

NEWS AND COMMENTARY

Lousy heirlooms

Lice help illuminate the recent evolutionary history of an Australian bird

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It is remarkable to consider that in the year 2008, most human societies still harbor human head and body lice (Insecta: Phthiraptera: *Pediculus humanus*). Although distressing for those infested, this is testimony to the evolutionary durability of these hardy parasites. Our closest living relatives, the chimpanzees, also continue to suffer from infestations of the chimpanzee louse *P. schaeffi*, which is the closest living relative of *P. humanus*. The lineages leading to humans and chimps, as well as to the two *Pediculus* lineages, coalesce contemporaneously in common ancestors approximately 6 million years ago (Reed *et al.*, 2004). Because parasites tend to tag along for the evolutionary ride, biologists have long used parasites to understand the evolutionary relationships of their hosts (Klassen, 1992). The practice is based on the observation that parasite lineages can be transmitted from parent to offspring, and eventually from ancestral to descendent species. Because parasites tend to be morphologically conservative relative to hosts, their shared distributions have sometimes suggested recent shared ancestry among the host species. Charles Darwin wondered, in a letter to parasitologist Henry Denny in 1844, 'When the same bird in immensely remote countries, has the same parasite, do you never observe some slight difference in color size or proportions of such parasites?' Largely (and wisely) abandoned due to the difficulties of assessing homoplasy before the advent of modern phylogenetics, a steady stream of recent studies have generated a renaissance in the use of studying parasites to glean information about their host's histories (Nieberding and Olivieri, 2007). At the molecular level, parasites tend to evolve more rapidly than their hosts. This is particularly germane to the lice of birds and mammals, which can exhibit greater phylogeographic (Whiteman *et al.*, 2007) and phylogenetic (Hafner *et al.*, 1994) divergence than their hosts. It has also been

used effectively in exploring the biology of hosts with small (bottlenecked) populations, as in endangered right whales whose cyamid 'lice' populations harbor considerably greater genetic variability than their hosts (Kaliszewska *et al.*, 2005). Using this reasoning, Toon and Hughes (2008) in this issue of *Heredity* report the results of a comparative population genetic and phylogeographic study of the Australian magpie *Gymnorhina tibicen* (Passeriformes: Artamidae) and two species of chewing louse, *Philopterus* sp. and *Brueelia semiannulata*, adding fresh insight into the host's evolutionary history.

Two putative Pleistocene refugia in Australia, one in the east and another in the west, explain the most salient features of the distributions and phylogeographic patterns of many extant species in Australia, including the present-day population structure of *G. tibicen*. There is shallow phylogeographic structuring in *G. tibicen* from the west to east (based on mitochondrial DNA (mtDNA) sequence data); the eastern and western populations were estimated to have diverged from one another at least 50 000 years ago (Toon *et al.*, 2007). However, nuclear microsatellite data showed evidence of contemporary gene flow between the two populations. The mitochondrial nuclear discordance was hypothesized to be due to male-biased gene flow between these populations. Toon and Hughes (2008) investigated whether genetic information from the two chewing lice of the magpie might shed additional light on this question, given natural history differences in the two louse species found on the host: *Philopterus* sp. is relatively host-specific and lives only on the head and nape feathers and *B. semiannulata* is less host-specific and occurs primarily on the body feathers. The authors expected the former to potentially match host history, because it is likely to be less dispersive, and the latter to reflect contemporary events (for example,

gene flow), because they suggest that it could be transmitted more easily between magpies (*sensu*; Clayton *et al.*, 2004).

In their analysis of mtDNA sequence data, the authors show that a previously identified east–west phylogeographic break in the host is also present in the mtDNA sequence data of the louse *Philopterus* sp. Approximately 75% of the mtDNA variation in *Philopterus* was partitioned between eastern and western mtDNA clades of the host. Moreover, this louse exhibited a greater degree of population structure than the host and harbored a third, cryptic clade comprising samples collected near Alice Springs that was not observed in the host, whose members fell into the eastern clade. The additional information afforded by the parasite pointed to the possibility of a previously unknown area of endemism in the host that could reflect a third magpie refugium during the Pleistocene.

Strikingly, the population genetic and phylogeographic structure of the second louse species, *B. semiannulata*, which is less host-specific and more of a habitat generalist on body feathers, did not match its host's structure and instead showed strong north–south structuring, which remains unexplained. These results are intriguing, because they suggest that *B. semiannulata* gene flow has not occurred despite gene flow in its host populations.

The evidence presented by Toon and Hughes (2008) that Australian magpies and their lice reciprocally illuminate their evolutionary histories is compelling. Nonetheless, important gaps remain, including the fact that small sample sizes did not allow for a detailed comparison of host and parasite inter-population migration rates or population divergence times, nor was there an attempt to test statistically whether either louse coexpanded with the host out of Pleistocene refugia. This study adds to the growing body of evidence suggesting that parasite species can give us important information about their hosts that would be difficult or impossible to come by in the hosts themselves, particularly in cases where the host populations are highly inbred or have not had sufficient time to accumulate informative substitutions. This study also illustrates how carefully one must consider the natural history of the parasite in these analyses. Although both parasite species showed marked structure across the range of the host, the two lice told different stories.

While the number of studies using parasites to infer host history is rising, the analytical framework for testing whether hosts and parasite populations share a common evolutionary history remains underdeveloped. At the macroevolutionary scale, cophylogenetic analytical methods are relatively sophisticated and allow one to test for cospeciation between hosts and parasite lineages as well as a suite of other processes, provided phylogenies are robust. When macroevolutionary studies are linked to ecological and microevolutionary studies, strong inferences are possible (Clayton *et al.*, 2004), although in other host-parasite systems, microevolutionary and macroevolutionary studies yielded contradictory results (Gómez Díaz *et al.*, 2007).

Researchers using parasites to infer host history should correlate host and parasite population structure (gene flow), population divergence times (estimated using the coalescent) and phylogenetic branching patterns when possible, but are these methods sufficient to show that host and parasite evolutionary histories are actually linked? The emerging field of cophylogenomics has the potential to add an additional layer of inquiry in studies relying on parasites to infer host history. It is possible to use existing statistical tests to determine whether populations of a host and parasite (or any two interacting species) have coexpanded from an ancestral area (Templeton, 2008). Using coalescent simulations, one can also construct Bayesian skyline

plots to determine whether changes in host and parasite effective population size are contemporaneous, or whether the signal present in the parasite data yields additional insight into ecological forces experienced by both parties (Biek *et al.*, 2006). Especially interesting would be to include magpie and parasite samples from the entire species range, including Papua New Guinea, as well as anthropogenically introduced populations such as those in New Zealand. Because colonization dates are either known or can be estimated using external information, this could provide for a better-calibrated test of whether host and parasite populations coexpanded after the Pleistocene.

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