ABSTRACT: Parasites are incredibly diverse. An important factor in the evolution of this diversity is the fact that many parasite species are restricted to 1, or just a few, host species. In addition, some parasites exhibit geographic specificity that is nested within their specificity to a particular species of host. The environmental factors that restrict parasites to particular regions within the host’s range are poorly understood, and it is often difficult to know whether such patterns of geographic specificity are real, or merely artifacts of uneven host sampling. For over a decade, we sampled communities of ectoparasitic lice (Phthiraptera) from birds and mammals, exhibit pronounced host specificity, often resulting from adaptation by parasites to particular features of their hosts (Bush and Clayton, 2006; Poulin and Keeney, 2007). However, such features are not the only factors governing host use; some parasites appear restricted to a subset of the host’s geographic range by environmental influences that are poorly understood. It is often difficult to know whether such patterns of geographic specificity are real, or if they are simply artifacts of uneven host sampling. In this article, we use data collected over more than a decade to document a significant pattern of geographic specificity among communities of chewing lice living on western scrub-jays (Aphelocoma californica). We then consider different hypotheses to explain the underlying causes of this geographic specificity.

Parasites represent a large fraction of the earth’s biodiversity (Price, 1980; Poulin and Morand, 2004). A main cause of this diversity is the fact that many parasites are more or less host specific; they use only a subset of the hosts available at a given location (Thompson, 1994; Poulin, 2007). Host specificity may often result from adaptation by parasites to particular features of their hosts (Bush and Clayton, 2006; Poulin and Keeney, 2007). However, such features are not the only factors governing host use; some parasites appear restricted to a subset of the host’s geographic range by environmental influences that are poorly understood. It is often difficult to know whether such patterns of geographic specificity are real, or if they are simply artifacts of uneven host sampling. In this article, we use data collected over more than a decade to document a significant pattern of geographic specificity among communities of chewing lice living on western scrub-jays (Aphelocoma californica). We then consider different hypotheses to explain the underlying causes of this geographic specificity.

Chewing lice (Insecta: Phthiraptera), which are parasites of both birds and mammals, exhibit pronounced host specificity, with an average of 2 bird host species per louse species (Price et al., 2003). Clay (1964) pointed out that many lice are further restricted to subsets of the host’s geographic range. For example, Clay (1976) reported that the louse Quadraceps ridgwayi occurs on New World and Australasian populations of the oyster catcher Haematopus ostralegus, but is absent from populations of this same host in Africa and Eurasia. In some cases, geography explains the distributions of lice better than does the relatedness of their hosts. Indeed, Weckstein (2004) showed that toucan lice are more likely to be found on sympatric, unrelated toucans, than on more closely related toucans that are allopatric. Unfortunately, many examples of geographic specificity in lice and other parasites are based on scattered sampling and very small numbers of host individuals per site (Clay, 1964). In this article we report geographic patterns derived from a comprehensive survey of a broadly distributed host, the western scrub-jay. We explore possible explanations for these patterns, and we conclude that geographic specificity may result from interactions between biotic and abiotic factors. Specifically, we hypothesize that the pattern is a result of interspecific competition between lice that is mediated by variation in ambient humidity. A better understanding of factors influencing geographic specificity will provide a more sophisticated view of the determinants driving ectoparasite diversity.

MATERIALS AND METHODS

From 1987 to 2003, we collected specimens of western scrub-jays and their lice from 16 localities representing 8 of 9 host subspecies present in the United States, all except the restricted-range A. c. cana, which is most likely of hybrid origin (see Peterson, 1991; American Ornithologists’ Union, 1998; Fig. 1A). This sampling regime crossed the geographic distributions of 2 distinct subspecies groups (Petitka, 1951) that likely merit species status (Peterson, 1990; K. Semple-De LANeY, pers. comm.), i.e., the californica group of Oregon, California, and Baja California, and the woodhouseii group of the Great Basin, Rocky Mountains, southwestern desert regions, and central Mexico. Jays in both the californica and woodhouseii groups were sampled in the spring and summer months when they can be lured with taped bird calls. Overall, 330 individual jays were sampled for lice (Table I).

Lice were recovered by either postmortem ruffling or body washing (Clayton and Drown, 2001). Birds subjected to postmortem ruffling were killed and sealed individually in a Tupperware container for 10–15 min with a cotton wad soaked in ethyl acetate. The feathers of each bird were then ruffled over a piece of white paper for approximately 1 min, with each major body region (wings, head, under parts) ruffled for at least 15 sec. Birds subjected to the body-washing method were treated as described in Clayton and Drown (2001). After postmortem ruffling or body washing, the lice were collected and preserved in 70–95% ethanol for subsequent identification. For each sampling locality, we calculated the prevalence of 3 species of lice: Philopterus crassipes, Brueelia deficiens, and Menecanthus eury sternus. These species of lice differed in their geographic distributions. Philopterus crassipes was distributed broadly, being found at 12 of 16 sampling localities (Fig. 1B, Table I). The
FIGURE 1. (A) Geographic distribution of 8 of the 9 subspecies of western scrub-jay (*Aphelocoma californica*) occurring in the United States. *Aphelocoma c. cana* (not shown) is restricted to Eagle Mountain, Riverside County, California (Curry et al., 2002). Letters in black circles indicate jay populations sampled for lice (for sample sizes see Table I). (B) Distribution of 3 species of lice on the 2 *A. californica* subspecies groups *californica* and *woodhousei*. Area within the perimeter of the dotted line has <55% mean annual relative humidity (National Climate Data Center, 2002).
The distributions of these lice cannot be explained by the codivergence of host lineages and louse species. Cospeciation of lice with host lineages would result in sister taxa of lice on related hosts. Our results show no evidence of such divergence at the level of host subspecies. All 3 species of lice were found on 2 or more host subspecies. Similarly, there was no evidence of codivergence of lice with host subspecies groups. Although Myrsidea sp. and B. deficiens had distributions that were roughly concordant with the 2 groups, these genera of lice are not sister taxa, indicating that this is not a case of codivergence.

The observed distributions of lice could be the result of chance sorting events. Jays founding the californica group may have had only P. crassipes and Myrsidea sp., whereas jays founding the woodhouseii group may have had P. crassipes and B. deficiens. However, this hypothesis fails to explain how the A. c. texana jay population became infested with Myrsidea sp. Furthermore, Peterson (1990) showed that the californica and woodhouseii subspecies groups are incompletely isolated, because of persistent and low-level gene flow. Because bird populations that exchange genes can also exchange lice (Whiteman et al., 2007), there are presumably opportunities for lice to move between these 2 interbreeding host groups. Nevertheless, B. deficiens is not found on jays in the californica group, whereas Myrsidea sp. is largely absent from jays in the woodhouseii group. This pattern is consistent with the existence of some factor(s) that select(s) against geographic overlap between the 2 species of lice.

Abiotic factors such as humidity are known to influence the geographic distribution of bird lice (Moyer et al., 2002). Jays in the woodhouseii group generally inhabit regions of the west where the mean annual relative humidity is less than 55% (Fig. 1B). Two species of lice, P. crassipes and B. deficiens, were found throughout this arid woodhouseii region; P. crassipes was even found on jays in Clark County, southern Nevada, where the mean annual relative humidity is just 42% (National Climate Data Center, 2002). In short, P. crassipes and B. deficiens can clearly withstand arid conditions. In contrast, Myrsidea sp. was found mainly on jays in more humid regions, suggesting that this species is less tolerant of arid conditions.

Different species of lice are known to differ in their ability to tolerate arid conditions. This difference is correlated with higher-level taxonomy. Lice of the suborder Ischnocera are capable of extracting water vapor from very dry air. In fact, their ability to extract water under arid conditions is among the best known in arthropods (Rudolph, 1983). Both P. crassipes and B. deficiens are ischnoceran lice. Myrsidea sp. belongs to the suborder Amblycera. The ability to extract water vapor is less common among lice in this suborder, and amblycieran taxa that do take up water vapor are less efficient at extracting and retaining water than ischnocerans (Rudolph, 1983). The differential ability of these 3 species of lice to extract water vapor may explain why the 2 ischnoceran lice can live in arid regions, while the amblycieran louse is absent. This hypothesis is consistent with the results of another study of louse communities on passerines in arid environments. Carrillo et al. (2007) found that trumpeter finches (Bucanetes githagineus) living in an arid region of Spain were infested with Brueelia sp. and Philopterus sp., but not with Myrsidea sp., even though Myrsidea is known to tolerate arid conditions.

**DISCUSSION**

Three species of lice were relatively common on the western scrub-jays sampled. However, these 3 species differed in their geographic distributions. Philopterus crassipes was broadly distributed throughout the entire host species range. The other 2 species of lice were much more restricted in distribution. Myrsidea sp. was found mostly among the californica subspecies group of the Pacific coast and California, and B. deficiens was found exclusively within the woodhouseii subspecies group of the interior and southwest.
from related finch species (Price et al., 2003). Although water physiology may explain the absence of Myrsidea from the woodhouseii group, it is not likely to explain the reciprocal absence of Brueelia from jays in the californica group, given that ischnoceran lice should not be restricted by higher humidity (Moyer et al., 2002). Other ecological factors, such as interspecific competition, may be responsible for the absence of B. deficiens from jays in the californica group. Interspecific competition is known to occur among bird lice (Bush and Malenke, 2008), and perhaps Myrsidea competitively excludes B. deficiens. Indeed, competition mediated by humidity has recently been shown to occur among lice on doves (Malenke, 2008). In contrast, P. crassipes, which is typically restricted to the head of the host, may not compete with either of the more generalist “body” lice Brueelia and Myrsidea. Experiments testing competitive interactions between Brueelia and Myrsidea under different humidity regimes would further our understanding of ecological factors that influence the distribution of western scrub-jay lice.

ACKNOWLEDGMENTS

We thank D. Kim, J. Malenke, and E. McConnell for assistance with this project. We thank 2 anonymous reviewers for their comments on the manuscript. Our work was supported by grants to ATP (NSF BSR-8700850), DHC (NSF PEET DEB-0118794), and to ATP and DNC (NSF 02-186).

LITERATURE CITED


