

SPECIATION PATTERNS OF ECTOPARASITES AND “STRAGGLING” LICE

LAJOS RÓZSA

Department of Parasitology and Zoology, University of Veterinary Science, H-1400 Budapest, P.O. Box 2, Hungary

(Received 3 February 1993; accepted 25 April 1993)

Abstract—RÓZSA L. 1993. Speciation patterns of ectoparasites and “stragglings” lice. *International Journal for Parasitology* 23: 859–864. Two competing views have been expressed to explain ectoparasite speciation patterns, one emphasizing co-speciation and one emphasizing host-switching. Though recent authors preferred a combination of these views, the available phylogenetic trees cannot be interpreted without revisiting island biogeography theory. Parasite extinction due to a temporal decline in host population size seems to be a prerequisite of subsequent speciation by host-switch. The need for a re-evaluation of “stragglers” (ectoparasites found on non-specific hosts) is emphasized.

INDEX KEY WORDS: Fahrenholz’s rule; co-speciation; resource tracking; island biogeography; extinction; rare species; stragglers.

INTRODUCTION

IN THE PAST decades there has been intensive research on the ecology and coevolution of helminths and their vertebrate hosts. On the other hand, ectoparasites seem to be neglected in this regard. The ectoparasitic way of life differs from that of the helminths in some major points. Ectoparasite assemblages tend to be less species-rich. Helminth species live in an aquatic habitat and therefore are potentially subject to attack by the host immune system and allelopathic agents excreted by other helminths. On the contrary, ectoparasites live in a rather dry environment where mechanical host defences, like grooming, preening and bathing seem to exert a selective pressure upon the parasites.

Some ideas, like Fahrenholz’s rule and “hosts as islands”, mentioned in this short paper refer to all kinds of parasites. Others, like the resource tracking hypothesis and the case of stragglers refer to ectoparasites exclusively. Consequently, some cases of helminths will be mentioned as well, though my argument aims at ectoparasite speciation patterns.

THE TWO HYPOTHESES

Permanent ectoparasites tend to be highly host-specific (Marshall, 1981). To take lice (Phthiraptera) as an example, infestation is supposed to occur only through body-to-body contact. Regular occurrence of such contacts can be imagined only between individuals of the same species, such as the parent–

offspring and sexual contacts (a clear exception is the predator–prey contact). This is the basis of Fahrenholz’s rule which states: in groups of permanent parasites the phylogenetic relationship of the parasites usually corresponds directly with that of their hosts (Fahrenholz, 1913). The term host–parasite co-speciation has become the common synonym for this rule.

The classic text-book example for Fahrenholz’s rule is the case of flamingoes, which were related to the order of storks (Ciconiiformes) by some ornithologists and to the order of geese (Anseriformes) by others. As three of the four louse genera of flamingoes (*Trinoton*, *Anatoecus* and *Anaticola*) are specialized strictly to anseriform birds and flamingoes, while the fourth (*Colpocephalum*) genus is regarded as a generalist, this parasite fauna was argued to be strong evidence for the close phylogenetic relationship between geese and flamingoes (Eichler, 1941; Hopkins, 1942). While Fahrenholz’s rule served as evidence for this relationship, this relationship served as evidence for the rule. Many authors have emphasized that knowledge of parasite phylogeny can be useful in elucidating the phylogenetic relationships of their hosts (see, e.g. Uchikawa, 1987, as a case study). In the meantime, considerable information has emerged to contradict this assumption.

A numerical taxonomic study of quill mites of the family Syringophilidae indicates a parasite phylogenetic pattern not congruent at all with host phylogeny (Johnston & Kethley, 1973).

Since new biochemical methods have emerged, our view about avian phylogeny has strikingly changed. The DNA-DNA hybridization studies of Sibley, Ahlquist & Monroe (1988) on the classification of birds suggests that the text-book story of flamingoes and lice is strikingly false. Geese and flamingoes are distant taxa and there is a close relationship between flamingoes and storks.

In a phylogenetic study based on protein electrophoretic data of eight rodent species of the family Geomyidae and their 10 species of the ischnoceran family Trichodectidae, four out of nine branching points of the parasite cladogram were not congruent or not contemporaneous with the branching points on the host cladogram (Hafner & Nadler, 1988). Though the authors regard this result as "the strongest evidence yet for co-speciation in a host-parasite assemblage", one can doubt the general value of this evidence. Geomyid species are specialized to an extreme way of life. These are fossorial and solitary rodents, with highly allopatric geographical distribution and therefore exceptionally ideal for undisturbed host-parasite co-speciation. In spite of that, only five out of the nine parasite speciation events were congruent with host speciation.

A cladistic study involving all described species (351) and subspecies of trichodectid lice of mammals was based on the analyses of 187 characters (Lyal, 1985). Interpreting this cladogram as a phylogeny and comparing it to host phylogenies, the author concluded that while "the predominant pattern of louse relationships is broadly congruent with host relationships (...), a substantial proportion (20.7%) of speciation events of the lice could only be explained by invoking secondary infestation of distantly related hosts by the lice" (Lyal, 1987). Secondary infestations among closely related host species – denied by Fahrenholz's rule also – could not be documented by this taxonomic method.

The phylogenetic tree of 11 species of amblyceran lice, and that of their eight marsupial host species and subspecies, were compared by Barker (1991). The author concluded, that "Lice of the *Heterodoxus octoseriatus* group have not coevolved absolutely or even closely with their hosts. Clearly, host-switching has been an important process in the evolution of associations between species of lice and taxa of rock-wallabies ...".

Resource tracking is an alternative hypothesis to interpret ectoparasite speciation patterns. It is argued that hosts exert strong selective pressures on their ectoparasites through preening and grooming activities, therefore ectoparasites are selected to conform for any given topographic region of the host as refuges to avoid host defences. Consequently, "successful

host-transfers through evolutionary time are most likely to occur between hosts that share similar topographic features" (Kethley & Johnston, 1975). There are many host switch events to illustrate the validity of this view. Consider the case of flamingoes, one can suppose that geese and flamingoes are not related phylogenetically, however, the structure of the bill and therefore the preening mechanism is similar in these taxa.

After an intensive taxonomic study of pocket gophers and their lice—an ideal taxa to fit Fahrenholz's rule—Timm (1983) has concluded that "Fahrenholz's rule and resource tracking are not conflicting hypotheses. Rather they apparently represent the ends of a continuum based on the dispersal opportunities and niches available to parasites". He argued that avian ectoparasites have had more opportunities to disperse to non-specific hosts by means of phoresy on hippoboscids flies, and "have more niches" in the highly diverse plumage than mammalian ectoparasites with less access to phoresy and living in a topographically less differentiated pelage. Therefore, according to him, avian ectoparasite taxa tend to fit better to resource tracking, while mammalian ectoparasite taxa—and especially the exceptional group of pocket gophers—tend to fit better to Fahrenholz's rule.

However, one should bear in mind that in view of the data mentioned above (Lyal, 1987; Hafner & Nadler, 1988), the ischnoceran fauna of mammals, and even that of the pocket gophers are far from being close to the end of this continuum. Furthermore, the case of marsupials and their amblyceran lice represents just the opposite end of it (Barker, 1991).

In spite of all this, a combination of the two hypotheses still seems to be satisfactory to interpret the phylogenetic patterns of parasites. However, two questions remain unanswered in this context. Why cannot negative interactions among parasite species prohibit host-switch colonisation? What is the reason for parasite host-switches between host species that are neither phylogenetically, nor topographically, the closest to each other?

GEOGRAPHICAL IMPACT ON HOST SPECIFICITY

The grebe species *Podiceps auritus* and *P. caspicus* are each divided into a pair of Palaearctic and Nearctic populations or subspecies. These birds harbour four species of the ischnoceran genus *Aquanirmus*. Conspecific populations of these grebes living on different continents are closer to each other than to the populations of the other species living in the same area. This is true for the phylogenetic distances and for the structural similarities of their plumage as well. Therefore, both Fahrenholz's rule and the resource

tracking hypothesis predict the same cladogram for the four *Aquanirmus* species, namely two pairs of sibling species in which each pair is formed of species parasitizing conspecific grebe populations on different continents. In fact, the four species clearly belong to two "species groups" (subgenera?) contrary to the prediction: the closely related *A. colymbinus* and *A. podicipis* utilize the Palearctic, whereas the closely related *A. bucomfishi* and *A. americanus* utilize the Nearctic populations and subspecies of *P. auritus* and *P. caspicus*, respectively (Edwards, 1965).

The two species of gannets, *Sula sula* and *S. leucogaster*, are circumtropical sea-birds parasitized by three species of the ischnoceran genus *Pectinopygus*. All three louse species occur on both bird species. The geographical distribution of the two birds is sympatric, while that of their lice is allopatric. Taking *Pectinopygus garbei* as an example, it is found to be specific to both host species in the Atlantic area, where the other two louse species do not occur (Clay, 1964). The host specificity of some parasite species clearly has a geographic determination. This pattern is also contradicted by Fahrenholz's rule and resource tracking hypothesis.

A study on the host specificity of the *Strigiphilus curtisani* species group (Ischnocera: Philopteridae) showed that all species found on two or more host species occur on sympatric and syntopic hosts. On the contrary, there were no louse species shared by allopatric hosts, even if these were closely related (Clayton, 1990).

The available data is not sufficient to consider how general is the geographical modification of host specificity. It should be noted, however, that it also occurs on the level of higher taxa. Amblycera, a suborder of lice (Phthiraptera), parasitizes birds exclusively, in the Northern Hemisphere and Africa. However, there are amblyceran families (Boopidae, Trimenoponidae and Gyropidae) that parasitize mammals (marsupials and rodents) in Australia and South America (Clay, 1970).

These examples illustrate that host-switches may play a role in the determination of parasite speciation patterns. Parasite transfers among host species are influenced by the geographical availability of potentially switching species, so geographically determined host specificity may occur. Host-switching was known by early authors discussing parasite speciation, who called it "secondary infestation" and regarded it as a rare, random accident in parasite phylogeny. Authors stressing the validity of Fahrenholz's rule suggested that such accidental host-switches tend to be prohibited by competition among parasite species (Clay, 1949). Site-segregation is a clear tendency in coexisting parasite species, i.e. coexisting species tend

to inhabit different anatomical sites on the host. This is the basis to suppose that competition or at least some kind of negative interaction exist among ectoparasite species.

On the other hand, authors of the resource tracking hypothesis considered all secondary infestations as cases supporting the validity of their argument (Kethley & Johnston, 1975), but did not give an explanation why negative interactions did not prevent them.

Here I argue, that the only way to interpret the high host-switch rates mentioned above is to presume that spontaneous parasite extinction is common in nature, resulting in a possibility for other parasite species to colonise new host species and thus to establish new, permanent phylogenetic lineages.

PARASITE EXTINCTIONS

Island biogeography theory predicts a positive correlation between area size and species richness of islands (MacArthur & Wilson, 1967). This can be applied to caves, lakes, plantations etc., which may act as habitat islands.

The idea that animal host species may act as habitat islands for parasites was tested by Dritschilo, Cornell, Nafus & O'Connor (1975). They have shown that the number of ectoparasitic and phoretic mite species reported from North American cricetid rodents and the area size of these host give a species-area curve which shows a good fit with the equation found for island species.

The social groups of primates can act as "islands" for parasitic protozoa. The number of intestinal protozoan species in mangabeys (*Cercocebus albigena*) is a function of group size (Freeland, 1979). While studying the species richness of parasite burdens of brown trout (*Salmo trutta*) in British lakes Kennedy (1978) noted a significant correlation between the lake size and the number of parasite species.

The area size of the host species accounts for 68% of the variation in the number of helminth species of the British freshwater fish species. Differences in feeding habits and variation in host body size has a relatively little impact on the species-richness of the helminth assemblage (Price & Clancy, 1983).

The lack of similar studies on the correlation between the number of louse species and the area size of their hosts is probably the result of (1) the relatively low number of louse species per host species making it difficult to obtain statistically significant data (especially for mammalian lice), and (2) the high inter-specific variability of topographical complexity of the structure of host body surface (especially for avian lice).

However, there are some cases of bird populations which have undergone a temporal decline regarding

their population size and consequently lost some of their parasite species. The house sparrow (*Passer domesticus*) is a native of the Palaearctic and it was introduced to the Nearctic at least 16 times between 1850 and 1881. Only 35 out of the 69 ectoparasite species reported from the European populations were found in America (Brown & Wilson, 1975).

The European starling (*Sturnus vulgaris*) is parasitized in Europe by four louse species, one of which (*Sturnioides sturni*) is absent from North America where the host was introduced in 1890 (Boyd, 1951). Comparing the helminth fauna of the American and European populations yields a more pronounced result. While the European population harbours 76 helminth species, only 17% of these were found in the American population. Interestingly, this reduced helminth fauna has doubled its species richness by host-switches acquiring 13 more species during a century (Freeland, 1983).

The louse genera *Cuculotogaster* and *Lipeurus* are represented by many species on the galliform birds of the Palaearctic, but absent from those of the Nearctic, presumably due to the extinction in the population of ancient galliforms crossing the Behring land bridge (Clay, 1972).

In the same way as host-switching, parasite extinction is not a direct deterministic outcome of host population decline, rather it is the result of a long stochastic process. *Lutridia exilis*, a trichodectid louse living on the otter (*Lutra lutra*), was regarded as a rare species, even before the severe decline of the otter population in Britain in the 1950's. It was collected in Britain only twice (1929, 1930) in an area uninhabited by otters later on. In spite of considerable efforts to detect the presence of this species in Britain (154 otters examined during 25 years) it was not collected again until once in 1987 (Jefferies, Hanson & Lyal, 1989). The British otter population is probably too scarce to maintain the louse population and these data seem to document the random extinction of *Lutridia exilis* in Britain. This louse is indeed an endangered species of the British fauna.

Contemporary changes in host taxon size and parasite species richness can be detected at higher taxonomical levels as well. In periods of adaptive radiation host taxa tend to harbour a parasite assemblage of increasing species richness. The marsupial fauna of Australia is monophyletic, derived from a single population of ancestors colonizing the continent from the Antarctica (Kirsch, 1977). They have radiated to occupy most of the niches currently occupied by eutherian mammals on other continents. An examination of the origin of their helminth fauna revealed that a few nematode and cestode groups may have been present in the original colonizing mar-

supials, while others have been acquired from the reptiles, birds and monotremes already living in Australia, or from the rodents and bats colonizing the continent much later from the north. This high host-switch rate is clearly contemporaneous with the adaptive radiation of the host taxon (Beveridge, 1986).

In spite of all these, Kuris, Blaustein & Alio (1980) doubt the validity of island biogeography theory in case of host species as islands. They claim that host density, range overlap and species diversity should not be ignored. The authors argue that the available host-parasite species lists of the major zoological collections are not appropriate for such studies, because these serve identification and therefore new species are added, but the disappearing species are never removed from such lists. The case of the grey whale (*Eschrichtius gibbosus*) and its four crustacean ectoparasite species is mentioned as an example. Though there was a major decline in the whale population size because of whaling, all the four parasite species survived (Grüner, 1975).

Contrary to the critical arguments of Kuris *et al.* (1980), I presume that island biogeography theory provides an appropriate tool to interpret the high rate of spontaneous parasite extinctions. Thus a temporal decline in host population size (area size, abundance or both) may lead to the extinction of some parasite species. If it is followed by an expansion in host population size, the vacant niches arising can allow successful host-switches and result in parasite speciations. The ability of any ectoparasite species to switch to a vacant niche depends on the topographical similarities between the two hosts and the geographical proximity of the parasite species.

RARE PARASITE STRAINS AND SPECIES

Presumably most host-switches end with an immediate extinction. There is little chance to survive on a non-specific host, parasitized by potential competitors. The chance of reproduction is also minimal, except the case of host-switching by a fertilized female. In spite of that, the pattern of ectoparasite phylogenies has been greatly modified by successful host-switches. This is a good reason to presume, that host-switches must have been quite common in the evolutionary past and be the same in the present. However, actually switching ectoparasites have been rarely if ever noted. The reason is a myth about the so-called "stragglers".

Early authors worked with ectoparasites collected from shot birds and mammals. The carcasses were put in the same bag for hours to take them home, so the lice shocked by the fall of temperature had an ability to move from one carcass to the other. To sign the false host-parasite relations resulted by this methodological fault these lice were labelled as "stragglers".

Today host individuals are isolated from each other and typically survive the study. However, "stragglers" are common in recent studies as well, with a rather modified meaning of the same term. It indicates ectoparasites found in unexpected host-parasite relations. I feel that this practice may well lead to the misinterpretation of data. One can think that the occurrence of a parasite on a particular host should be classified either as a normal or as an accidental one, on the basis of traditional preconceptions. However, "straggling" is not an artifact in recent cases, rather it is host-switching in process. An excellent case study on the louse *Halipeurus gravis gravis* is a good example, in which adults of both sexes were collected while "straggling" on an aspecific host individual (Zonfrillo, 1991). Actually switching ectoparasites or their scarce descendants are often observed, but typically misinterpreted.

The population size of parasites are supposed to be limited by interspecific factors like host defence against parasites, competition or mutualism between parasite species. In all these cases two species exert mutual selective pressure upon each other. It should be emphasized, that only large populations of parasites can be imagined to exert selective pressure upon their host species or on other parasite species. Ectoparasite lineages in the process of host-switching or extinction are scarce in their numbers therefore irrelevant in such interspecific relations. Consequently, parasites in the process of host-switching or extinction exhibit erratic changes in population size.

Host-switching is an inherently random event. If any parasites survive and breed at all, the progeny would establish a scarce strain exhibiting random changes in its size and random extinction after a random period of time. Only a very small amount of host-switches may result in speciation. However, phylogenetic trees document many cases that resulted well-established abundant parasite species.

Acknowledgements—I thank C. Arme, T. Kassai, M. Müller and L. Papp for their critical comments on an earlier version of the manuscript. This work was supported by the OTKA 1/3 1267 grant.

REFERENCES

- BARKER S. C. 1991. Evolution of host-parasite associations among species of lice and rock-wallabies: coevolution? *International Journal of Parasitology* **21**: 497–501.
- BEVERIDGE I. 1986. Coevolutionary relationships of the helminth parasites of Australian marsupials. In: *Coevolution and Systematics* (Edited by STONE A. R. & HAWKSWORTH D. L.), pp. 93–117. Clarendon Press, Oxford.
- BOYD E. M. 1951. A survey of parasitism of the starling *Sturnus vulgaris* in North America. *Journal of Parasitology* **37**: 56–84.
- BROWN N. S. & WILSON G. I. 1975. A comparison of the ectoparasites of the house sparrow (*Passer domesticus*) from North America and Europe. *American Midland Naturalist* **94**: 154–165.
- CLAY T. 1949. Some problems in the evolution of a group of ectoparasites. *Evolution* **3**: 279–299.
- CLAY T. 1964. Geographical distribution of the Mallophaga (Insecta). *Bulletin of the British Ornithological Club* **84**: 14–16.
- CLAY T. 1970. The Amblycera (Phthiraptera: Insecta). *Bulletin of the British Museum of Natural History (Entomology)* **25**: 73–98.
- CLAY T. 1972. Geographical distribution of the avian lice (Phthiraptera): a review. *Journal of the Bombay Natural History Society* **71**: 536–547.
- 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.
- DRITSCHLO W., CORNELL H., NAFUS D. & O'CONNOR B. 1975. Insular biogeography: Of mice and mites. *Science* **190**: 467–469.
- EDWARDS R. L. 1965. Revision of the Genus *Aquanirmus* (Mallophaga: Philopteridae) parasitic on Grebes (Podicipidae). *Canadian Entomologist* **97**: 920–935.
- EICHLER W. 1941. Wirtsspezifität und stammesgeschichtliche Gleichlaufigkeit bei Parasiten im allgemeinen und bei Mallophagen im besonderen. *Zoologischer Anzeiger* **132**: 254–262.
- FAHRENHOLZ H. 1913. Ectoparasiten und Abstammungslehre. *Zoologischer Anzeiger* **41**: 371–374.
- FREELAND W. J. 1979. Primate social groups as biological islands. *Ecology* **60**: 719–728.
- FREELAND W. J. 1983. Parasites and the coexistence of animal host species. *American Naturalist* **121**: 223–236.
- GRÜNER H. E. 1975. Amphipoda II. Caprellidea II. Family Cyamidae. *Crustaceorum Catalogus* **5**: 79–104.
- HAFNER M. S. & NADLER S. A. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature*, London **332**: 258–259.
- HOPKINS G. H. E. 1942. The Mallophaga as an aid to the classification of birds. *Ibis* **14**: 94–106.
- JEFFERIES D. J., HANSON H. M. & LYAL C. H. C. 1989. A further record of *Lutridia exilis* (Nitzsch) (Phthiraptera, Trichodectidae) in Britain, with notes on the presence and absence of lice on otters. *Entomologists' Monthly Magazine* **125**: 245–249.
- JOHNSTON D. E. & KETHLEY J. B. 1973. A numerical phenetic study of the quill mites of the family Syringophilidae (Acari). *Journal of Parasitology* **59**: 520–530.
- KENNEDY C. R. 1978. An analysis of the metazoan parasiticoenoses of brown trout *Salmo trutta* from British lakes. *Journal of Fish Biology* **13**: 255–263.
- KETHLEY J. B. & JOHNSTON D. E. 1975. Resource tracking in bird and mammal ectoparasites. *Miscellaneous Publications of the Entomological Society of America* **9**: 231–236.
- KIRSCH J. A. W. 1977. The comparative serology of the Marsupialia, and a classification of Marsupials. *Australian Journal of Zoology, Supplementum Series* **52**: 1–152.
- KURIS A. M., BLAUSTEIN A. R. & ALIO J. J. 1980. Hosts as islands. *American Naturalist* **116**: 570–586.

- LYAL C. H. C. 1985. A cladistic analysis and classification of trichodectid mammal lice (Phthiraptera: Ischnocera). *Bulletin of the British Museum of Natural History (Entomology)* **51**: 187–346.
- LYAL C. H. C. 1987. Co-evolution of trichodectid lice and their mammalian hosts. *Journal of Natural History* **21**: 1–28.
- MACARTHUR R. H. & WILSON E. O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MARSHALL A. G. 1981. *The Ecology of Ectoparasitic Insects*. Academic Press, London.
- PRICE P. W. & CLANCY K. M. 1983. Patterns in the number of helminth parasite species in freshwater fishes. *Journal of Parasitology* **69**: 449–454.
- SIBLEY Ch. G, AHLQUIST J. E. & MONROE B. L. 1988. A classification of the living birds of the world based on DNA–DNA hybridization studies. *Auk* **105**: 409–423.
- TIMM R. M. 1983. Fahrenholz's rule and resource tracking: a study of host–parasite coevolution. In: *Coevolution*. (Edited by NITECKI M. H.), pp. 225–265. University of Chicago Press, Chicago.
- UCHIKAWA K. 1987. Myobiid mites (Trombidiformes: Myobiidae) associated with the vampire bats (Chiroptera: Phyllostomatidae) and information on host taxonomy deduced from them. *Journal of Parasitology* **73**: 640–645.
- ZONFRILLO B. 1991. The feather louse *Halipeurus gravis gravis* Timmermann, 1961 (Mallophaga: Philopteridae) from a sooty shearwater *Puffinus griseus* in Scotland. *Seabird* **11**: 17–18.