

GEOGRAPHIC VARIATION IN THE COMMUNITY STRUCTURE OF LICE ON WESTERN SCRUB-JAYS

Sarah E. Bush, Christopher W. Harbison*†, David L. Slager*, A. Townsend Peterson*, Roger D. Price‡, and Dale H. Clayton*

Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas 66045. e-mail: sbush@ku.edu

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 western scrub-jays (*Aphelocoma californica*) throughout their range in the United States, and found 3 common species of lice. *Phlopterus crassipes* was found throughout the host range, whereas the other 2 species of lice had more restricted distributions. *Brueelia deficiens* was found only on the *woodhouseii* host subspecies group, and *Myrsidea* sp. was found largely on the *californica* host subspecies group. We suggest that differential tolerance to arid conditions and interspecific competition has led to the restricted geographic distributions of these 2 species of lice.

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 *Quadriceps ridgwayi* occurs on New World and Australasian populations of the oystercatcher *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 (Pitelka, 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: *Phlopterus crassipes*, *Brueelia deficiens*, and *Myrsidea* sp. A given louse species was considered to be present at a site if at least 1 individual was found. We have not reported data on louse intensity because the 2 sampling methods used are not strictly comparable for this level of detail (Clayton and Drown, 2001).

RESULTS

The 330 birds yielded over 550 lice. Lice taxa included *P. crassipes*, *Myrsidea* sp., *B. deficiens*, and *Menecanthus eury-sternus*. These species of lice differed in their geographic distributions. *Phlopterus crassipes* was distributed broadly, being found at 12 of 16 sampling localities (Fig. 1B, Table I). The

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* Department of Biology, University of Utah, Salt Lake City, Utah 84112.

† Present address: Department of Biology, Siena College, Loudonville, New York 12211.

‡ Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108.

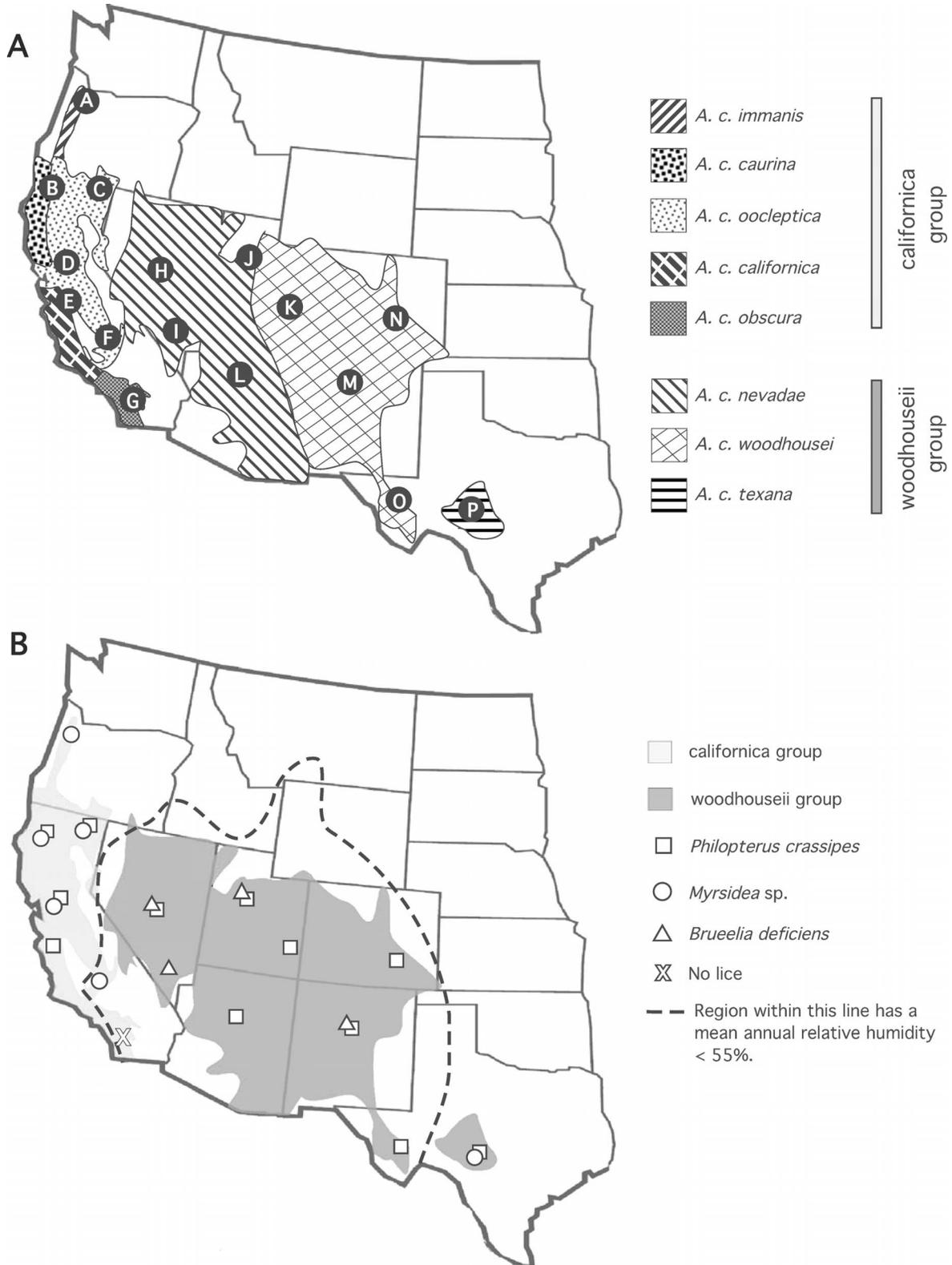


FIGURE 1. (A) Geographic distribution of 8 of the 9 subspecies of western scrub-jay (*Aphelocoma californica*) occurring in the United States. *Aphelocoma c. cana* (not shown) is restricted to Eagle Mountain, Riverside County, California (Curry et al., 2002). Letters in black circles indicate jay populations 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 *woodhouseii*. Area within the perimeter of the dotted line has <55% mean annual relative humidity (National Climate Data Center, 2002).

TABLE I. Prevalence of lice on western scrub-jay (*Aphelocoma californica*) populations (A–P) and on the 2 scrub-jay subspecies groups. Letters indicate the location of each population in Figure 1A.

Host population	N	Prevalence		
		<i>Philopterus crassipes</i>	<i>Myrsidea</i> sp.	<i>Brueelia deficiens</i>
A	16	0	19	0
B	16	6	6	0
C	21	24	10	0
D	26	4	19	0
E	24	17	0	0
F	20	0	10	0
G	16	0	0	0
<i>californica</i> group (A–G)	139	8	9	0
H	53	4	0	11
I	24	0	0	4
J	14	64	0	21
K	6	17	0	0
L	22	9	0	0
M	22	36	0	5
N	12	8	0	0
O	22	32	0	0
P	16	6	38	0
<i>woodhouseii</i> group (H–P)	191	16	3	6

occurrence of *P. crassipes* among populations of the *californica* subspecies group did not differ significantly from that among populations of the *woodhouseii* subspecies group (Fisher's exact, $P = 0.70$).

Unlike *P. crassipes*, the other 2 species of lice were restricted to particular subsets of the host species' geographic range (Fig. 1B, Table I). *Myrsidea* sp. was found in 5 of 7 localities within the *californica* subspecies group, but only 1 of 9 localities within the *woodhouseii* subspecies group. *Brueelia deficiens* was collected from none of 7 localities of the *californica* subspecies group, but was collected at 4 of 9 localities of the *woodhouseii* subspecies group. The geographic distributions of these 2 species of lice differed significantly with regard to host subspecies group (Fisher's exact, $P = 0.048$). Indeed, their distributions were essentially complementary. Among the 16 jay populations sampled, *Myrsidea* sp. and *B. deficiens* were never collected at the same locality.

A single *M. eurysternus* louse was collected from a jay in northern Utah in 2002. Given that we found just a single specimen, and that this louse is a generalist known from over 170 species of birds (Price et al., 2003), we consider this record to be a case of "straggling" from another host (Rózsa, 1993).

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.

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 amblyceran 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 amblyceran 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

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.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1998. Checklist of North American birds. American Ornithologists' Union, Washington, DC, 829 p.
- BUSH, S. E., AND D. H. CLAYTON. 2006. The role of body size in host specificity: Reciprocal transfer experiments with feather lice. *Evolution* **60**: 2158–2167.
- , AND J. R. MALENKE. 2008. Host defense mediates interspecific competition in ectoparasites. *Journal of Animal Ecology* **77**: 558–564.
- CARRILLO, C. M., F. VALERA, A. BARBOSA, AND E. MORENO. 2007. Thriving in an arid environment: High prevalence of avian lice in low humidity conditions. *Ecoscience* **14**: 241–249.
- CLAY, T. 1964. Geographical distribution of the Mallophaga (Insecta). *Bulletin of the British Ornithological Club* **84**: 14–16.
- . 1976. Geographical distribution of the avian lice (Phthiraptera): A review. *Journal of the Bombay Natural History Society* **71**: 536–547.
- CLAYTON, D. H., AND D. M. DROWN. 2001. Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). *Journal of Parasitology* **87**: 1291–1300.
- CURRY, R. L., A. T. PETERSON, AND T. A. LANGEN. 2002. Western scrub-jay. *Birds of North America* **712**: 1–35.
- MALENKE, J. R. 2008. The ecology of local adaptation in feather-lice. Ph.D. Thesis. University of Utah, Salt Lake City, Utah, 151 p.
- MOYER, B. R., D. M. DROWN, AND D. H. CLAYTON. 2002. Low humidity reduces ectoparasite pressure: Implications for host life history evolution. *Oikos* **97**: 223–228.
- NATIONAL CLIMATE DATA CENTER. 2002. Climate atlas of the United States, version 2.0. National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Asheville, North Carolina.
- PETERSON, A. T. 1990. Evolutionary relationships of the *Aphelocoma* jays. Ph.D. Thesis. University of Chicago, Chicago, Illinois, 235 p.
- . 1991. Gene flow in scrub jays: Frequency and direction of movement. *Condor* **93**: 926–934.
- PITELKA, F. A. 1951. Speciation and ecological distribution of American jays of the genus *Aphelocoma*. University of California Publications in Zoology **50**: 195–464.
- POULIN, R. 2007. Evolutionary ecology of parasites. Princeton University Press, Princeton, New Jersey, 342 p.
- , AND D. B. KEENEY. 2007. Host specificity under molecular and experimental scrutiny. *Trends in Parasitology* **24**: 24–28.
- , AND S. MORAND. 2004. Parasite biodiversity. Smithsonian Books, Washington, DC, 224 p.
- PRICE, P. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey, 237 p.
- PRICE, R. D., R. A. HELLENTHAL, R. L. PALMA, K. P. JOHNSON, AND D. H. CLAYTON. 2003. The chewing lice: World checklist and biological overview. Illinois Natural History Survey, Special Publication No. 24, Champaign, Illinois, 501 p.
- RÓZSA, L. 1993. Speciation patterns of ectoparasites and “stragglings” lice. *International Journal for Parasitology* **23**: 859–864.
- RUDOLPH, D. 1983. The water-vapour uptake system of the Phthiraptera. *Journal of Insect Physiology* **29**: 15–25.
- THOMPSON, J. N. 1994. The coevolutionary process. University of Chicago Press, Chicago, Illinois, 376 p.
- WECKSTEIN, J. D. 2004. Biogeography explains cophylogenetic patterns in toucan chewing lice. *Systematic Biology* **53**: 154–164.
- WHITEMAN, N. K., R. T. KIMBALL, AND P. G. PARKER. 2007. Co-phylogeography and comparative population genetics of the threatened Galapagos hawk and three ectoparasite species: Ecology shapes population histories within parasite communities. *Molecular Ecology* **16**: 4759–4773.