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Clever birds are lousy: Co-variation between avian innovation and the taxonomic richness of their amblyceran lice

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ABSTRACT

Lice (Insecta: Phthiraptera) are ectoparasites that reduce host life expectancy and sexual attractiveness. Their taxonomic richness varies considerably among their hosts. Previous studies have already explored some important factors shaping louse diversity. An unexplored potential correlate of louse taxonomic richness is host behavioural flexibility. In this comparative study, we examine the relationship between louse generic richness, innovative capabilities (as a proxy for behavioural flexibility), and brain size while controlling for host species diversity, phylogeny, body size and research effort. Using data for 108 avian families, we found a highly significant positive relationship between host innovative capabilities and the taxonomic richness of amblyceran lice, but a lack of a similar relationship in ischnoceran lice. Host brain size had only a marginal impact on amblyceran diversity and no correlation with ischnoceran diversity. This suggests that the effect in Amblycera is not mediated by metabolic limitations due to the energetic costs of brain size and maintenance, rather directly caused by the ecological differences between hosts with differing cognitive capabilities. We propose four alternative and mutually non-exclusive hypotheses that may explain this phenomenon.

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1. Introduction

Avian lice are interesting candidates to explore environmental factors affecting parasite biodiversity for several reasons. Firstly, animal lice (Insecta: Phthiraptera) are pathogens in the sense that they reduce host life expectancy (Brown et al., 1995) and flight performance (Barbosa et al., 2002), as well as increase metabolism (Booth et al., 1993) and reduce sexual attractiveness (Clayton, 1990; Kose and Møller, 1999; Kose et al., 1999). Secondly, the diversity and host distribution of avian lice has been extensively reviewed (Price et al., 2003). Finally, avian lice are relatively diverse compared with the species richness of mammalian lice (Johnson and Clayton, 2003).

In spite of this, a complete understanding of the taxonomic richness of avian louse fauna is still lacking. One particular methodological problem is that louse species richness data are biased by differences in research effort (Walther et al., 1995). Moreover, parasites can be inherited from host ancestors (Page, 2003) and, therefore, host phylogeny limits species composition. Thus studies of

parasite richness must always control for potential biases due to differences in sampling effort and host phylogeny.

Some environmental correlates of louse taxonomic richness have already been explored, incorporating some kind of controls for the biases mentioned above. For example, past bottlenecks in host population size may result in a long-lasting reduction of louse richness (Paterson et al., 1999; MacLeod et al., 2010). Moreover, an evolutionary switch to an aquatic way of life (or, more precisely, to diving behaviour) reduces louse richness compared with louse assemblages inhabiting non-aquatic sister-clades of birds (Felső and Rózsa, 2006). Interestingly, higher levels of avian physiological defences such as stronger T-cell immune response or relatively larger uropygial glands co-vary positively with the taxonomic richness of amblyceran lice, while they do not interact with the richness of ischnoceran lice (Møller and Rózsa, 2005; Møller et al., 2010). Finally, the population size of marine birds and – to a lesser extent – their geographic range co-varies positively with louse richness (Hughes and Page, 2007).

One other intriguing environmental correlate of avian parasites might be host behavioural flexibility. It can be quantified as feeding innovation rates and its neural correlate, relative brain size (Lefebvre et al., 1997). Bird clades that show high rates of novel feeding techniques tend to have large brains (Overington et al.,

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2009). Both of these traits are associated with a higher prevalence of endoparasites (Garamszegi et al., 2007), as well as a stronger immune response in the form of an enlarged spleen and bursa of Fabricius (Møller et al., 2004). This relationship might be facilitated by the exposure of innovative clades to a wider set of habitats (Overington, S.E., 2011. Behavioural Innovation and the Evolution of Cognition in Birds. Ph.D. Thesis. McGill University, Canada), resulting in a higher rate of contact with a diversity of potential parasites. The positive relationship between endoparasite infestation, immune response, innovation rate and relative brain size is all the more intriguing in that it runs counter to the known cost of parasites on brain development. In bats and rodents, Bordes et al. (2008, 2010) followed such logic in predicting a negative effect of parasite species richness on brain size due to a trade-off between energetic costs of immune defence and those of brain maintenance. In contrast, they found a positive association similar to the one reported in birds.

In this paper, we examine the relationship between avian ectoparasite richness, innovation rate and brain size while controlling for host species diversity, body size, phylogeny and research effort. We predict that ectoparasite richness should be positively associated with innovation rate and relative brain size.

2. Materials and methods

2.1. Host taxonomic levels used in the study

We examined variation in avian traits at the family level. Correlates of innovation rate and relative brain size are routinely studied at this level (Sol et al., 2005a,b; Overington et al., 2009). The avian family level is also convenient for the measure of ectoparasite diversity and helps to account for missing information at the species level.

2.2. Taxonomic richness of hosts and lice

Species richness of bird families was obtained from the checklist of Sibley and Monroe (1990), because the innovation and relative brain size data also refer to bird families recognised by this checklist. As host species richness among avian families varied across several magnitudes (1–993) we log-transformed species richness data in all subsequent analyses.

We used generic richness as a proxy for louse taxonomic diversity because it has several advantages over species richness. Firstly, a widely distributed bird species often hosts congeneric louse species, each restricted to different non-overlapping parts of the host distribution. Thus, parasite species richness of widely distributed bird species would over-estimate the true parasite richness that each local bird population harbours (Clay, 1964). Secondly, taxonomists often use different species concepts to describe louse diversity (Mey, 2003), making species richness an unreliable measure. Some taxonomists automatically described congeneric lice from different hosts as distinct species while other authors lump many species into a single one from a wide range of hosts (see Price (1975) as an example). Finally, the bias caused by uneven sampling intensity is stronger at the species level than at the generic level. The number of louse genera found per avian family was obtained from Price et al. (2003).

However, Price et al. (2003) used a bird checklist which differs slightly from that used in the innovation and brain size datasets. Therefore, the louse lists were fitted to the families recognised by Sibley and Monroe (1990) by dividing or unifying certain families. We collected richness data separately for amblycercan and ischnocercan lice. This is because the life histories and the important factors affecting distribution and evolution in these louse suborders are

quite different, as already shown by several previous studies (see e.g. Johnson and Clayton, 2003; Møller and Rózsa, 2005; Felső and Rózsa, 2006; Whiteman et al., 2006; Møller et al., 2010). Louse generic richness data was not log-transformed, as it did not vary across several magnitudes (see Section 3).

We controlled for uneven louse sampling effort in two different ways. Firstly, we used generic richness to quantify parasite diversity, which is less biased by sampling than species richness. Arguably, a larger proportion of louse species awaits description than the proportion of unknown louse genera. Secondly, for each host family we calculated a study effort rate defined as the number of species known to be associated with lice divided by the total number of species. Then we excluded all bird families below the 10% effort rate, an arbitrary limit thus reducing the sample size from 108 to 99. As all results in the subsequent analyses were qualitatively identical to those obtained using the whole dataset, we do not report these results.

2.3. Quantifying rates of feeding innovation

We used a current extended version of the database on avian innovations collated by Lefebvre and colleagues (Lefebvre et al., 1997; Overington et al., 2009). In birds, feeding innovations are defined as new foods or new ways of searching, handling or ingesting food (Kummer and Goodall, 1985; Lefebvre et al., 1997; Reader and Laland, 2003). The innovation database currently contains over 2,300 reports for 808 species in six zones of the world (North America, Western Europe, Australia, New Zealand, southern Africa and the Indian subcontinent), compiled from volumes of 64 ornithology journals published mostly between 1960 and 2002. These journals include academic serials (e.g. *Auk*, *British Birds*, *Ibis*, *Emu*) as well as publications that are edited by local birding organisations (e.g. *Florida Field Naturalist*, *Nebraska Bird Review*). Reports are included in the database if they contain keywords such as 'novel', 'opportunistic', 'first description', 'not noted before' or 'unusual' (Lefebvre et al., 1997). Although the degree to which the noted behaviour is a departure from the species' repertoire may vary, the strength of this database is that it relies on the knowledge of local birders and ornithologists, as well as that of journal editors and reviewers. All of the reports, and the claim of novelty they contain, have thus been subject to some form of peer review. The reliability and validity of the database has been checked for biases stemming from species number per clade, research effort, population size, likelihood of noticing and reporting a case, popularity of a species among observers, inter-classifier (most often blind to the hypothesis) agreement (0.827–0.910), journal identity, geographical zone and historical period (Nicolakakis and Lefebvre, 2000; Lefebvre et al., 2001). In this paper, we corrected innovation frequency by research effort, defined as the number of articles listed for each species in the online version of the *Zoological Record* (available at: www.library.dialog.com/bluesheets/html/bl0185.html). Both innovation rate and research effort were summed for families by adding species level data and log transforming the totals.

2.4. Relative brain size and body mass for avian families

The avian brain size database includes 1,714 species, comprising both directly measured brain mass and endocranial volumes converted to mass (as described in Mlikovsky, 1989a,b,c, 1990; DeVoogd et al., 1993; Székely et al., 1996; Garamszegi et al., 2002; Iwaniuk and Nelson, 2002; Iwaniuk (Iwaniuk, A.N., 2003. The Evolution of Brain Size and Structure in Birds. Ph.D. Thesis. Monash University, Australia); Sol et al., 2005a). These data represent mean values of male and female specimens. Previous work (Overington et al., 2009) has shown that the combination of data

from multiple sources does not bias the relationship with innovation rate: data on 1,197 species from a single experimenter (Iwaniuk, 2003, Ph.D. thesis, see above) using one technique (endocranial volume, which is not influenced by potential errors related to freezing, desiccation or perfusion that can affect fresh brains) yields similar conclusions to that of the dataset collated from multiple sources. The relationship between innovation rate and relative size of the neural substrate is also robust with respect to both anatomical level and origin of the dataset, yielding similar results at the level of: the whole brain – combined dataset or limited endocranial dataset of Iwaniuk (2003, Ph.D. thesis, see above), reported in Overington et al. (2009); the cerebral hemispheres – data from Portmann (1947), reported in Lefebvre et al. (1997); or the mesopallium and nidopallium – data from Boire (Boire, D., 1989. *Comparaison quantitative de l'encéphale, de ses grandes subdivisions et de relais visuels, trijumeaux et acoustiques chez 28 espèces d'oiseaux*. Ph.D. Thesis. Université de Montréal, Canada) and Rehkämper et al. (1991), reported in Timmermans et al. (2000). The relationship is also independent of the known confounding effect of development mode of brain size (Bennett and Harvey, 1985).

Body mass is a well-known covariate of brain size in birds as well as a potential confounding variable in comparative studies in general (Garland et al., 1992), and particularly in studies focused on avian louse assemblages (Rózsa, 1997). Body mass data were taken from the same sources as brain mass. We averaged brain volumes and body masses within each family and calculated the residuals from a log–log linear regression of the mean body size and brain size of species for each family. As the usage of residuals from linear regression is often criticised (Freckleton, 2002, 2009) we also computed the ratio of brain size to body mass. However, as the results obtained by using this ratio were qualitatively identical to the results obtained when analysing residual brain size, we report only the latter.

2.5. Phylogenetic trees

We constructed three different phylogenetic trees of bird families in Mesquite 2.74 (available at www.mesquiteproject.org) to take evolutionary history into account (Felsenstein, 1985, 2004). One of these trees was constructed by Sibley and Ahlquist (1990) with branch length values based on DNA–DNA hybridisation. This tree was obtained from the Analysis of Phylogenetics and Evolution ('ape') package (Paradis et al., 2004) in R 2.11.1 (available at www.R-project.org). The phylogenetic hypothesis of Sibley and Ahlquist (1990) is often still used in comparative studies because it provides the most complete available tree with real branch lengths (Overington et al., 2009). However, more recent studies based on nuclear and mtDNA sequences suggested that several relationships in Sibley and Ahlquist (1990) tree might not be correct (Barker et al., 2004; Alström et al., 2006; Hackett et al., 2008).

Therefore, we constructed two other trees, one based on Barker et al. (2004) and Hackett et al. (2008), and another one based on Barker et al. (2004), Alström et al. (2006) and Hackett et al. (2008). The non-passerine branching pattern from Hackett et al. (2008) was combined with passerine topology from Barker et al. (2004) and the latter was modified in one of the trees according to Alström et al. (2006). These trees differ from each other in the phylogeny of Passeriformes. The relationships among these families are still uncertain, possibly due to the rapid radiation of Passeriformes (Barker et al., 2004; Alström et al., 2006). Although these phylogenies provide more up-to-date branching patterns, they come without branch length values. Therefore, we used arbitrary branch lengths computed with PDAP:PDTREE module 1.15 (available at www.mesquiteproject.org/pdap_mesquite) in Mesquite 2.74. This module allows the calculation of arbitrary branch

lengths using several methods, e.g. all branch lengths equal to one, branch lengths according to the method of Grafen (1989), Pagel (1992) or Nee (Purvis, 1995).

The results obtained by using different trees (and different arbitrary branch lengths in the case of newer trees) were qualitatively identical; therefore, we report only the analysis based on Sibley and Ahlquist (1990) tree. This choice was reasonable as this was the only phylogenetic model to contain real branch length information and provides a perfect fit to data according to the diagnostic plots (see Section 2.6).

Our phylogenetic trees contained polytomies, probably due to the uncertainty about the true bifurcating patterns. Polytomies in the phylogenetic trees can cause inflation in the type I error in the analysis of independent contrasts (Grafen, 1989; Purvis and Garland, 1993); however, this problem was resolved by bounded degrees of freedom, as recommended by Purvis and Garland (1993) and tested by Garland and Díaz-Uriarte (1999).

2.6. Statistical analyses

We used the method of independent contrasts to control for phylogenetic non-independence (Felsenstein, 1985). Calculations were carried out with PDAP:PDTREE module 1.15 in Mesquite 2.74. We plotted the absolute values of standardised phylogenetically independent contrasts versus their S.D.s as the most widespread and reliable diagnostic check to test whether the branch lengths fitted the data (Garland et al., 1992; Díaz-Uriarte and Garland, 1996, 1998). According to diagnostic plots, the model using the phylogenetic tree by Sibley and Ahlquist (1990) provided a perfect fit. The more recent trees by Barker et al. (2004), Alström et al. (2006) and Hackett et al. (2008) with arbitrary branch lengths did not provide a perfect fit, probably due to the lack of real branch length information. We simulated character evolution under the Brownian motion model (Felsenstein, 1985). Although this model might not perfectly represent the process of evolutionary changes, several authors have shown that even with errors in branch lengths and deviations from Brownian motion the method of independent contrasts is robust and reliable (Díaz-Uriarte and Garland, 1996, 1998).

The correlated evolution between two continuous variables can be tested simultaneously by using the method of independent contrasts in Mesquite 2.74. Therefore, we created standardised contrasts for each variable and performed multiple linear regressions to test the explanatory power of all variables on the louse taxonomic richness at the same time. All regressions were computed through the origin (Felsenstein, 1985; Garland et al., 1992). Multicollinearity between the explanatory variables was checked by variance inflation factor (VIF) (Reiczigel et al., 2007). These analyses were carried out with R 2.11.1 using the packages 'R Commander' (available at www.cran.r-project.org/package=Rcmdr) and 'faraway' (available at www.maths.bath.ac.uk/~jff23). We calculated the *K* phylogenetic signal measure (Blomberg et al., 2003) using the 'picante' package (Kembel et al., 2010). All reported *P*-values are two-tailed and a *P* value of 0.05 was considered significant. The full dataset of all variables is available from the corresponding author.

3. Results

Both amblyceran (range: 0–10 genera, mean = 1.92) and ischnoceran (range: 0–14 genera, mean = 2.26) richness varied extensively across the 108 avian families involved. The *K* phylogenetic signal measure (Blomberg et al., 2003) of our variables varied between 0.61 and 2.10 suggesting some degree of phylogenetic non-independence. The phylogenetic signal was significant

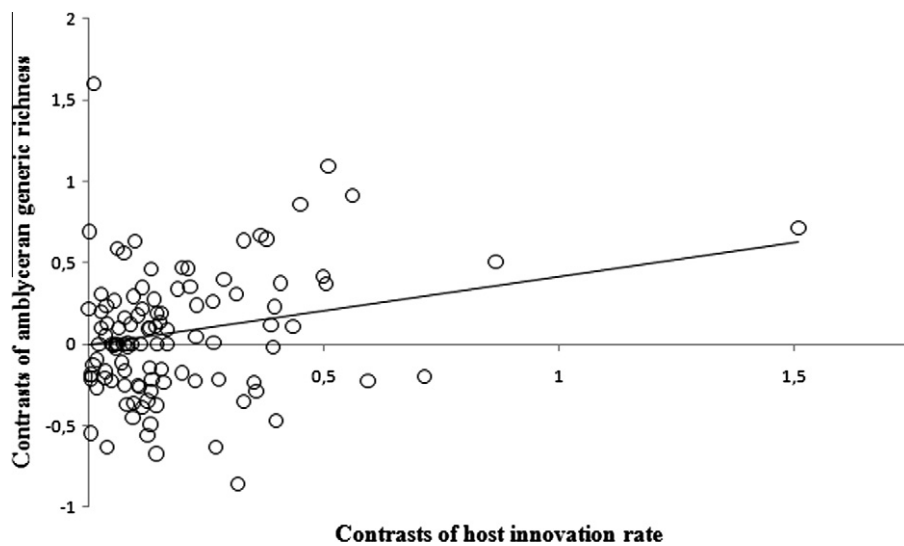


Fig. 1. Co-variation of avian innovation rate and amblyceran richness.

($P < 0.001$) in residual brain size ($K = 0.99$), body mass ($K = 1.91$), ratio of brain size to body mass ($K = 2.10$), and amblyceran generic richness ($K = 0.80$); hence we controlled for phylogeny in all analyses.

In a phylogenetically controlled comparison, host innovation rate per family, co-varied positively with amblyceran richness ($n = 107$, slope = 0.42, $r = 0.30$, $P = 0.002$, Fig. 1), but no similar significant relationship appeared with ischnoceran richness ($n = 107$, slope = 0.18, $r = 0.08$, $P = 0.388$). Relative brain size also showed a significant correlation with amblyceran richness ($n = 102$, slope = 0.37, $r = 0.19$, $P = 0.049$), however, it did not correlate with ischnoceran richness ($n = 102$, slope = 0.51, $r = 0.18$, $P = 0.076$).

We found a strong positive correlation between amblyceran and ischnoceran richness across avian families ($n = 107$, slope = 0.98, $r = 0.65$, $P < 0.001$). The (log) species richness of avian families showed a highly significant positive correlation both with amblyceran ($n = 107$, slope = 1.43, $r = 0.65$, $P < 0.001$) and ischnoceran richness ($n = 107$, slope = 2.05, $r = 0.62$, $P < 0.001$). However, species richness of avian families co-varied with neither innovation rate ($n = 107$, slope = 0.21, $r = 0.14$, $P = 0.161$) nor residual brain size ($n = 102$, slope = -0.01 , $r = -0.01$, $P = 0.992$).

One can presume that body mass might act as a confounding variable since more innovative birds may tend to be larger and, consequently, may harbour more diverse louse burdens. Therefore, we checked the relationship between avian (log) body masses and innovative capabilities. Contrary to our expectations, there was no relationship between these variables ($n = 102$, slope = -0.07 , $r = -0.03$, $P = 0.741$). Additionally, we found no correlation between (log) host body mass and either amblyceran ($n = 102$, slope = -0.29 , $r = -0.09$, $P = 0.345$) or ischnoceran generic richness ($n = 102$, slope = -0.39 , $r = -0.08$, $P = 0.396$).

In our multiple linear regression models the response variables were the standardised contrasts of either amblyceran or ischnoceran richness. The explanatory variables were the standardised contrasts of host innovative capability, relative brain size, (log) species richness and (log) body mass of avian families, and the generic-level richness of the other louse suborder. Significant predictors of amblyceran richness were avian (log) species richness (slope = 0.83, $P < 0.001$), innovative capabilities (slope = 0.30, $P = 0.001$), and ischnoceran richness (slope = 0.26, $P < 0.001$, adjusted R^2 of the model = 0.56). There was no multicollinearity between the explanatory variables (VIF values, respectively: 1.64, 1.02 and 1.62). Significant predictors of ischnoceran richness were avian (log) species richness (slope = 1.13, $P < 0.001$), and amblycer-

an richness (slope = 0.65, $P < 0.001$, adjusted R^2 of the model = 0.48). There was no multicollinearity between the explanatory variables (VIF values, respectively: 1.75, 1.75).

4. Discussion

To our knowledge, this is the first reported study to explore ecological correlates of the taxonomic richness of louse infestations across a considerably wide range of avian families, comprehensively sampling avian diversity. In particular, we included a large proportion – 108 out of 146 – of the families recognised by Sibley and Monroe (1990).

Our results show that both amblyceran and ischnoceran generic richness co-varied positively with host taxonomic richness. The relationship between host taxonomic richness and louse richness was predicted several decades ago by Eichler (1942). This effect is often called “Eichler’s rule”. The positive relationship between amblyceran and ischnoceran richness – independent of the parallel effect of “Eichler’s rule” – has already been reported by Møller and Rózsa (2005) and is strongly supported by our present results. Ecological interpretation of this phenomenon is not well understood. It seems likely that an increase in host diversity might increase amblyceran and ischnoceran richness as parallel but independent effects. However, this effect was not responsible for the relationship of amblyceran richness with innovation rate or residual brain size, as species richness of avian families co-varied with neither of these variables. The lack of co-variation between innovation rates and host species richness was not surprising given the fact that the innovation rate was already controlled for research effort, which is highly correlated with avian species richness (Lefebvre et al., 2001).

The most surprising result of the present study was a highly significant positive relationship between host residual innovation frequency and the taxonomic richness of amblyceran lice (Fig. 1), in contrast to the lack of a similar relationship in the case of ischnoceran lice. The correlation between host innovative capabilities and amblyceran richness was not influenced by the three outlier points (Fig. 1). According to model diagnostic plots, these points were not influential and results obtained by excluding them were qualitatively identical. This co-variation was robust, as we found qualitatively identical results by using any of the phylogenetic trees and arbitrary branch length transformations described above. This was not a spurious effect of host taxonomic richness, as it was

not significantly associated with either innovation rate or residual brain size.

Host behavioural flexibility interacts with amblyceran richness; however, host brain size has only a marginal impact. This finding is paralleled by results of Bordes et al. (2010) who found that only the taxonomic richness of mites, but not the richness of helminths or fleas, was predicted by differences in host brain size. These results again raise doubts about the hypothesis that parasite richness is affected by the high costs of producing and maintaining large brains in the host. It seems more likely that it is not the large brains per se that are important, but cognitive capabilities that co-vary directly with the taxonomic richness of parasite assemblages. In birds, the metabolic costs of maintaining a large brain do not seem to be as high as they are in mammals. Isler and van Schaik (2006a) found a strong association between basal metabolic rate and brain size (both corrected for body size) in 347 mammalian species, but not in 224 species of birds (Isler and van Schaik, 2006b).

Here we propose four alternative and mutually non-exclusive hypotheses that might possibly explain the co-variation of host innovative capabilities and amblyceran richness. Firstly, Sol et al. (2005a) have shown that more innovative birds are also better at colonising new zones in which they have been introduced. Perhaps as a consequence, more innovative species also tend to have more subspecies (Sol et al., 2005b) and innovative parvorders (a taxon between infraorder and family) more species (Nicolakakis et al., 2003) than less innovative ones. Host diversity is known to be associated with louse diversity (Eichler, 1941), so if innovativeness contributes to avian diversity, then we also expect innovativeness and louse diversity to co-vary. While this effect might partly contribute to amblyceran richness on more innovative taxa, we emphasise that the relationship between amblyceran richness and host innovative capabilities was also significant independently of the parallel effect of “Eichler’s rule”.

Secondly, Overington et al. (in press) has shown that more innovative birds exploit a wider diversity of habitats than less innovative ones. These clades might thus have a greater chance of contacting other avian taxa in these habitats, enabling lice specific to other birds to switch more frequently to innovative birds.

Thirdly, birds with more sophisticated cognitive capabilities are also likely to be more social. Logical arguments from resource defence theory, confirmed by a game theory model, suggest that the spatial and temporal predictability of food should drive both sociality and generalism/opportunism in the same direction (Overington et al., 2008). Burish et al. (2004) reported that the volume of the telencephalic portion of the brain is correlated with social complexity in birds; while Emery et al. (2007) show that the birds with the largest brain sizes are those that live in small groups of 5–30 individuals. More social birds are likely to have more opportunities for louse transmission, which may lead to a higher prevalence of lice in social species as shown by Rékási et al. (1997). This in turn might lower the risk of extinction for lice at low host population sizes (Paterson et al., 2010), leading to higher diversity over time. Additionally, several studies have shown that louse prevalence is higher in more social individuals of the same species (Hoi et al., 1998; Monello and Gompper, 2010). In a study comparing prevalence and intensity of Amblycera versus Ischnocera on Galapagos Hawks (*Buteo galapagoensis*), both prevalence and intensity increased with larger group sizes for Amblycera, but not for Ischnocera (Whiteman and Parker, 2004). This difference might explain the difference between Amblycera and Ischnocera in the correlation we found between innovation and louse diversity, in which only amblyceran diversity was significantly correlated with innovativeness. Based on these studies, it seems conceivable that in periods of host population bottlenecks, louse extinction rates are higher for Amblycera on more solitary birds.

Finally, birds that show more feeding innovations might also innovate in other domains that affect louse richness, for example grooming. However, this possibility would work against the relationship we have found here, unless these innovations are more efficient against Amblycera than they are against Ischnocera. Former studies have shown that more advanced host defences increase amblyceran taxonomic diversity (Møller and Rózsa, 2005; Møller et al., 2010). Intriguingly, innovative birds such as grackles and starlings have been seen “anting” with a variety of compounds, including marigold flowers (Dennis, 1985), moth balls (Borgelt, 1960; Clark et al., 1990) and lime (Clayton and Vernon, 1993). Clayton and Vernon (1993) experimentally tested the efficiency of lime against ischnocerans and found that a component of lime oil, *D*-limonene, was lethal to the lice. More research is needed to see whether the innovative use of grooming compounds has an effect that might mitigate some of the parasite risk factors in birds.

To summarise, avian cognitive capabilities co-vary positively with the taxonomic diversity of amblyceran lice – but are not affected by the diversity of ischnoceran lice. Testing the potential causes and consequences of this effect will be a challenging task for future authors.

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