then no switch can occur. Where species of hosts are

allopatric (like most of the pocket gophers) opportunities for host-switching do not exist normally. Cospeciation between species of host and lice that are allopatric, therefore, is not remarkable; it is not a special feature of parasitism.

Competitive exclusion may preclude many host switches and thus it is an important factor in studies of the evolution of parasite-host associations (Rózsa, 1993). A successful switch of a species of louse to a new host could be prevented by competition from one already on that host. The question is whether species of lice that do not live together can coexist should a species move onto a host already infested by another species of louse. Choe & Kim (1988) demonstrated that coexisting lice do not exclude one another but this is not evidence that other species of lice, like sister-species that may have similar niches, can coexist with existing lice should they switch to the host. I agree with Page *et al.* (1995) that rigorous tests of competition involve experiments; however, it is only recently that the idea that competition among species of lice may promote cospeciation has been considered worthy of attention.

I support the 6-point proposal of Page *et al.* (1995) for tests of cospeciation but make 2 comments. First, accurate alpha-level taxonomy of host and parasites is indeed vital if the evolution of lice and their hosts is to be interpreted accurately. Multivariate analyses of morphological features may help (e.g., Hellenenthal & Price, 1980) but genetics has proven instructive also (e.g., Hafner & Nadler, 1988; Barker *et al.*, 1991). There are cases where analyses of morphology do not allow closely related species to be distinguished, whereas genetic studies should always allow different species to be distinguished if sufficient genes are studied. Second, the elegant methods developed by Page can overestimate cospeciation where host-switching has occurred among sister-species of hosts (pseudo-cospeciation). This is more likely than switching between more distantly related hosts because sister-species of hosts can have geographic distributions that are adjacent to one another and sister-species of hosts may be similar biologically for example, have similar fur, feathers and skin.

Finally, I emphasize that lice should be collected comprehensively from their hosts. Most collections of lice are incomplete and their hosts have not been examined from large parts (often most) of their geographic ranges. Comprehensive collections allow real comparisons and robust conclusions about the associations and evolution of lice and their hosts. Studies on comprehensive collections should lead to fewer *ad hoc* arguments for species which have not been discovered (e.g., Page, 1990).

Is cospeciation typical for extant and ancestral lice? The people that study lice will continue to evolve the answer.

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REFERENCES

- Barker S. C. & Close R. L. 1990. Zoogeography and host associations of the *Heterodoxus octoseriatus* group and *H. ampullatus* (Phthiraptera: Boopidae) from rock-wallabies (Marsupialia: Petrogale). *International Journal for Parasitology* 20: 1081–1087.
- Barker S. C. 1991. Evolution of host-parasite associations among species of lice and rock-wallabies: coevolution? (J. F. A. Sprent Prize Lecture, August 1990). *International Journal for Parasitology* 21: 497–501.
- Barker S. C., Briscoe D. A., Close R. L., Dallas P. 1991. Genetic variation in the *Heterodoxus octoseriatus* group (Phthiraptera): a test of Price's model of parasite evolution. *International Journal for Parasitology* 21: 555–563.
- Barker S. C., Briscoe D. A., Close R. L. 1992. Phylogeny inferred from allozymes in the *Heterodoxus octoseriatus* group of species (Phthiraptera: Boopidae). *Australian Journal of Zoology* 40: 411–422.
- Barker S. C. 1994. Phylogeny and classification, origins, and evolution of host-louse associations of lice. *International Journal for Parasitology* 24: 1285–1291.
- Choe L. C. & Kim 1988. Microhabitat preference and coexistence of ectoparasitic arthropods on Alaskan seabirds. *Canadian Journal of Zoology* 66: 987–997.
- Clay T. & Moreby C. 1967. Mallophaga (biting lice) and Anoplura (sucking lice). Part II. Keys and locality lists of Mallophaga and Anoplura. In: *Entomology of Antarctica*. (Edited by Gressitt J. L.), Vol. 10 Antarctic Research Series, pp. 157–196. American Geophysical Union, Washington, DC.
- Eldridge M. D. B. & Close R. L. 1992. Taxonomy of rock wallabies, *Petrogale* Marsupialia: Macropodidae). I. A revision of the eastern *Petrogale* with the description of three new species. *Australian Journal of Zoology* 40: 605–625.
- Hafner M. S. & Nadler S. A. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* 332: 258–259.
- Hellenenthal R. A. & Price R. D. 1980. A review of the *Geomydoecus subcalifornicus* complex (Mallophaga: Trichodectidae) from *Thomomys* pocket gophers (Rodentia: Geomyidae), with a discussion of quantitative techniques and automated taxonomic procedures. *Annals of the Entomological Society of America* 73: 495–503.
- Hopkins G. H. E. 1951. Stray notes on Mallophaga, XI. *Annals and Magazine of Natural History* 4: 371–377.
- Kim K. C. 1988. Evolutionary parallelism in Anoplura and eutherian mammals. In: *Biosystematics of Haematophagous Insects* (Systematics Association special volume 37),

- (Edited by Service M. W.), pp. 91–114. Clarendon Press, Oxford.
- Lyal C. H. C. 1985. Phylogeny and classification of the Psocodea, with particular reference to the lice (Psocoda: Phthiraptera). *Systematic Entomology* **10**: 145–165.
- Lyal C. H. C. 1986. Coevolutionary relationships of lice and their hosts: a test of Fahrenholz's Rule. In: *Coevolution and Systematics*, (Edited by Stone A. R.), pp. 77–121.
- Lyal C. H. C. 1987. Co-evolution of trichodectid lice (Insecta: Phthiraptera) and their mammalian hosts. *Journal of Natural History* **21**: 1–28.
- Marshall A. G. 1981. *The Ecology of Ectoparasitic Insects*. Academic Press, London.
- Page D. M. 1990. Temporal congruence and cladistic analysis of biogeography and cosepeciation. *Systematic Zoology* **39**: 205–226.
- Page D. M. 1994. Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics* **10**: 155–173.
- Page D. M., Paterson A. M. & Clayton D. H. 1995. Lice and speciation: a response to Barker. *International Journal for Parasitology*.
- Paterson A. M., Gray R. D. & Wallis G. P. 1993. Parasites petrels and penguins: does louse presence reflect seabird phylogeny? *International Journal for Parasitology* **23**: 515–526.
- Paterson A. M., Gray R. D. & Wallis G. P. 1995. Of lice and men: the return of the "comparative parasitology" debate. *Parasitology Today* **11**: 158–160.
- Paterson A. M. & Gray R. D. in press. Host-parasite cosepeciation. II. In: *Host-parasite Evolution: General Principles and Avian Models*, (Edited by Clayton D. H. & Moore J.). Oxford University Press, Oxford.
- Rózsa, L. 1993. Speciation patterns of ectoparasites and "straggling" lice. *International Journal for Parasitology* **23**: 859–864.



POINTS IN QUESTION

More "Misconceptions" About the Measurement of Aggregation

I commented on the paper by R. Poulin on aggregated parasite distributions (*International Journal for Parasitology* 1993, **23**: 937–944) in *International Journal for Parasitology* 1994, **24**: 919–920. Dr Poulin kindly took the effort to reply (*International Journal for Parasitology* 1995, **25**: 863–864). However, it seems to me that most points brought forward in my comment were not really resolved in his reply or were regarded as not important. The 2 most outstanding points in my view will be addressed here in more detail than in my earlier comments.

First, I argued that the index of discrepancy (D) as proposed by Poulin does not present a new look at parasite aggregation. The definition of aggregation has not changed, has it? I argued further that expressing degree of aggregation as some proportion of the total parasite population harboured by some proportion of the host population is essentially the same as the index D . Poulin states that such a measure will correlate with the index D , but only within a certain range of aggregations. That indeed is true to some extent, but does not change the fact that both measures are essentially the same. Let me illustrate this using Fig. 2 of Poulin's original paper, here redrawn in Fig. 1 with 3 different artificial host-parasite distributions. Before going on it is important to state 2 conditions applying to Fig. 1: (1) for each value of D there exists only one unique line between the points [0, 0] and [1, 1]; and (2) the lines for all possible values for D have only 2 points in common, namely [0, 0] and [1, 1], so that between these points no line intersects with another line which makes each point on a line as unique as the line itself. I think Poulin will agree, since he stated in his original paper:

"The more concave the curve, the greater the degree of aggregation". These conditions result in that each point on a line (except [0, 0] and [1, 1]) uniquely belongs to the value for D calculated from the areas defined by that same line. Thus, expressing degree of aggregation as some proportion of the total parasite population harboured by some proportion of the host population is essentially the same as expressing it by the index D . The problem Poulin referred to arises when prevalence is very low. If, for example, the

selected fixed proportion of hosts is set at 0.8, any parasite distribution for which prevalence is 20% or less cannot be discriminated any longer by the proportion of parasites harboured by 80% of the hosts since that proportion will be zero (see Fig. 1). However, this problem can be simply circumvented by choosing another proportion of hosts at which to look at. Alternatively, we can choose a fixed proportion of the parasite population and find out what proportion of the hosts belongs to it (in Fig. 1 set at 0.2 on the vertical axis). Another alternative is to draw the diagonal from [0, 1] to [1, 0] and look at the intersects (in Fig. 1 identified by the closed circles). Admitted, D is more elegant since it expresses degree of aggregation in a single value, whereas expressing it in proportions of hosts and parasites requires 2 values. None the less, both measures uniquely belong to one and the same line and therefore can be used interchangeably, provided of course that the above stated conditions do apply and that they are not fruits of my vivid imagination.

A related point to the above is Poulin's statement that the index D is a more adequate measure of aggregation than other measures, among them the coefficient k in the negative binomial distribution. He found a negative correlation (r) of -0.744 between k and D , and concluded that "they probably quantify related things". This leaves room for assuming that D partly measures something else than k . I wonder whether that's the case. Knowing that the range of possible values for D has an upper boundary (unity) as opposed to the range of possible values for k , it might be suspected that the relationship between k and D is nonlinear. If you plot D against k , it becomes clear that the relationship is indeed nonlinear. So, the correlation Poulin presented is misleadingly low. If you take a simple natural logarithmic transformation for k , the correlation between k and D already becomes -0.897 . The remaining unexplained variability between the 2 parameters may well be accounted for by the fact that D is calculated from the observed frequency distribution, whereas k is a coefficient from a fitted negative binomial distribution. I suspect that "the related things k and D