

POINTS IN QUESTION FLAMINGO LICE CONTRAVENE FAHRENHOLZ

THE idea that highly host-specific, that is stenoxene, parasites and their hosts speciate in synchrony is almost a century old. Fahrenholz's rule, which is based on this assumption, states that the phylogenetic relationship of two parasite species reflects that of their host (1913, *Zoologischer Anzeiger* **41**: 371–374). Since three of the four genera of chewing lice (*Mallophaga*) of the flamingoes (*Phoenicopteriformes*) are represented in the louse fauna of the order of geese (*Anseriformes*), but none in that of storks (*Ciconiiformes*), it was widely accepted since Eichler (1941, *Zoologischer Anzeiger* **132**: 254–262) that flamingoes are related to geese and not to storks.

However, recent DNA–DNA hybridization studies (Sibley, Ahlquist & Monroe, 1988, *The Auk* **105**: 409–423) on the classification of birds have revealed a surprisingly close relationship between storks and flamingoes and their lack of affinity to geese. Nevertheless, many parasitologists still overestimate the role of co-speciation (synchronized speciation of host and parasite) in the phylogeny of parasites (e.g. see Brooks, 1987, *International Journal for Parasitology* **17**: 291–297).

Recent evidence indicates that modes of stenoxene parasite speciation other than co-speciation also play an important role. Theoretically, three such modes can be identified.

1. All parasite species must have an ancestor which was not a parasite. "Becoming a parasite" is a rare but relevant mode of parasite speciation. It is typical in periods when an essentially new host taxon emerges with much greater anatomical complexity than that of its ancestors. For example the epidermis of mammals and birds is covered by much more complicated structures than that of their reptile ancestors. The appearance of birds and mammals in the Triassic and Jurassic is associated with some free-living species becoming ectoparasites. The ancestors of most of the present mammalian and avian ectoparasites (e.g. *Phthiraptera*, *Siphonaptera*) were free-living animals before the Triassic and did not parasitize the epidermis of ancient reptiles.

2. In certain cases parasites can utilize a new host species even if it was not phylogenetically related to their former host species. Such a host-shift (host-switch or host jump) will result in the evolution of a new parasite species existing simultaneously with the original species continuing to parasitize the old host.

3. Parasites can also invade a previously unutilized site (organ, tissue or surface area) of their host species. A typical example is the case of lice of some antelopes. Their foot louse species are each derived from the body louse of the same host species (Eichler, 1989, *Programme & Abstracts of 13th WAAVP Conference*, Berlin, p. 30). However, site-shift does not necessarily result in parasite speciation.

Host-shift seems to be quite a common phenomenon. In a case study (Hafner & Nadler, 1988, *Nature* **332**: 258–259) on the rodent family *Geomyidae* and its mallophagan fauna, three of nine branching points of the parasite phylogenetic tree were host-shifts, although the taxa studies were chosen precisely in a way to minimize its probability (the distribution of these rodent species does not overlap, the transmission of these lice is thought to occur only through host-to-host contact, etc.). The fact that there are so many such shifts indicates that host populations with anatomical sites not utilized by parasites (vacant niches for parasites) are often available.

Vacant niches arise when parasite species become extinct but their hosts survive. It is probably quite a common phenomenon because of a process resembling the 'bottleneck effect' of population genetics. The essence of a 'parasitological bottleneck' is that a decrease in the size of the host population—and even a temporary decrease—will tend to result in the extinction of some of its specific parasite species. For instance two of the three louse species of the house sparrow are absent in North America since they became extinct during the course of the introduction of their hosts to that continent (Brown & Wilson, 1974, *American Midland Naturalist* **94**: 154–165). Similarly, mouse species with restricted distribution in North America have less acarine parasite species than others with wide geographical distribution (Dritschilo, Cornell, Nafus & O'Connor, 1974, *Science* **190**: 467–469). If the population size of a host species fluctuates in an evolutionary time-scale, parasite extinctions will occur in the periods of decrease, while parasite speciations by host-shifts and site-shifts will be induced by the vacant niches arising in the periods of population increase.

Host-shift is even more common in the case of parasites of plants than in the case of parasites of animals. Anyone comparing the local host-specific insect parasite faunas of a widely distributed plant species will find a very few or no common species, as reported by Strong, McCoy & Rey (1977, *Ecology* **58**: 167–175) for parasites of sugarcane, or by Lawton (1982, *Journal of Animal Ecology* **51**: 573–595) for those of bracken. On the other hand, taking feral pigeon populations living in different continents as an example, their respective louse species composition shows a moderate level of variation (e.g. see Brown, 1971, *The Journal of Parasitology* **57**: 1379–1380; Cerny, 1970, *Angewandte Parasitologie* **11**: 244–248; Selim, El-Kasaby & El-Refaii, 1968, *Angewandte Parasitologie* **9**: 74–83).

There is no doubt that co-speciation also exists as an alternative mode of parasite speciation, but this is probably not the only major factor influencing their phylogeny. Co-speciation is likely to have a more

pronounced role in the phylogeny of the parasites of animals living in relatively stable climax communities with little fluctuations in the size of host populations.

It must also be recognized that Fahrenholz's rule was applied originally only in the case of stenoxene parasites. However many or most of the parasite species are not so strictly host-specific and therefore able to contravene the 'rules' of parasite speciation.

On the other hand, co-adaptation (the other component of co-evolution) is not questioned as a major factor in the evolution of hosts and parasites, because of the evidence of mutual selective pressure between them. Parasites—by definition—decrease the fitness of their hosts even if they are not apparently pathogenic in a veterinary or medical sense. Since the defence ability of hosts is genetically influenced and host populations are polymorphic for the corresponding loci, parasites exert selective pressure upon the host populations. The main reason for parasite mortality is often the various defence activities of the host populations, such as grooming in the case of avian *Mallophaga* species (e.g. see Nelson & Murray, 1971, *International Journal for Parasitology* 1: 21–29). In an evolutionary time scale, lice can quite easily shift among goose and flamingo species, probably because the structure of their bill and, therefore, their grooming techniques are similar, regardless of the great phylogenetic distance between them.

L. ROZSA
Department of Parasitology & Zoology,
University of Veterinary Science,
H-1400 Budapest, Pf.2,
Hungary.

Acknowledgement—I thank C. Arme and T. Kassai for helpful comments and suggestions.