

RESEARCH NOTE

Diving behavior reduces genera richness of lice (Insecta, Phthiraptera) of mammals

Bernadett Felső^{1*} and Lajos Rózsa²

¹Zoological Institute, Faculty of Veterinary Science, Szent István University, Rottenbiller Str. 50, Budapest, H-1078 Hungary;

²Animal Ecology Research Group, Hungarian Academy of Sciences, Hungarian Natural History Museum, Budapest, Ludovika 2 Str., H-1083 Hungary; Collegium Budapest, Institute for Advanced Study

Abstract

Lice of mammals spend the entire life cycle in the host hair, thus, the microclimate found near the mammal skin is likely to influence the structure of louse communities. Here we use a comparative approach to examine the effect of mammals' diving behavior on the taxonomic richness of their lice. We compared the mean genera richness of lice, and – as potential confounding variables – the mean species richness of host, and the mean body mass of host between diving clades and their non-diving sister clades. Louse genera richness was significantly lower in clades of aquatic mammals than on their non-diving sister clades. Host species richness was not significantly different between these clades. Body mass was significantly higher in clades of aquatic mammals, however, the direction of this difference cannot explain the difference in parasite taxonomic richness. This study suggests that mammals' diving behavior can effectively shape their ectoparasite communities.

Key words

Lice, genera richness, mammals, diving behavior

Lice depend on an intimate and permanent association with their host; they are well adapted to the warm, humid microhabitat near the host skin and cannot survive off the host for more than a few hours or days (Johnson and Clayton 2003). These microhabitats are influenced by host characters and the outside physical environment. Previous studies already identified several ecological factors that can influence the structure of louse communities. Host body size covaries positively with louse taxonomic richness (Rózsa 1997, Clayton and Walther 2001). Similarly, host population size and density can also influence the taxonomic richness of lice. Accordingly, past bottlenecks in host population size are known to cause a long-lasting decrease in louse richness (Rózsa 1993, Paterson *et al.* 1999). Moreover, taxonomically richer clades are also known to harbor more diverse parasite taxa than their sister clades, a relationship known as “Eichler's rule” (Klassen 1992). The availability of water can also shape louse communities, because low ambient humidity can reduce louse diversity (Moyer *et al.* 2002).

Finally, birds' diving behavior reduces genera richness of avian lice (Felső and Rózsa 2006). The aim of our present study is to search for a similar effect in mammal ectoparasite communities. Diving behavior is an influential determinant of the water content of pelage. Even though water rarely penetrates deeply beyond the surface of the pelage of aquatic mammals it can be expected to influence humidity within the pelage. Therefore, we test whether mammals' diving behavior affects the taxonomic richness of lice while taking into account host species richness and body mass as potential confounding variables.

Diving mammals were defined as species that dive beneath the water surface with their whole body, while non-diving mammals were terrestrial ones based on Csorba (1995). Mammals with no body size data provided by Silva and Downing (1995) were excluded from the analyses.

Widely distributed host species often have congeneric louse species, each restricted to different non-overlapping parts of the host distribution, thus exhibiting an allopatric dis-

*Corresponding author: bernadett.f@freemail.hu

tribution. Consequently, parasite species richness of widely distributed host species would overestimate the true parasite richness that each local host population must face (Clay 1964). To remove this confounding effect, we used genera richness rather than species richness to quantify the taxonomic richness of lice. This procedure also partly resolves the problem that species richness would provide unequivocal estimates due to uncertainty of the status of morpho-species (Møller and Rózsa 2005). The number of louse genera occurring on a particular host genus was obtained from Price *et al.* (2003). To calculate the mean species richness of host genera for a clade,

we summed the number of mammal species in each clade and divided it by the number of genera in that clade. Data were obtained from Dagleish (2005). Host body mass data were derived from Silva and Downing (1995). Species with 2 or more data (female and male, or ranges) were characterized by average values. Clade averages were obtained in 2 different ways. First, we summed weights of all species of the clade we examined and divided it by the number of species (species average). Second, we divided the mean weights of genera by number of genera for each clade (genera average). This second approach gave qualitatively identical results in all analy-

Table I. Host sister clades included in the analyses. See the text for definitions and sources

Taxa	Diver clade			Non-diver clade			
	mean genera richness of lice	mean species richness of host genera	mean body mass (kg)	taxa	mean genera richness of lice	mean species richness of host genera	mean body mass (kg)
<i>Chironectes minimus</i>	0	1	0.795	<i>Lutreolina</i> , <i>Didephis</i> , <i>Philander</i>	0	2.333	1.092
<i>Potamogale</i> , <i>Micropotamogale</i>	0	1.5	0.376	<i>Tenrec</i> and allies	0	1	0.556
<i>Desmana</i> , <i>Galemys</i>	0	1	0.221	<i>Talpa</i>	0	3.714	0.066
<i>Condylura cristata</i>	0	1	0.043	<i>Parascalops</i> and allies	0.5	1.5	0.051
<i>Neomys</i> , <i>Chimarrogale</i>	0.5	3.333	0.028	<i>Soriculus</i>	1	10	0.011
<i>Sorex palustris</i>	0	2	0.012	<i>Sorex</i> <i>monticolus</i> and allies	0	3	0.007
Lutinae	0.75	1.857	11.052	Mephitinae	1	3	1.318
<i>Mustela vison</i>	1	1	0.96	<i>Mustela altaica</i> and allies	2	7	0.16
<i>Ursus maritimus</i>	0	1	269.75	<i>Ursus arctos</i>	1	1	161.153
<i>Cynogale bennettii</i>	1	1	4.25	<i>Hemigalus</i> , <i>Chrotogale</i>	0	1	2.844
Pinnipedia	0.937	1.888	384.313	Procyonidae	1	3	3.596
Cetacea, Hippopotamidae	0	2.119	19141.8	Ruminantia	1.474	2.814	114.733
Sirenia	0	2	391.329	Proboscidea	1	2	2488.86
<i>Oryzomys</i>	2	36	0.052	<i>Zygodontomys</i>	2	2	0.068
Castoridae	0	2	20.756	Sciuridae	1.372	5.392	0.560
Thyromidae	1	2	2.805	Bathyergidae	0.4	2.4	0.213
Myocastoridae	1	1	7.4135	Echimyidae	1.35	3.9	0.33
Hydrochaeridae	0	1	38.944	Caviidae	2.4	2.8	1.527
<i>Arvicola</i> , <i>Ondatra</i>	1.5	1.5	0.464	<i>Clethrionomys</i> , <i>Eothenomys</i>	1.5	8	0.029

ses; thus, only the calculations with species averages will be provided below. Clade body mass values were log-transformed.

Felsenstein's (1985) independent contrast method was used to control for effects of phylogenetic association between taxa. Independent differences are created by comparing the values for sister taxa in the phylogeny. We compared the mean genera richness of lice, the mean species richness of host, and the mean body mass of host between diving mammals and their non-diving sister clades. The phylogenetic tree used for our analyses was derived from several previously published phylogenies (Bininda-Emonds *et al.* 1999, Liu *et al.* 2001, Arnason and Janke 2002, Grenyer and Purvis 2003, Cardillo *et al.* 2004, Jansa and Weksler 2004, Luo *et al.* 2004). We could gather data on a total of 19 branching points between diving vs. non-diving mammals (Table I). Branch length values were not considered in our analyses, as we adopted a punctuated model of evolution.

First, we used a 1-sample t-test on the mean of the contrasts of louse richness, host body mass, and host taxonomic richness between clades of aquatic mammals vs. non-diving mammals. Here, the null hypothesis is that contrasts deviate from the mean randomly, thus their mean equals zero. Second, we searched for an interaction between contrasts louse richness and contrasts of potential confounding variables (host body mass and host richness) by multiple linear regression forced through the origin as recommended by Grafen (1989). Computations were carried out with GraphPad InStat 3.06 and 'R' statistical program. All statistical tests are 2-tailed.

Mean genera richness of lice is significantly lower on clades of diving mammals (t-test on mean of contrasts, $n = 19$, $P = 0.0264$, Fig. 1). Species richness of host genera does not differ between sister clades (1 sample t-test on means of contrasts, $n = 19$, $P = 0.9651$), while host body mass differ between sister clades, diving mammals are significantly heavier than non-diving mammals (1 sample t-test, $n = 19$, $P = 0.002$). Contrasts of louse genera richness are not predicted by contrasts of host taxonomic richness (linear regression forced through the origin $t = 0.6354$, $df = 18$, $P = 0.5332$). Contrasts of host body mass are correlated negatively with contrasts of louse genera richness (linear regression through the origin, $t = -2.59$, $df = 18$, $P = 0.018$). The direction of this relationship was opposite to the direction that could explain our results on the relationship between diving behavior and louse richness, since – contrary to expectations – clades of heavier hosts harbor fewer genera of lice. After all, we controlled for potential interactions between louse genera richness and confounding variables by a multiple regression force through the origin. This model explains about 60% of the variability of louse genera richness (adjusted $R^2 = 0.6058$, F-statistic: 15.6 on 4 and 34 df, $P < 0.001$), and indicates that effects of diving behavior and host species richness are both significant predictors ($F = 12.926$, $P < 0.001$; $F = 36.536$, $P < 0.001$, respectively). An extreme outlier seems to affect this result; the host species contrast at *Oryzomys/Zygodontomys*. Excluding this data point results in a new model that explains slightly less of

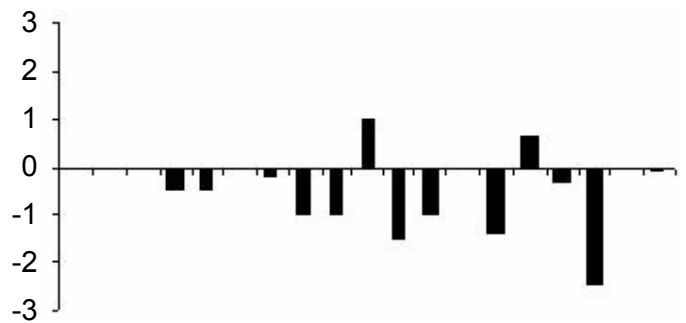


Fig. 1. The contrasts of the mean genera richness of lice between diving and non-diving mammals' clades (in the sequence of Table I, $x =$ diving vs. non-diving pairs, $y =$ contrasts). Negative values indicate that non-diving mammals have greater louse genera richness

the variability of louse genera richness (adjusted $R^2 = 0.5836$, F-statistic: 17.82 on 3 and 33 df, $P < 0.001$), and indicates that only diving behavior predicts louse richness significantly ($F = 47.4929$, $P < 0.001$). Thus the effect of mean species richness of host clades appears to be an artefact of an extreme outlier. Our data indicate that between-clade differences in host body size and taxonomic richness are unlikely to affect between-clade differences in louse richness.

The evolutionary interaction between mammal diving behavior and louse taxonomic richness described above is similar to that already described in case of birds and avian lice. At least four alternative hypotheses can explain this pattern. First, louse richness can decline due to a direct effect of water in the pelage. Second, pelage may differ between diving vs. non-diving mammals in their structural characteristics. There can be also differences in the quality or quantity of grooming behavior between diving and non-diving mammals. Finally, the composition of skin glands excretion may also differ between aquatic and terrestrial mammals. Whether host diving behavior also affects other characteristics of lousiness, such as louse prevalence, body size, or intensity of infestations, is not known.

Acknowledgements. We thank Andrea Harnos for help in statistic analyses. The 2nd author was supported by the Hungarian National Research Fund (T 049157).

References

- Arnason U., Janke A. 2002. Mitogenomic analyses of eutherian relationship. *Cytogenetic and Genom Research*, 96, 20–32.
- Bininda-Emonds O.R., Gittleman J.L., Purvis A. 1999. Building large trees by combining phylogenetic information: complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews*, 74, 143–175.
- Cardillo M., Bininda-Emonds O.M., Boakes E., Purvis A. 2004. A species-level phylogenetic supertree of marsupials. *Journal of Zoology*, 264, 11–31.
- Clay T. 1964. Geographical distribution of the Mallophaga (Insecta). *Bulletin B.O.C.*, 84, 14–16.

- Clayton D.H., Walther B.A. 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. *Oikos*, 94, 455–467.
- Csorba G. 1995. Mammals. In: *Zootaxonomia* (Ed. L. Papp). Budapest (In Hungarian).
- Dalgleish B. 2005. Available from <http://www.phthiraptera.org> (cited 08 September 2005).
- Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist*, 125, 1–15.
- Felső B., Rózsa L. 2006. Reduced taxonomic richness of lice (Insecta: Phthiraptera) in diving birds. *Journal of Parasitology*, 92, 867–869.
- Grafen A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society, B*, 326, 119–157.
- Grenyer R., Purvis A. 2003. A composite species-level phylogeny of the ‘Insectivora’ (Mammalia: Order Lipotyphla Haeckel, 1866). *Journal of Zoology*, 260, 245–257.
- Jansa S.A., Weksler M. 2004. Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. *Molecular Phylogenetics and Evolution*, 31, 256–276.
- Johnson K.P., Clayton D.H. 2003. The biology, ecology, and evolution of chewing lice. In: *The chewing lice: world checklist and biological overview* (Eds. R.D. Price, R.A. Hellenthal, R.L. Palma, K.P. Johnson and D.H. Clayton). Illinois Natural History Survey Special Publication, 24.
- Klassen G.J. 1992. Coevolution: a history of the macroevolutionary approach to studying host-parasite associations. *Journal of Parasitology*, 78, 573–587.
- Liu F.R., Miyamoto M.M., Freire N.P., Ong P.Q., Tennant M.R., Young T.S., Gugel K.F. 2001. Molecular and morphological supertrees for eutherian (placental) mammals. *Science*, 291, 1786–1789.
- Luo J., Yang D., Suzuki H., Wang Y., Chen W., Campbell K.L., Zhang Y. 2004. Molecular phylogeny and biogeography of Oriental voles: genus *Eothenomys* (Muridae, Mammalia). *Molecular Phylogenetics and Evolution*, 33, 349–362.
- Møller A.P., Rózsa L. 2005. Parasite biodiversity and host defenses: Chewing lice and immune response of their avian hosts. *Oecologia*, 142, 169–176.
- Moyer B.R., Drown D.M., Clayton D.H. 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos*, 97, 223–228.
- Paterson A.M., Palma R.L., Gray E.R. 1999. How frequently do avian lice miss the boat? Implications for coevolutionary studies. *System of Biology*, 48, 214–223.
- Price R.D., Hellenthal R.A., Palma R.L. 2003. World checklist of chewing lice with host. In: *The chewing lice: world checklist and biological overview* (Eds. R.D. Price, R.A. Hellenthal, R.L. Palma, K.P. Johnson and D.H. Clayton). Illinois Natural History Survey Special Publication, 24.
- Rózsa L. 1993. Speciation patterns of ectoparasites and “stragglers” lice. *International Journal for Parasitology*, 23, 859–864.
- Rózsa L. 1997. Patterns in abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). *Journal of Avian Biology*, 28, 249–254.
- Silva M., Downing J.A. 1995. CRC handbook of mammalian body masses. CRC Press Inc., Boca Raton, Florida.