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Research paper

Speciation and diversification of parasite lineages: an analysis of congeneric parasite species in vertebrates

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Abstract. The evolutionary diversification of living organisms is a central research theme in evolutionary ecology, and yet it remains difficult to infer the action of evolutionary processes from patterns in the distribution of rates of diversification among related taxa. Using data from helminth parasite communities in 76 species of birds and 114 species of mammals, the influence of four factors that may either be associated with or modulate rates of parasite speciation were examined in a comparative analysis. Two measures of the relative number of congeneric parasite species per host species were used as indices of parasite diversification, and related to host body mass, host density, latitude, and whether the host is aquatic or terrestrial. The occurrence of congeneric parasites was not distributed randomly with respect to these factors. Aquatic bird species tended to harbour more congeneric parasites than terrestrial birds. Large-bodied mammal species, or those living at low latitudes, harboured more congeneric parasites than small-bodied mammals, or than those from higher latitudes. Host density had no apparent association with either measures of parasite diversification. These patterns, however, reflect only the present-day distribution of parasite diversification among host taxa, and not the evolutionary processes responsible for diversification, because the apparent effects of the factors investigated disappeared once corrections were made for host phylogeny. This indicates that features other than host body size, host density, latitude, and whether the habitat is terrestrial or aquatic, have been the key driving forces in the diversification of parasitic helminth lineages.

Key words: adaptive radiation, comparative analysis, gastrointestinal helminths, host body mass, latitude, phylogeny, species flocks

Introduction

Patterns in the present-day distribution of species diversity and the evolutionary processes responsible for generating these patterns have attracted much scientific interest in recent years (Ricklefs and Schluter, 1993; Huston, 1994; Rosenzweig, 1995). Most hypotheses attempting to explain the spatial variation in species diversity invoke differences among habitats, in terms of age, heterogeneity or amount of solar radiation received, as the principal mechanisms responsible for spatial variation in rates of speciation and diversification. The fact that these hypotheses are not mutually exclusive, and the large

number of confounding variables involved in habitat comparisons, has made it difficult to assess the merit of individual mechanisms. In particular, it is rarely easy to distinguish between factors associated with high rates of diversification, and factors causing this diversification (Dial and Marzluff, 1989). Still, investigations of the causes of species diversity remain at the core of evolutionary ecology (Rosenzweig, 1995; Maurer, 1999).

Parasite communities represent excellent models to test ideas regarding differences in rates of diversification among related taxa and the evolution of species diversity. The historical relationships between their habitats (i.e. the phylogeny of their hosts) can often be resolved more easily than those of free-living organisms, and they can be included in comparative analyses. Many ecological correlates of species diversity in parasite communities, especially in gastrointestinal helminths of vertebrate hosts, have already been identified (Bush *et al.*, 1990; Poulin, 1995, 1997). These correlates of the current distribution of parasite diversity may have been key determinants over evolutionary time of the rates of host colonization as well as rates of within-host speciation by parasite lineages. An investigation of the occurrence of congeneric parasite species within the same host species may yield more information on the factors favouring diversification than studies focusing on species richness in general. It has been argued that strict habitat selection leads to a higher frequency of sympatric speciation in parasites than in free-living animals (Price, 1980; de Meeüs *et al.*, 1995, 1998); the occurrence of congeneric parasite species can therefore be a direct indication of the diversification of a lineage. Early investigations of multiple parasite congeners suggested that they provided evidence for radiation of species flocks, especially in certain taxa of nematodes from terrestrial vertebrates (Schad, 1963; Inglis, 1971). More recently, Kennedy and Bush (1992) surveyed published studies and found that congeneric helminths were common in parasite communities of birds and mammals, although most genera were represented by a single species. The issue of why multiple congeners are more frequent in some parasite communities (i.e. in some host species) than others remains unexplored.

Many factors could promote speciation of parasite lineages in particular host species. Bush *et al.* (1990) suggested that multiple helminth congeners characterize the parasite communities of aquatic birds and contribute to their high species richness. Thus whether the host is aquatic or terrestrial may influence its share of congeneric parasites. Host body size and host density are often reliable predictors of species richness in parasite communities (Poulin, 1997; Morand and Poulin, 1998). Larger-bodied host-species offer more space for parasite attachment, possibly a greater variety of niches, and more permanent habitats as they are longer-lived than small-bodied hosts. Host species occurring at high population densities make transmission of parasites more effective and their extinction less likely. If these features facilitate the

colonization of host species by new parasite species over evolutionary time, they may also favour intrahost speciation by some or most parasite lineages. Finally, latitude may be associated with the occurrence of congeneric parasites in the same host species. Rohde (1992, 1998) argued that the greater diversity of fish ectoparasites at low latitudes was due mostly to higher temperature-mediated rates of mutation, evolution and speciation in the tropics. The influence of temperature on speciation in internal parasites of endothermic hosts is probably nil, but known latitudinal trends in the diversity of free-living invertebrates (see Rosenzweig, 1995) suggest that tropical helminth parasites have a wider variety of intermediate hosts to choose from, and could diversity accordingly. Kennedy (1995) observed much richer endoparasite communities in tropical eels than in their temperate relatives, and proposed other mechanisms that could lead to the diversification of parasite assemblages at low latitudes.

Here I investigate the patterns in the occurrence of congener parasites in communities of gastrointestinal helminths of bird and mammal hosts. First, I examine whether the occurrence of congener parasites is associated with terrestrial or aquatic habitats, host body size, host density, or latitude. Correlations between these variables and the frequency of congener parasites serve to describe the present-day distribution of congener parasites, and thus the potential hot spots of diversification. Second, in a comparative analysis controlling for host phylogeny, I assess the potential role of each of the above factors in the diversification of parasite genera over evolutionary time. The results are discussed with respect to some of the classical examples of multiple helminth congeners in vertebrates, traditionally viewed as probable instances of parasite radiation.

Methods

Data on congeneric species of gastrointestinal helminths of bird and mammal hosts were obtained from the compilation of published results presented in the Appendix of Poulin (1995). The original authors' parasite taxonomy was accepted, even though this can create some additional error. I recorded the number of helminth species (digeneans, cestodes, acanthocephalans, and nematodes), the number of helminth genera, and the number of helminth genera represented by more than one species, for each sample of hosts. Host sample size, or the number of hosts examined for parasites in each study, was also recorded; sampling effort is an important confounding factor as it usually correlates positively with the number of parasite taxa found in surveys of wild hosts (Poulin, 1995; Walther *et al.*, 1995). The data on numbers of helminth species or genera are not representative of the entire parasite fauna of the various host species, but of local helminth communities found in particular

host populations. It is at the level of the host population that parasite diversity changes over evolutionary time, with parasite species being acquired or lost in some populations but not others. When data were available for more than one populations of a host species, the data were averaged across populations, weighting for sample size, to give mean values for each host species.

Information on the four other variables that may influence the number of congeneric helminth species per host species was also recorded. Host body size was taken as adult body mass, obtained from Dunning (1993) for birds and Grzimek (1990) for mammals. Host population density was available for mammals only, and was obtained from the compilation of Damuth (1987). The latitude at which the host population was sampled, was also recorded with no distinction made between the northern and southern hemispheres (most studies were performed in North America). Finally, the habitat of the host species was recorded as either terrestrial or aquatic, depending on where individuals of the species spend most of their time and obtain the majority of their food.

Bird and mammal hosts were analysed separately. All continuous data were log-transformed prior to analysis. The first series of analyses attempted to identify the potential correlates of within-genus helminth diversification across host species. Treating host species as independent observations ignores the potentially strong influence of phylogeny (see below), but allows one to find out which host attributes are associated with higher rates of helminth diversification. The number of parasite species per host species was regressed against the number of parasite genera per host species, and residuals of this regression were used as measures of relative number of helminth species per helminth genus. Similarly, the number of parasite genera represented by more than one species was regressed against the number of parasite genera, with the residuals used as measures of the relative number of multispecific genera. These relative values were then used as dependent variables in multiple regressions, with host sample size, host body mass, host density (for mammals only) and latitude used as predictor variables. Finally, two separate single-factor ANOVAs were used to test for the influence of host taxonomic order and host habitat on both the relative number of helminth species per genus and the relative number of multispecific genera.

Subsequent analyses controlled for phylogenetic influences. If trends identified in the above analyses disappear once the effect of host phylogeny are removed, then they are merely a reflection of other processes and were probably unimportant during the evolution and diversification of host and parasite lineages. I used the phylogenetically independent contrasts method (Felsenstein, 1985) on log-transformed data, following the procedures outlined by Garland *et al.* (1992) and implemented using the software CAIC, Version 2 (Purvis and Rambaut, 1994). The method is widely used and has been shown to be relatively robust for testing hypotheses of correlated evolution when good estimates of the topology and branch lengths of the phylogeny are available (Purvis *et al.*, 1994;

Díaz-Uriarte and Garland, 1996, 1998). A phylogeny of the mammal species used here was reconstructed from the information provided by Garland and Janis (1993), de Jong (1998), Morand and Poulin (1998), Simmons (1998), Randi *et al.* (1998), and Bininda-Emonds *et al.* (1999). The avian phylogeny used here was that proposed by Sibley and Ahlquist (1991), supplemented by information on relationships among Anatidae from Livezey (1991, 1995). Branch lengths in the mammalian phylogeny were only available for certain parts of the tree; therefore, branch lengths estimates were derived using the method proposed by Grafen (1989). Branch lengths in the avian phylogeny were inferred from the divergence units computed by Sibley and Ahlquist (1991) in their DNA–DNA hybridization experiments. Phylogenetic contrasts were standardized for branch lengths as described in Garland *et al.* (1992). As in the previous analyses, contrasts in number of helminth species per host species were regressed against contrasts in number of helminth genera per host species, and residuals were computed to obtain contrasts in relative number of helminth species per helminth genus. Similarly, contrasts in number of parasite genera represented by more than one species were regressed against contrasts in number of parasite genera, with the residuals used as contrasts in relative number of multispecific genera per host species. These derived contrasts were then corrected for contrasts in host sample size, again using residuals from a regression, and then separately correlated with contrasts in host body mass, host density (for mammals only) and latitude. All regressions and correlations using phylogenetic contrasts were forced through the origin (see Garland *et al.*, 1992).

Results

Data were obtained for 76 species of birds and 114 species of mammals (density data were available for only 56 mammal species). Of these, two species of birds and six species of mammals harboured only a single helminth species. Excluding these host species from the analyses had no effect on any of the results; here, I only present the results obtained from the analyses using the entire data sets. The number of helminth species to number of genera ratio ranged from 1 to 2.19 among bird hosts, and from 1 to 2.77 among mammal hosts. The number of multispecific genera per host species ranged from 0 to 5 among bird species, and from 0 to 8 among mammals.

Analyses of parasites in avian hosts

Across bird species, the number of helminth genera per host species correlated strongly with the number of helminth species ($y = 1.056x - 0.017$, $r^2 = 0.972$, $p < 0.0001$) and with the number of multispecific genera per host species

($y = 0.388x - 0.162$, $r^2 = 0.289$, $p < 0.0001$). The residuals of these regressions were used as relative measures, corrected for number of genera, in multiple regressions that controlled for host sample size as a confounding factor. Neither of the two predictor variables tested, host body mass and latitude, had significant effects on the relative number of helminth species per genus (host mass: $r = 0.133$, $p = 0.251$; latitude: $r = 0.187$, $p = 0.108$) or on the relative number of multispecific genera per host species (host mass: $r = 0.201$, $p = 0.084$; latitude: $r = 0.121$, $p = 0.295$).

There were differences between terrestrial and aquatic birds with respect to both the relative number of helminth species per genus (ANOVA, $F_{1,74} = 3.67$, $p = 0.059$) and the relative number of multispecific genera per host species ($F_{1,74} = 5.93$, $p = 0.017$). Avian taxonomic order had no effect on either variable (relative number of helminth species per genus: $F_{7,68} = 0.75$, $p = 0.631$; relative number of multispecific genera per host species: $F_{7,68} = 1.19$, $p = 0.320$), but orders of aquatic birds tended to show higher values of both variables than terrestrial ones, at least among well-represented orders (Figure 1).

A total of 58 independent contrasts could be derived from the avian phylogeny used here. Using these contrasts, and thus controlling for potential phylogenetic influences, I again used the residual variance from regressions as measures of relative number of helminth species per genus and relative number of multispecific genera per host species. Neither of these two measures, respectively, correlated with contrasts in host body mass ($r = -0.069$, $p = 0.608$; and $r = -0.029$, $p = 0.830$) or contrasts in latitude ($r = 0.170$, $p = 0.203$; and $r = 0.063$, $p = 0.641$). There were too few independent contrasts between aquatic and terrestrial bird taxa to assess the influence of host habitat while removing phylogenetic influences.

Analyses of parasites in mammalian hosts

Across mammal species, the number of helminth genera per host species correlated strongly with the number of helminth species ($y = 1.132x - 0.033$, $r^2 = 0.939$, $p < 0.0001$) and with the number of multispecific genera per host species ($y = 0.476x - 0.145$, $r^2 = 0.303$, $p < 0.0001$). As before, the residuals of these regressions were used as relative measures, corrected for number of genera, in multiple regressions that also controlled for host sample size as a confounding factor. Latitude did not correlate with the relative number of helminth species per genus ($r = -0.095$, $p = 0.294$) but it correlated negatively with the relative number of multispecific genera per host species ($r = -0.228$, $p = 0.011$). Host body mass correlated positively and significantly with both the relative number of helminth species per genus ($r = 0.297$, $p = 0.0013$) and the relative number of multispecific helminth genera per host species

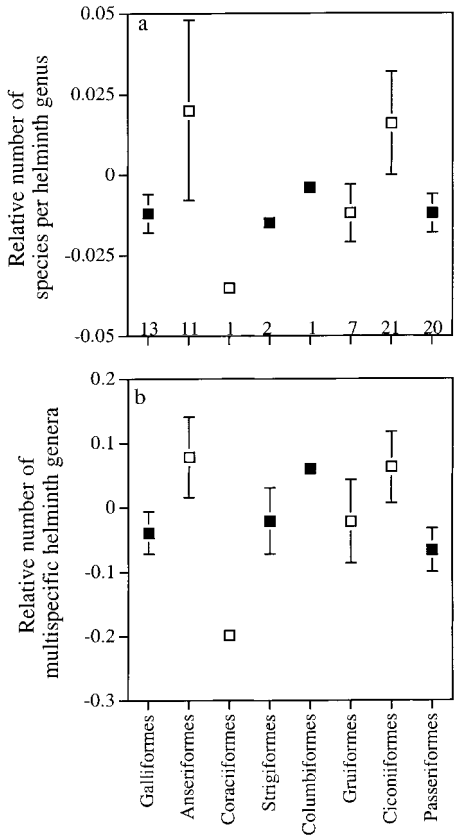

Figure 1. Mean (±SE) relative number of species per helminth genus (a) and relative number of multispecific genera per host species (b) for the avian orders represented in the data set. Terrestrial bird orders are denoted by black squares, and aquatic orders by open squares. The numbers on the *x*-axis in (a) indicate the number of bird species for which data were available.

($r = 0.301$, $p = 0.0009$). These relationships appear somewhat influenced by data on equid hosts (see Figure 2); however, both relationships remain statistically significant when the data for the three equid species are removed (relative number of helminth species per genus: $r = 0.198$, $p = 0.037$; relative number of multispecific helminth genera: $r = 0.222$, $p = 0.019$). Host density did not correlate with either measure of parasite diversification ($r = -0.102$, $p = 0.293$, and $r = -0.098$, $p = 0.294$, respectively).

Aquatic and terrestrial mammals did not differ with respect to relative number of helminth species per genus or relative number of multispecific genera per host species (ANOVAs, both $p > 0.7$). However, mammalian taxonomic order had significant effects on both variables (relative number of helminth species per genus: $F_{10,103} = 7.78$, $p = 0.0001$; relative number of multispecific genera per host species: $F_{10,103} = 8.23$, $p = 0.0001$).

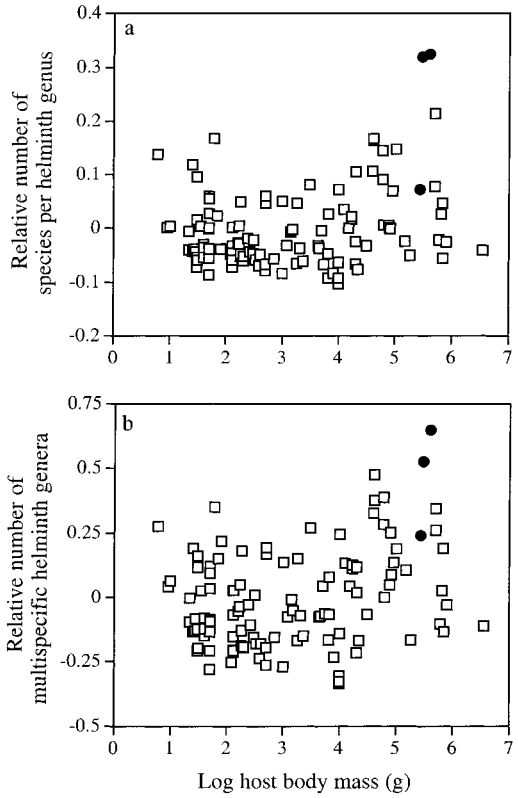

Figure 2. Relationship between host body mass and (a) the relative number of species per helminth genus and (b) the relative number of multispecific genera per host species, across 114 species of mammals. Both dependent variables are corrected for host sample size and latitude (see text). Black circles represent the three species of equids (horses) included in the data set.

Perissodactyls, marsupials and insectivores tended to show higher values of both variables than other orders (Figure 3).

Not surprisingly, with such a clear taxonomic influence, the effects of latitude and host body mass were different once analyses were repeated using the 87 sets of contrasts derived from the mammalian phylogeny instead of species values. Among contrasts, and after correcting for host sample size, host body mass did not correlate with relative number of helminth species per genus ($r = 0.066$, $p = 0.541$) or with relative number of multispecific genera per host species ($r = -0.038$, $p = 0.730$). Latitude tended to covary with the relative number of helminth species per genus ($r = 0.207$, $p = 0.054$), but did not correlate with the relative number of multispecific helminth genera ($r = -0.0004$, $p = 0.993$). Host density (only 42 sets of contrasts) did not correlate with either measure ($r = -0.151$, $p = 0.344$, and $r = -0.125$,

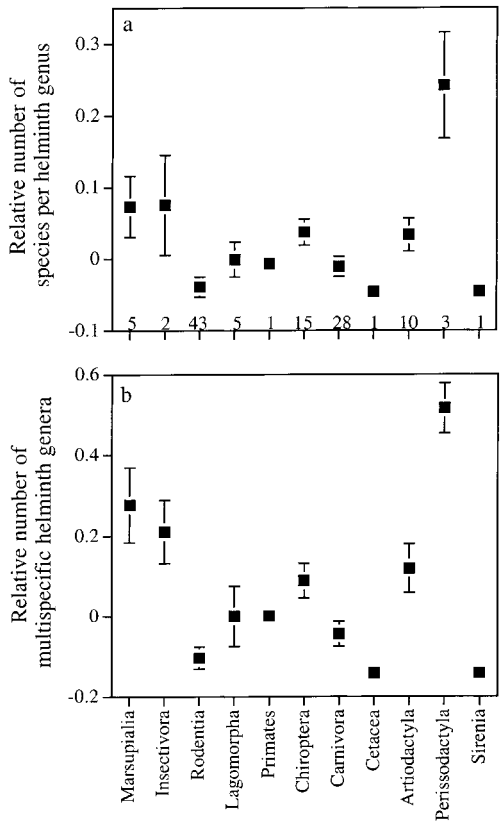

Figure 3. Mean (±SE) relative number of species per helminth genus (a) and relative number of multispecific genera per host species (b) for the mammalian orders represented in the data set. The numbers on the *x*-axis in (a) indicate the number of mammal species for which data were available.

$p = 0.431$, respectively). There were not enough independent contrasts between aquatic and terrestrial mammal taxa to assess the influence of host habitat on within-genus helminth diversification rates.

Discussion

The diversification of parasite lineages over evolutionary time can be determined to a large extent by the biological features of parasites. For instance, it appears from the skewed body size distributions of endoparasitic helminths, that small-bodied parasite taxa are more speciose than large-bodied ones (Poulin and Morand, 1997). This pattern is common in many other animal groups and may result from the shorter generation times of smaller-bodied taxa promoting speciation (Marzluff and Dial, 1991). Also, key innovations in

the evolution of certain parasite lineages, such as the gain or loss of a host in the life cycle, can promote speciation rates and lead to adaptive radiations (Brooks and McLennan, 1993). Here, I examined how properties of the hosts may influence parasite diversification. The occurrence of congeneric helminth parasites is not distributed randomly with respect to host features. Aquatic bird species tend to harbour more congeneric helminths than terrestrial birds. Large-bodied mammal species, and those living at low latitudes, harbour more congeneric helminths than small-bodied mammals, or than those of higher latitudes. These distributional patterns, however, may not reflect evolutionary processes. Substantial host taxonomic or phylogenetic influences must exist because the apparent effects of the four variables investigated cannot be confirmed in analyses using phylogenetically independent contrasts. This suggests that host body size, host density, latitude, and whether the habitat is terrestrial or aquatic, have not been important driving forces in the diversification of gastrointestinal helminth lineages. The fact that these variables are important determinants of total parasite species richness (see Poulin, 1997) but not of the frequency of congeners suggests that new species are added to parasite faunas mainly by sequential colonisation.

Two potential sources of error deserve to be mentioned. First, I used the original authors' parasite taxonomy, and most likely these authors differed in their sources of taxonomic information. Some taxonomic schemes show a tendency to lump species into few genera, whereas others tend to erect many more genera for the same number of species. Since it is extremely unlikely that there exists a systematic bias in this source of error with respect to variables such as latitude or host body size, it does not represent a problem in the present study. Second, the number of congeneric species can be underestimated when rare species are not found because of inadequate host sample sizes (Poulin, 1998). The most likely influence of sampling effort should be to reduce the likelihood of finding a positive relationship between host body size and the relative occurrence of congeneric parasites in mammals, since it is the large-bodied mammal species that are typically suffering from poor sampling (see appendix in Poulin, 1995). Here I did find a positive correlation between mammal body size and the occurrence of congeneric parasites, and thus sampling artefacts are unlikely to be important.

Several examples of multiple congeneric parasites coexisting in the same host species have been reported in the parasitology literature, most involving nematode parasites. The best known are the oxyurids of tortoises, the strongyloids of horses and elephants, and the cloacinids of kangaroos (Schad, 1963; Inglis, 1971; Bucknell *et al.*, 1996; Beveridge and Spratt, 1996); of these, horses and kangaroos were included in the present analyses. In some of these well-known cases, not only are some parasite genera represented by multiple species, but some subfamilies are also represented by many genera. How can

many related and similar parasite species coexist in a host population? Interspecific competition does not appear intense: most host individuals do not harbour the full set of congeneric parasite species present in the host population, and positive associations among congeneric species far outnumber negative ones (e.g. Bucknell *et al*., 1996). Congeners in these assemblages tend to have very restricted distributions in the stomach or intestine of their host, which may explain the apparent absence of strong contemporary competition. From an evolutionary perspective, the structural complexity of the anatomy of the digestive tract of large mammalian herbivores offers a wide range of niches to helminth parasites. The morphological differentiation among congeneric nematode species in these rich communities is primarily based around the buccal structures, suggesting that the diversification of parasite genera reflects specializations in their feeding mechanisms in habitats rich in diverse niches (Beveridge and Spratt, 1996). To the above examples featuring nematodes and large herbivorous mammals as hosts, Kennedy and Bush (1992) have added dactylogyrid monogeneans on fish hosts. In ectoparasite communities of fish, there can be up to 15 species of *Dactylogyrus*, although such high numbers of congeners are never seen in other genera of monogeneans. Other instances of multiple congeneric parasites mentioned by Kennedy and Bush (1992) include cestodes in aquatic birds and elasmobranchs, and digeneans in bats.

The cases discussed above probably represent real species flocks, being the product of the radiation of an ancestral taxon. There may be another explanation, though. Multiple congeners can indeed be the outcome of several intrahost speciation events, but they can also be the result of several independent host colonization events by congeneric parasites evolved in other hosts (Paterson and Gray, 1997). Since colonization events are considered to be rare events, and because sympatric speciation can be frequent in parasites (Price, 1980; de Meeüs *et al*., 1998), perhaps the most parsimonious explanation is to view these multiple congeners as the product of speciation and diversification within the host. Why has this occurred in certain hosts and not in others? The analyses reported here seeked to identify general trends. Although some host characteristics are associated with the occurrence of congeneric parasites in a statistical sense, they do not appear to have been key factors in the evolution and diversification of these congeners. For instance, whereas horses and kangaroos are relatively large-bodied and harbour many congeneric helminth species, other large mammals such as bears and cetaceans harbour relatively few congeneric parasites. The explanation is not merely one of difference in diet, as many large-bodied herbivorous ungulates also harbour relatively few congeners. It may be that certain combinations of host and parasite characteristics, and not just host features alone, allow high rates of within-host parasite diversification and lead to the development of the parasite species flocks observed in many present-day vertebrates.

References

Beveridge, I. and Spratt, D.M. (1996) The helminth fauna of Australasian marsupials: Origins and evolutionary biology. *Adv. Parasitol.* **37**, 135–254.

Bininda-Emonds, O.R.P., Gittleman, J.L. and Purvis, A. (1999) Building large trees by combining phylogenetic information: A complete phylogeny of the extant Carnivora (Mammalia). *Biol. Rev.* **74**, 143–175.

Brooks, D.R. and McLennan, D.A. (1993) Comparative study of adaptive radiations with an example using parasitic flatworms (Platyhelminthes: Cercomeria). *Am. Nat.* **142**, 755–778.

Bucknell, D., Hoste, H., Gasser, R.B. and Beveridge, I. (1996) The structure of the community of strongyloid nematodes of domestic equids. *J. Helminthol.* **70**, 185–192.

Bush, A.O., Aho, J.M. and Kennedy, C.R. (1990) Ecological versus phylogenetic determinants of helminth parasite community richness. *Evol. Ecol.* **4**, 1–20.

Damuth, J. (1987) Interspecific allometry of population density in mammals and other animals: The independence of body mass and population energy-use. *Biol. J. Linn. Soc.* **31**, 193–246.

de Jong, W.W. (1998) Molecules remodel the mammalian tree. *Trends Ecol. Evol.* **13**, 270–275.

de Meeüs, T., Hochberg, M.E. and Renaud, F. (1995) Maintenance of two genetic entities by habitat selection. *Evol. Ecol.* **9**, 131–138.

de Meeüs, T., Michalakis, Y. and Renaud, F. (1998) Santa Rosalia revisited: Why are there so many kinds of parasites in ''The garden of Earthly delights''? *Parasitol. Today* **14**, 10–13.

Dial, K.P. and Marzluff, J.M. (1989) Nonrandom diversification within taxonomic assemblages. *Syst. Zool.* **38**, 26–37.

Díaz-Uriarte, R. and Garland, T. Jr. (1996) Testing hypotheses of correlated evolution using phylogenetically independent contrasts: Sensitivity to deviations from Brownian motion. *Syst. Biol.* **45**, 27–47.

Díaz-Uriarte, R. and Garland, T. Jr. (1998) Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst. Biol.* **47**, 654–672.

Dunning, J.B. Jr. (1993) *CRC Handbook of Avian Body Masses*. CRC Press, Boca Raton, Florida.

Felsenstein, J. (1985) Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Garland, T. Jr., Harvey, P.H. and Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.

Garland, T. Jr. and Janis, C.M. (1993) Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J. Zool.* (*Lond.*) **229**, 133–151.

Grafen, A. (1989) The phylogenetic regression. *Phil. Trans. Roy. Soc. Lond.* **B 326**, 119–157.

Grzimek, B. (1990) *Encyclopedia of Mammals,* 5 Volumes. McGraw-Hill, New York.

Huston, M.A. (1994) *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.

Inglis, W.G. (1971) Speciation in parasitic nematodes. *Adv. Parasitol.* **9**, 201–223.

Kennedy, C.R. (1995) Richness and diversity of macroparasite communities in tropical eels *Anguilla reinhardtii* in Queensland, Australia. *Parasitology* **111**, 233–245.

Kennedy, C.R. and Bush, A.O. (1992) Species richness in helminth communities: The importance of multiple congeners. *Parasitology* **104**, 189–197.

Livezey, B.C. (1991) A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. *Auk* **108**, 471–507.

Livezey, B.C. (1995) Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). *Condor* **97**, 233–255.

Marzluff, J.M. and Dial, K.P. (1991) Life history correlates of taxonomic diversity. *Ecology* **72**, 428–439.

Maurer, B.A. (1999) *Untangling Ecological Complexity: The Macroscopic Perspective*. University of Chicago Press, Chicago.

Morand, S. and Poulin, R. (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evol. Ecol.* **12**, 717–727.

Paterson, A.M. and Gray, R.D. (1997) Host-parasite cospeciation, host switching, and missing the boat. In D.H. Clayton and J. Moore (eds) *Host-Parasite Evolution: General Principles and Avian Models*. Oxford University Press, Oxford, pp. 236–250.

Poulin, R. (1995) Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol. Monogr*. **65**, 283–302.

Poulin, R. (1997) Species richness of parasite assemblages: Evolution and patterns. *Annu. Rev. Ecol. Syst*. **28**, 341–358.

Poulin, R. (1998) Comparison of three estimators of species richness in parasite component communities. *J. Parasitol*. **84**, 485–490.

Poulin, R. and Morand, S. (1997) Parasite body size distributions: Interpreting patterns of skewness. *Int. J. Parasitol*. **27**, 959–964.

Price, P.W. (1980) *Evolutionary Biology of Parasites*. Princeton University Press, Princeton.

Purvis, A., Gittleman, J.L. and Luh, H.-K. (1994) Truth or consequences: Effects of phylogenetic accuracy on two comparative methods. *J. Theor. Biol*. **167**, 293–300.

Purvis, A. and Rambaut, A. (1994) *Comparative Analysis by Independent Contrasts (CAIC)*, version 2. Oxford University, Oxford.

Randi, E., Mucci, N., Pierpaoli, M. and Douzery, E. (1998) New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome *b* gene. *Proc. Roy. Soc. Lond*. **B 265**, 793–801.

Ricklefs, R.E. and Schluter, D. (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago.

Rohde, K. (1992) Latitudinal gradients in species diversity: The search for the primary cause. *Oikos* **65**, 514–527.

Rohde, K. (1998) Latitudinal gradients in species diversity: Area matters, but how much? *Oikos* **82**, 184–190.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Schad, G.A. (1963) Niche diversification in a parasite species flock. *Nature* **198**, 404–406.

Sibley, C.G. and Ahlquist, J.E. (1991) *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven, Connecticutt.

Simmons, N.B. (1998) A reappraisal of interfamilial relationships of bats. In T.H. Kunz and P.A. Racey (eds) *Bat Biology and Conservation*. Smithsonian Institution Press, Washington, pp. 3–26.

Walther, B.A., Cotgreave, P., Price, R.D., Gregory, R.D., and Clayton, D.H. (1995) Sampling effort and parasite species richness. *Parasitol. Today* **11**, 306–310.