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Reduced Taxonomic Richness of Lice (Insecta: Phthiraptera) in Diving Birds

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ABSTRACT: Avian lice occupy different habitats in the host plumage that the physical environment outside the host body may affect in several ways. Interactions between host plumage and water may be an important source of such effects. Here, we use a comparative approach to examine the effect of a host's diving behavior on the taxonomic richness of its lice. Louse genera richness was significantly lower in clades of diving birds than on their nondiving sister clades. Species richness of host and body mass did not differ significantly between these clades; thus, these factors did not bias our results. This study suggests that the hosts' diving behavior can effectively influence ectoparasite communities.

Lice (Phthiraptera) are obligate parasitic insects that complete their entire life cycle on the body of the host. Avian lice are adapted to the warm, humid microhabitat near the skin of the host and cannot survive off the host for more than a few hr or days (Tompkins and Clayton, 1999). As previous studies suggest, several environmental factors influence the composition of louse communities. Host body size may influence parasite taxonomic richness because it may determine the amount of available resources (Rózsa, 1997; Clayton and Walther, 2001). Host population size and density also can influence the taxonomic richness of lice. Furthermore, 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 known to harbor more diverse parasite taxa than their sister clades, a relationship known as ''Eichler's rule'' (Klassen, 1992). Finally, the availability of water can shape louse communities, because low ambient humidity can reduce louse diversity (Moyer et al., 2002).

Diving behavior is likely to be an influential determinant of the water content of avian plumage. Even though water rarely penetrates beyond the surface of the plumage of diving birds, it can be expected to influence the humidity within the plumage. Therefore, we test whether a hosts' diving behavior affects the taxonomic richness of avian lice. First, we compare genera richness of lice among clades of diving versus nondiving birds. Then, we control for between-clade differences of host taxonomic richness and host body mass as potential confounding variables.

Diving birds were defined as birds that dive beneath the water surface with their complete body to take food. Nondiving birds were defined as either terrestrial or aquatic birds that acquire food from the water surface. Only lice of the faunistically well explored areas were included, i.e., continental Europe, continental North America, and the pelagic birds of the Southern Hemisphere. Geographic distribution data for birds were derived from Sibley and Monroe (1990). Other areas, such as continental Australia, were excluded from our study, because the lice are not known from many bird species within these regions. Louse richness is known to be correlated with sampling effort (Walther et al., 1995), but we made no further control for this effect.

Widely distributed bird species often have congeneric louse species, each restricted to different nonoverlapping parts of the host distribution, thus exhibiting an allopatric distribution. Consequently, parasite species richness of widely distributed bird species would overestimate the true parasite richness that each local bird 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 morphospecies (Møller and Rózsa, 2005).

The number of louse genera occurring on a particular host genus was obtained from Price et al. (2003). Louse genera that occur only outside our study area were excluded from the data set, e.g., *Rediella* spp. known from the Madagascar pratincole, were not included in our measure to describe the louse genera richness of pratincoles. Then, each host clade was characterized by values of mean louse genera richness (the average number of louse genera found on the host genera of a clade). One particular branching point between diving birds and nondiving birds falls within a single genus (*Pelecanus*); thus, we did not need averages here.

To calculate the mean species richness of host genera for a clade, we summed the number of bird species in each clade and divided it with the number of genera in that clade. Data were obtained from Howard and Moore (1991).

Avian body mass data were derived from Dunning (1992). Species with 2 or more data points (female and male, or ranges) were characterized by average values. Clade averages were obtained by 2 methods. First, we summed weights of all species of the clade we examined and divided the sum by the number of species (species average). Second, we divided the mean weights of genera with number of genera for each clade (genera average). This second approach gave qualitatively identical results in all analyses; thus, only the calculations with species averages are 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 birds and their nondiving sister clades. Some diving clades (such as diving

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

Diver clade	Mean genera richness of lice	Mean species richness of host genera	Mean body mass (g)	Nondiver clade	Mean genera richness of lice	Mean species richness of host genera	Mean body mass (g)
Alcedo, Megaceryle	1	10.50	94.86	*Merops*	3	22	32.83
Aptenodytes and allies	1.20	2.40	7,159.27	*Fregata*	3	5	1,238.75
Cinclus	3	3	60.25	*Turdus, Mimus, Sturnus*	2.72	14.55	67.68
Fulica	5	11	677.60	*Gallinula*	6	9	333.79
Gavia	1	5	3,239.80	*Hydrobatidae*	3.14	3	40.21
Netta, Aythya	5	7.50	899.63	*Anser, Branta, Cygnus*	6	7	3,754.37
Pandion	3	1	1,485.50	*Accipitridae*	4.88	7.94	1,498.47
Pelecanus occidentalis	2	1	3438	Other *Pelecanus* spp.	3	6	6,550
Sterna and allies	3.75	10.50	158.49	*Larus* and allies	4	15.33	643.61
Sula, Anhinga, Phalacrocorax	2	12.25	1,674.03	*Ardeidae*	2.56	5.55	764.26
Uria and allies	2.40	2.30	420.82	*Glareola*	2	7	73.60

petrels or tropic birds) were not included in our analyses, because there are no nondiving sister clades to which they can be compared independently from other comparisons. The phylogeny used for our analyses was derived from Sibley and Alquist (1990). For avian phylogeny, a total of 11 branching points of diving bird versus nondiving birds can be found within the geographic limits outlined above (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 diving birds versus nondiving birds. Here, the null hypothesis indicates that contrasts deviate from the mean randomly, thus their mean equals zero. Second, we searched for an interaction between contrasts of louse richness and disparities of potential confounding variables (host body mass and host richness) by linear regression forced through the origin. Computations were carried out with GraphPad InStat 3.06 (GraphPad Software Inc., San Diego, California). All statistical tests are 2-tailed.

The mean genera richness of lice is significantly lower on diving birds (*t*-test on mean of contrasts, n = 11, $P = 0.0042$; Fig. 1). Species richness of host genera tends to be somewhat higher on nondiving birds (1-sample *t*-test on means of contrasts, n = 11, $P = 0.0874$), whereas host body mass does not differ between sister clades (1-sample *t*-test, n = 11, $P = 0.2492$). Contrasts of host taxonomic richness are not correlated with contrasts of louse genera richness (linear regression forced through the origin $t = 1.15$, df = 10, $P = 0.2771$). Similarly, contrasts of louse genera richness are not predicted by contrasts of host body mass (linear regression through the origin, $t = -1.889$, df = 10, $P = 0.0882$). The direction of this nonsignificant covariation was opposite to the direction that could confound our results, i.e., clades with higher host body size tend to harbor fewer genera of lice. Briefly, between-clade differences in host body size and taxonomic richness are unlikely to affect between-clade differences in louse richness.

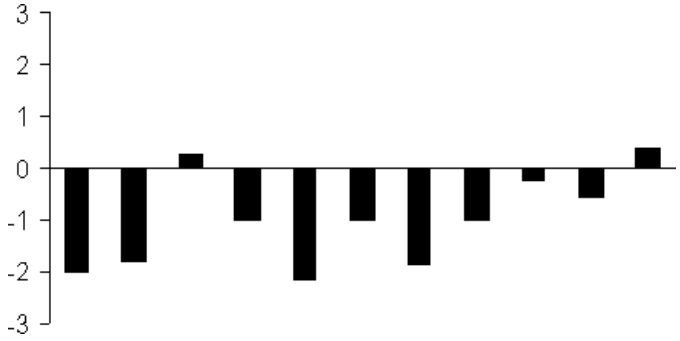

FIGURE 1. Contrasts of the mean genera richness of lice between diving and nondiving bird clades (sequence of Table I).

In one case, host geographic distribution data were equivocal. The marbled teal (*Marmaronetta angustirostris*) formerly occurred in our study range, but it recently became extinct; thus, we removed it from all analyses. Incorporating this host would further strengthen the relationship described here (data not shown).

Previous studies suggested that microhabitats in the avian plumage are relatively constant and independent from environmental effects. However, Moyer et al. (2002) demonstrated that air humidity outside the host body affects humidity in the plumage. Furthermore, they showed that low ambient humidity causes a sharp reduction in louse abundance. Here, we showed that high humidity inherent in the plumage of diving birds also can impact ectoparasite communities on an evolutionary time scale.

At least 3 alternative hypotheses can explain the pattern we described above. First, louse richness can decline due to a direct effect of water in the plumage. Second, avian plumage may differ between diving versus nondiving birds in their structural characteristics. Finally, preen-oil composition and use also may differ according to diving behavior, and a recent study seems to indicate that preen oil may have a role in combating lice (Moyer et al., 2003). On the contrary, however, since diving birds carry considerable quantities of air within their plumage, limited tolerance to oxygen shortage or to anaerobic lactic acidosis in lice is unlikely to account for the loss of louse genera in diving birds.

Whether host diving behavior also affects other characteristics of lousiness, such as louse prevalence, body size, or intensity of infestations, is not known. Similarly, we do not know whether louse richness is reduced in diving mammals compared with their nondiving sister clades, as indicated by anecdotal evidence.

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Transfer of *Borrelia Burgdorferi* s.s. Infection via Blood Transfusion in a Murine Model

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ABSTRACT: Without antibiotic treatment, the Lyme-disease–causing bacterium, *Borrelia burgdorferi* can be cultured from the peripheral blood of human patients nearly 6 wk post-tick bite. To determine if Lyme disease spirochetes can be transmitted from a spirochetemic donor mouse to a naive recipient during blood transfusion, blood taken from immunocompetent infected mice was transfused into either immunodeficient (SCID) mice, inbred immunocompetent animals (C3H/HeJ), or outbred mice. Nine of 19 (47.7%) immunodeficient mice, 7 of 15 (46.8%) inbred immunocompetent mice, and 6 of 10 (60.0%) outbred mice became infected with *B. burgdorferi* after transfusion. Our results indicate that it is possible to acquire *B. burgdoferi* infection via transfused blood in a mouse model of Lyme borreliosis.

Lyme disease is a systemic, tick-borne disease with clinical manifestations, which include dermatologic, rheumatologic, neurologic, and cardiac abnormalities. The causative agent of Lyme disease in the United States is the spirochete *Borrelia burgdorferi* sensu stricto, which has been isolated from cultures of blood from infected individuals early in the course of infection (Nadelman, Pavia et al., 1990). Depending upon the strain of *B. burgdorferi*, peak spirochetemia of the organism is reached between 7 and 10 days post-tick exposure (Dolan et al., 2004), but can be cultured from the blood of humans for close to 6 wk post-tick infestation (Schmidt et al., 1989). Previous studies have demonstrated that whole blood inoculated with *B. burgdorferi* (strain B31), separated into red cell frozen plasma and platelet fractions, and stored under blood banking conditions, had cultivable spirochetes in both the red cell (4 C) and fresh-frozen plasma fractions (−18 C) for up to 45 days, and in platelet concentrates (20–24 C) over a 6-day period. (Badon et al., 1989) Multiple investigators have found that *B. burgdorferi* was able to survive the standard blood processing procedures applied to transfused blood in the United States (Baranton and Saint-Girons, 1987; Nadelman, Sherer et al., 1988). In this study, we examined whether *B. burgdorferi* can be transfused successfully from a spirochetemic donor to a naive recipient via citrated blood transfusion in a mouse model of Lyme borreliosis.

Infected donor mice were generated by placing 5 laboratory-reared nymphal *Ixodes scapularis* ticks infected with *B. burgdorferi* (strain B-31), raised as previously described (Piesman, 1993), on each C3H/HeJ (Jackson Laboratories, Bar Harbor, Maine) or Imperial Cancer Research Fund (ICR) mouse. The ticks were allowed to feed until repletion. Ten days post-tick infestation, a time point previously shown to be peak spirochetemia in C3H mice (Dolan et al., 2004), 400 μl of sodium citrated blood was collected from donor mice by cardiac puncture. The citrate solution was prepared according to the American Association of Blood Banks technical manual and combined with blood at 14% (v/v) concentration (Brecher, 2005); 200 μl of the donor blood was placed in a microcentrifuge tube containing 20 μl of heparin for quantitative PCR (qPCR) analysis, and 200 μl (equivalent to 1 unit of blood transfused into a 150-kg patient) was transfused immediately into a recipient mouse via intravenous injection. In individual mice where intravenous inoculation was unsuccessful, an intraperitoneal injection was utilized. To quantify spirochetes, DNA was isolated from whole, heparinized donor blood with the use of a QIAGEN (Valencia, California) blood kit, and qPCR was run with the use of FLA primers and probe as previously described (Zeidner et al., 2001).

To test whether recipients with different levels of innate immunity could resist a spirochete transfusion, whole blood transfusions were performed in 3 study groups: (1) C3H/HeJ (Jackson Laboratories, Bar Harbor, Maine) infected donor mice transfused to severe combined immunodeficient (SCID-C3H/HeJ) recipient mice (Jackson Laboratories, Bar Harbor, Maine); (2) C3H/HeJ infected donor mice transfused to naive C3H/HeJ recipient mice; and (3) Imperial Cancer Research Fund (ICR) (obtained from a pathogen-free colony maintained at the Centers for Disease Control and Prevention [CDC], Fort Collins, Colorado) infected outbred donor mice to naive ICR outbred recipient mice.

Four weeks post-transfusion, ear biopsies were obtained from recipient mice and cultured in Barbor–Stoenner–Kelly medium (Barbour, 1984) to determine infection prevalence of *B. burgdorferi* (Sinsky and Piesman, 1989). Ear biopsies were obtained from donor mice 4 wk post-transfusion to confirm that recipient mice were transfused with infected blood. Recipients that received blood from an uninfected donor were removed from the study. Cultures of biopsied ears, hearts, and bladders were checked for the presence of spirochetes every 7 days for 4 wk by dark-field microscopy.

Blood transfusion from C3H/HeJ infected donor mice to SCID recipient mice resulted in 9 of 19 (47.7%) recipient mice becoming infected (Table I). Transfusion from infected C3H/HeJ donor mice to naive C3H/HeJ recipient mice resulted in 7 of 15 (46.6%) mice acquiring infection and transfusion from ICR donor mice to naive ICR recipient mice resulted in 6 of 10 (60%) becoming infected with *B. burgdorferi* (Table I). The number of spirochetes/milliliter delivered to the recipient mice did not affect successful transmission. The average number of bacteria/