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# Condition-Specific Competition Governs the Geographic Distribution and Diversity of Ectoparasites

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**ABSTRACT:** Understanding how environmental parameters interact to govern species distributions is a shared goal of ecology and biogeography. Biotic and abiotic conditions can change distributions by affecting the nature of interspecific interactions. Although documented in free-living systems, this context dependency has been neglected in parasite interactions. We investigated the influence of condition-specific competition on the specificity of two species of feather lice (Phthiraptera: Ischnocera) that share a host, the mourning dove (*Zenaidura macroura*). We show that relative humidity restricts the range of one species, *Columbicola macrourae*3 (i.e., the *C. macrourae* lineage found on mourning doves), to the more humid eastern United States. The second species, *Columbicola baculoides*, an arid-adapted species, is restricted to drier regions of the western United States by *C. macrourae*3, which outcompetes it in experiments. Thus, arid conditions in the West provide *C. baculoides* with a climatic refuge from the competitively superior *C. macrourae*3, effectively doubling parasite diversity on one host species. These results support the hypothesis that abiotic factors can determine species distributions on the stressful end of an environmental gradient while interspecific competition governs distributions at the benign end. The balance between these factors is subject to change as environmental conditions change, even if the host distribution remains unaffected.

**Keywords:** context dependency, humidity, lice, birds, environmental gradient.

## Introduction

The building blocks of community structure are individual species distributions. Species distributions are not static characteristics of organisms but are affected by factors such as abiotic environmental conditions, competition, and predation (MacArthur 1972). These factors can act alone or in concert to maintain diversity by facilitating species coexistence; alternatively, they can cause local extinction, thus reducing diversity. Understanding how environmen-

tal parameters interact in a context-dependent way to govern species distributions is a shared goal of ecology and biogeography (Brown 1984). In this article, we explore the influence of context dependency on parasite distributions.

Abiotic environmental conditions and interspecific competition have been shown to interact in the form of “condition-specific competition” (Dunson and Travis 1991; Taniguchi and Nakano 2000; Twomey et al. 2008). At the mild or benign end of an environmental gradient, species distributions are governed by interspecific competition; at the harsh end, stressful abiotic conditions reduce competition (Greenslade 1983; Parsons 1996). A classic example involves the littoral distribution of two competing species of barnacles, *Chthamalus stellatus* and *Balanus balanoides* (Connell 1961). *Chthamalus stellatus* was outcompeted in deeper water by the faster-growing, larger *B. balanoides*. However, higher on the shoreline, *B. balanoides* was more sensitive to desiccation and heat, allowing *C. stellatus* to survive in the absence of competition. Thus, both species of barnacle coexisted along a given shoreline, with a zone of overlap where interactions were strongest.

The strengths of other kinds of interspecific interactions also vary across abiotic gradients. According to the stress-gradient hypothesis, for example, species of plants interact facilitatively at the stressful end of an abiotic gradient but competitively at the benign end (Maestre et al. 2009). Another well-studied example involves context-dependent competition versus predation between species of mosquitoes (Juliano 2009). In this case, the relative impacts of competition and predation change along a gradient in the size and permanence of habitats. Regardless of system, the most important result is that ecological context changes competitive interactions, thus facilitating the coexistence of competitors on a landscape level. The consequence is an increase in diversity.

Although parasites represent one-half or more of all living species (Price 1980; DeMeeùs and Renaud 2002), the influence of condition-specific competition on parasite distributions has received little attention. This may be, in

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part, because parasite distributions have traditionally been investigated from a host-centric point of view that concentrates on factors influencing the geographic distribution of the host rather than the parasite itself (Price 1980; Combes 2001; Poulin 2006). Although this framework has been useful in understanding much about the evolutionary ecology of parasites, it ignores many of the nonhost factors that have been studied extensively in free-living systems. It also ignores the possible influence of co-occurring members of a parasite community on the geographic distributions of one another. Finally, it ignores the possibility that these different factors may interact to govern parasite distributions.

We investigated whether abiotic environmental conditions and interspecific competition might interact to shape parasite communities. We studied a host-ectoparasite system consisting of birds and their feather lice (Phthiraptera: Ischnocera), partly because recent work suggests that abiotic factors (ambient humidity) and interspecific competition play important roles in the ecology of these parasites (Moyer et al. 2002b; Bush and Malenke 2008). Bush et al. (2009) recently published correlational data to suggest that ambient humidity governs the geographic distribution and community structure of lice on western scrub jays (*Aphelocoma californica*). Similarly, of 10 species of lice infesting domestic chickens in Nigeria, some are distributed on chicken populations across the country, while others show geographic distributions correlated with the length of the regional wet season (Fabiya 1996).

We concentrated on *Columbicola*, a genus of feather lice that parasitizes pigeons and doves of the world (Aves: Columbiformes). Like other feather lice, *Columbicola* are permanent parasites that spend their entire lives on the body of their host (Marshall 1981). The 3–4-week direct life cycle begins with the egg, which is glued to the feathers, and progresses through three nymphal instars to the adult stage. *Columbicola* are transmitted between hosts primarily during periods of direct contact, such as between parents and their offspring in the nest (Clayton and Tompkins 1994). They feed on feathers and dead skin, which are metabolized with the aid of endosymbiotic bacteria (Fukatsu et al. 2007). The feather damage caused by *Columbicola* has a chronic effect on the host that leads to reduced survival (Clayton et al. 1999) and reduced mating success (Clayton 1990). The principal defense against these parasites is host preening (Clayton et al. 2005). Preening exerts a selective effect on *Columbicola* body size because the lice escape from preening by inserting themselves between the feather barbs; lice that fit well between the barbs are selectively favored (Clayton et al. 1999). Preening and body size interact to reinforce the host specificity of *Columbicola* species (Clayton et al. 2003; Bush et al. 2006).

*Columbicola* and other species of feather lice are sen-

sitive to ambient relative humidity (RH) because they obtain all of their moisture directly from atmospheric water vapor (Rudolph 1983). Rudolph (1983) documented variation among species of lice in the ability to retain water under conditions of low ambient humidity (critical threshold ranging from 43% to 52% RH). Any adaptation allowing survival at a lower humidity would enable a species to exploit more arid regions of the host's range. Consistent with this hypothesis, Moyer et al. (2002b) reported field and laboratory data showing that lice on Columbiformes are sensitive to humidity and that low humidity can drive louse populations to local extinction, at least in the lab. In contrast, *Columbicola* do not appear to be sensitive to ambient temperature variation (Clayton et al. 1992), probably because they live close to the host's skin, which provides constant warmth but not constant humidity (Moyer et al. 2002b). Large-scale differences in RH may provide an environmental gradient across which interspecific competition and abiotic conditions can interact to determine louse distributions.

To test this hypothesis, we used *Columbicola baculoides* and *Columbicola macrourae*, two species of *Columbicola* that parasitize the mourning dove (*Zenaidura macroura*), a widespread, abundant North American species found across diverse habitats (Baskett et al. 1993). *Columbicola baculoides* has been documented from five hosts, most of which are South American species. *Columbicola macrourae* is a generalist species that infests 15 different host species (Price et al. 2003). However, recent molecular and ecological evidence suggests that this single morphospecies is actually an assemblage of host-specific cryptic sibling species (Johnson et al. 2002; Malenke et al. 2009). The *C. macrourae* lineage found on mourning doves is known as *C. macrourae*<sub>3</sub>; we use this convention hereafter.

Mourning doves are distributed across a large east-west humidity gradient in North America, with *C. baculoides* and *C. macrourae*<sub>3</sub> appearing to partition their host's geographic range (Clayton and Price 1999; Adams et al. 2005). We began by testing whether *C. baculoides* and *C. macrourae*<sub>3</sub> are, in fact, restricted to different regions of the host's broad geographic range. We did this by using host records from museum collections, the taxonomic literature, and new specimens collected for this study. We also carried out in vivo experimental work with captive mourning doves infested with different combinations of *C. baculoides* and *C. macrourae*<sub>3</sub>. The infested birds were kept in animal rooms set at different humidities. This approach allowed us to test for effects of ambient humidity and interspecific competition on the fitness of each species of louse. Finally, we carried out in vitro experiments with lice in an incubator to measure proximal effects of ambient humidity on fitness parameters of the two species of lice more precisely.

## Material and Methods

### *Biogeographic Sampling*

The geographic distributions of *Columbicola baculoides* and *Columbicola macrourae*3 in the continental United States were estimated, using new specimens of lice collected from wild mourning doves by the authors; these estimates were combined with data from existing specimens in the following institutions: K. C. Emerson Entomology Museum, Oklahoma State University; University of Minnesota Entomology Museum; U.S. National Museum of Natural History; and the Price Institute for Parasite Research, University of Utah. Additional data were taken from published records. We included data only if the identity of specimens was verified by us or by a reliable taxonomic publication that listed the specimens in question (table 1). We compared the resulting distributions of *C. baculoides* and *C. macrourae*3 with climatological data adapted from the Climate Atlas of the United States (NOAA 2002).

### *Manipulation of Abiotic and Competitive Conditions*

To create live cultures of the two species of lice for use in experiments, we started with 25 infested mourning doves trapped in Tucson, Arizona (for *C. baculoides*), and eight infested mourning doves trapped in Lake Placid, Florida (for *C. macrourae*3). The birds from the two localities were brought back to our animal facility at the University of Utah, where they were kept in two separate animal rooms maintained at high humidity (>65% RH). Birds were isolated in 30 × 30 × 56-cm wire cages, kept on a 12L : 12D cycle, and given ad lib. food, grit, and water. To generate sufficient numbers of lice for the experiments, each culture bird was fitted with a C-shaped plastic “bit” inserted between the upper and lower mandibles of its bill. Bits spring shut slightly in the nares (nostrils) to prevent dislodging. They create a 1–3-mm gap between the mandibles that impairs the forceps-like action of the bill required for efficient preening; the result is a dramatic increase in lice over a period of several weeks (Clayton 1990). Bits do not interfere with feeding, and they have no other apparent side effects (Clayton and Tompkins 1995). Subsamples of lice from these “culture” birds were examined to confirm that Arizona birds had only *C. baculoides* and Florida birds had only *C. macrourae*3.

We used another 36 mourning doves trapped in Tucson, Arizona, as hosts to be infested with different combinations of lice. These birds were also housed in individual cages, but in a room set at very low humidity (<30% RH) for ≥10 weeks to eliminate “background” louse infestations (Harbison et al. 2008). After this drying period, the louse-free birds were divided randomly into six replicate

groups of six birds each. Live adult lice removed from culture birds with CO<sub>2</sub> (Moyer et al. 2002a) were then used to infest two birds in each replicate group with 25 *C. baculoides*, two other birds with 25 *C. macrourae*3, and two birds with 25 *C. baculoides* and 25 *C. macrourae*3. The louse populations on each replicate group (six birds) were paired on the basis of time of experimental infestation. We chose to infest birds with 25 lice of each species to approximate the number found on wild mourning doves in Utah (mean = 23.8, *n* = 15 birds collected for this study). We used an additive experimental design with constant focal densities in order to detect interspecific competition while maintaining relatively constant intraspecific competitive effects (Goldberg and Scheiner 1993).

After experimental infestation, one-half of the birds in each replicate group (balanced by louse treatment) were placed in an empty animal room at low humidity (~45% RH); the remaining three birds in each group were placed in another empty room with high humidity (~70% RH). This design allowed us to compare the population sizes of *C. baculoides* and *C. macrourae*3 under low- and high-humidity conditions. We chose 45% RH for the low-humidity treatment because this level would be challenging for the lice but not immediately lethal (J. R. Malenke, unpublished data). The high-humidity room was set at 70% RH because this is the RH at which we typically culture lice (D. H. Clayton, unpublished data). The two animal rooms were kept at a relatively constant temperature of 18°C. Temperature and humidity were monitored and recorded with digital data loggers throughout the experiment.

The experiment was conducted for 6 weeks, which is equivalent to nearly two louse generations. At the end of this time, birds were dispatched and their louse populations were quantified, using a body-washing method that can account for 99% of the lice on a bird (Clayton and Drown 2001). *Columbicola baculoides* and *C. macrourae*3 were identified under a dissection microscope. Single-species populations of *C. baculoides* and *C. macrourae*3 from the humid and dry rooms were compared to evaluate the effect of ambient humidity on population size as a proxy for louse fitness. The mixed-species populations were compared with the single-species populations to test for interspecific competition.

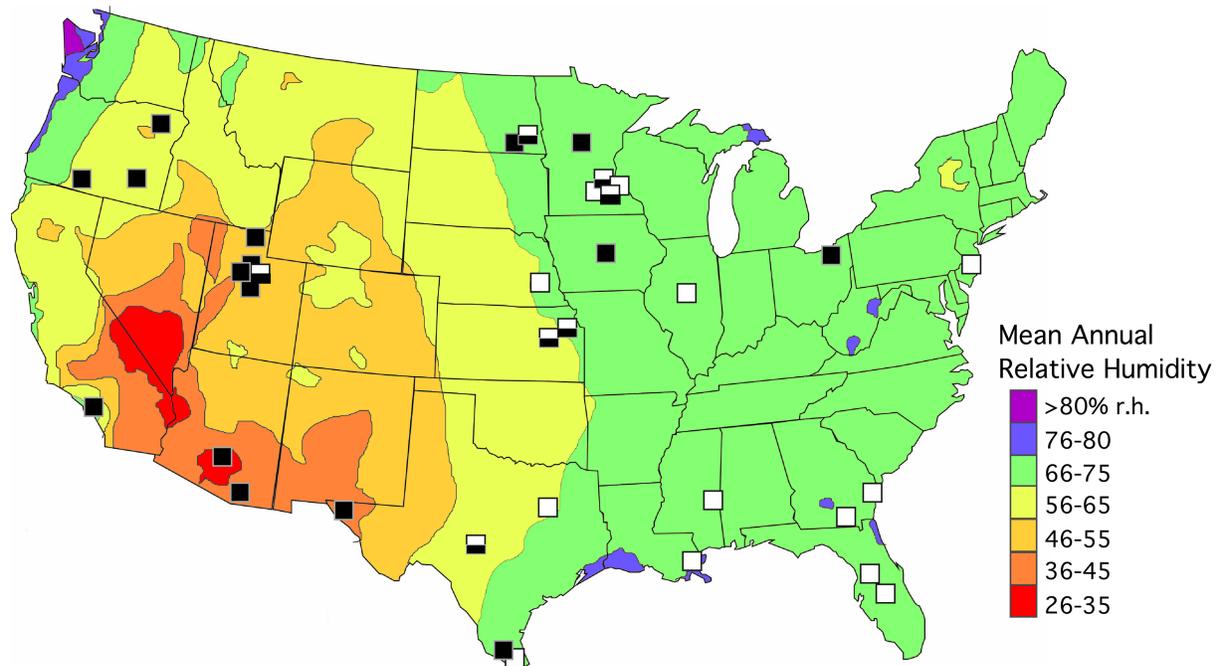
### *Louse Fitness Comparisons across Humidity Levels*

We measured the effect of humidity on the survival and reproduction of *C. baculoides* and *C. macrourae*3 kept in vented glass vials in a Percival incubator set to one of four RH treatments (~70%, 60%, 50%, and 40%). Incubator temperature was set at 35°C to simulate conditions close to that of the body of the host (Nelson and Murray 1971).

**Table 1:** *Columbicola macrouae3* (*C. mac3*) and *Columbicola baculoides* (*C. bac*) specimen data from the continental US

| Louse species, no. lice | Location                   | Year      | Source                                     |
|-------------------------|----------------------------|-----------|--|
| <i>C. mac3</i> :        |                            |           |  |
| 2                       | Gainesville, Florida       | 1978      | Clayton and Price 1999                     |
| 68                      | Lake Placid, Florida       | 2004      | New specimens; this study                  |
| 3                       | Savannah, Georgia          | 1940      | Tendeiro 1962                              |
| 6                       | Valdosta, Georgia          | 1936      | Clayton and Price 1999                     |
| ?                       | Illinois                   | 1948–1954 | Hanson et al. 1956                         |
| 64 <sup>A</sup>         | Lawrence, Kansas           | 2007      | New specimens; this study                  |
| 4 <sup>B</sup>          | Leavenworth, Kansas        | 1956      | Tendeiro 1962                              |
| 7                       | New Orleans, Louisiana     | 1934      | Clayton and Price 1999                     |
| 3                       | New Orleans, Louisiana     | 1934      | Tendeiro 1962                              |
| 2 <sup>C</sup>          | Anoka, Minnesota           | 1961      | Clayton and Price 1999                     |
| 1                       | Minneapolis, Minnesota     | 1940      | Clayton and Price 1999                     |
| 1 <sup>D</sup>          | Savage, Minnesota          | 1958      | Clayton and Price 1999                     |
| 2                       | St. Paul, Minnesota        | 1896      | Tendeiro 1962                              |
| 2                       | St. Paul, Minnesota        | 1961      | Clayton and Price 1999                     |
| 3                       | State College, Mississippi | 1935      | Clayton and Price 1999                     |
| 3                       | State College, Mississippi | 1937      | Clayton and Price 1999                     |
| 3                       | Dunbar, Nebraska           | 1940      | Tendeiro 1962                              |
| 4                       | Riverton, New Jersey       | 1919      | Tendeiro 1962                              |
| 2 <sup>E</sup>          | Leonard, North Dakota      | 1930      | Tendeiro 1962                              |
| 4                       | Cedar Hill, Texas          | 1922      | Tendeiro 1962                              |
| 1 <sup>F</sup>          | Roosevelt, Texas           | 1919      | Tendeiro 1962                              |
| 2                       | McAllen, Texas             | 1999      | New specimens; this study                  |
| 12 <sup>G</sup>         | Utah County, Utah          | 2005      | New specimens; this study                  |
| <i>C. bac</i> :         |                            |           |  |
| 9                       | Robbins Butte, Arizona     | 1997      | Moyer et al. 2002b                         |
| 74                      | Tucson, Arizona            | 2004      | New specimens; this study                  |
| 3                       | Pasadena, California       | 1937      | Clayton and Price 1999                     |
| 1                       | Ames, Iowa                 | 1934      | Tendeiro 1962                              |
| 16 <sup>A</sup>         | Lawrence, Kansas           | 2007      | New specimens; this study                  |
| 2                       | Leavenworth, Kansas        | 1955      | USNM                                       |
| 7 <sup>B</sup>          | Leavenworth, Kansas        | 1956      | Tendeiro 1962                              |
| 1 <sup>C</sup>          | Anoka, Minnesota           | 1961      | University of Minnesota, Entomology Museum |
| 2                       | Little Falls, Minnesota    | 1961      | University of Minnesota, Entomology Museum |
| 2 <sup>D</sup>          | Savage, Minnesota          | 1958      | Clayton and Price 1999                     |
| 1                       | Fargo, North Dakota        | 1934      | USNM                                       |
| 1 <sup>E</sup>          | Leonard, North Dakota      | 1930      | Tendeiro 1962                              |
| 2                       | Gates Mills, Ohio          | 1932      | Tendeiro 1962                              |
| 2                       | Hereford, Oregon           | 1932      | Clayton and Price 1999                     |
| 15                      | Keno, Oregon               | 1934      | Tendeiro 1962                              |
| 3                       | Steen Mountains, Oregon    | 1934      | USNM                                       |
| 4                       | El Paso, Texas             | 1930      | Tendeiro 1962                              |
| 1 <sup>F</sup>          | Roosevelt, Texas           | 1919      | Tendeiro 1962                              |
| 2                       | McAllen, Texas             | 1998      | New specimens; this study                  |
| 3                       | Levan, Utah                | 1945      | Clayton and Price 1999                     |
| 4                       | Logan, Utah                | 1939      | Clayton and Price 1999                     |
| 3                       | Logan, Utah                | 1945      | Tendeiro 1962                              |
| 1                       | Salt Lake County, Utah     | 2007      | New specimens; this study                  |
| 28                      | Salt Lake County, Utah     | 2008      | New specimens; this study                  |
| 14                      | Skull Valley, Utah         | 1964      | Clayton and Price 1999                     |
| 1                       | Tooele, Utah               | 1953      | USNM                                       |
| 2                       | Tooele, Utah               | 1964      | USNM                                       |
| 3                       | Tooele, Utah               | 1964      | USNM                                       |
| 322 <sup>G</sup>        | Utah County, Utah          | 2005      | New specimens; this study                  |

Note: *C. mac3* indicates the *C. macrouae* lineage found on mourning doves. Matching letters on records for *C. mac3* and *C. bac* are instances in which the two species were collected in the same location on the same day, often from the same host individual; see text. USNM = U.S. National Museum, Smithsonian Institution, Washington, DC.



**Figure 1:** Distribution of two species of *Columbicola* lice on mourning doves in the United States in relation to mean annual relative humidity. Black squares indicate collecting localities for *Columbicola baculoides*; white squares are *Columbicola macrourae3* (i.e., the *C. macrourae* lineage found on mourning doves) collecting localities; black and white squares are localities where both *C. baculoides* and *C. macrourae3* were present. Records are from museum specimens, taxonomic literature, and new specimens collected for this study (table 1). Climatological data are adapted from the Climate Atlas of the United States (NOAA 2002).

Three mourning dove feathers were placed in each vial, together with 10 *C. baculoides* or 10 *C. macrourae3* from culture birds. The sex ratio of lice in each vial was also recorded. After a period of 2 weeks, the survival of adult and nymphal lice in each vial was scored, as was the number of eggs. Humidity and temperature were monitored continuously throughout the experiment with a data logger. Mean relative humidities and temperatures ( $\pm 1$  SD), respectively, of the four different treatments were as follows: 70.0%  $\pm$  2.4% RH, 34.6°  $\pm$  0.3°C; 64.2%  $\pm$  2.3% RH, 34.4°  $\pm$  0.3°C; 49.6%  $\pm$  2.1% RH, 34.9°  $\pm$  0.3°C; and 41.7%  $\pm$  0.8% RH, 34.6°  $\pm$  0.5°C.

We also compared the abilities of *C. baculoides* and *C. macrourae3* to conserve water at low humidity (40% RH) in the incubator by measuring water loss. We estimated water loss, using changes in louse body mass over the course of 8-h trials (Rudolph 1983). Because of their small size, we grouped 10 adult lice on a square of Parafilm (25 cm<sup>2</sup>), which absorbs very little moisture (N. Newbold, unpublished data). Each replicate consisted of a petri dish containing a square of Parafilm and either 10 *C. baculoides*, 10 *C. macrourae3*, or no lice. At the start of the trial, each of three squares of Parafilm was weighed on a sensitive

digital balance (to 0.001 mg) three times, lice were added to two of the squares, and then all three squares were weighed three more times. The starting mass of lice was taken as the difference in the average mass of each square before and after the addition of lice. At the end of the 8-h trial, each square was weighed three more times; lice and their feces were then brushed away, and each square was weighed three final times. The end mass of lice was taken as the difference in the average mass of each square with and without lice (and their frass). Louse mass was compared before and after the incubator treatment.

A total of 25 paired trials were run across four testing periods; the mean RH and temperature ( $\pm$ SD), respectively, in the incubator for the different testing periods were as follows: 44.0%  $\pm$  2.9% RH, 34.9°  $\pm$  0.3°C; 39.6%  $\pm$  4.1% RH, 35.1°  $\pm$  0.9°C; 40.2%  $\pm$  4.2% RH, 34.4°  $\pm$  0.5°C; and 42.4%  $\pm$  3.6% RH, 34.4°  $\pm$  0.4°C.

## Results

### *Biogeographic Sampling*

We documented 16 localities in which mourning doves had *Columbicola baculoides*, 13 localities in which they had

*Columbicola macrourae*3, and seven localities in which they had both species of lice, often on individual hosts (see “Discussion”; fig. 1). *Columbicola macrourae*3 was significantly more likely to be recorded from localities with high mean annual RH (>65% RH), while *C. baculoides* was found primarily at localities with low humidity ( $\leq 65\%$  RH; Fisher’s exact test:  $P = .012$ ,  $n = 43$ ,  $df = 1$ ). RH and therefore louse species covaried with geography: *C. baculoides* was found primarily in the western United States, while *C. macrourae*3 was found primarily in the east. The two species co-occurred in the Midwest (table 1; fig. 1). Six of the seven localities in which mourning doves had both species of lice were from the central United States, where the mean annual RH varies between 56% and 75%. The seventh locality in which mourning doves had both species of lice was northern Utah, where both species were present on birds returning from migration in the spring but only *C. baculoides* remained on birds in August (see “Discussion”).

#### Manipulation of Abiotic and Competitive Conditions

We evaluated the effect of humidity on the fitness of *C. baculoides* and *C. macrourae*3 by comparing population sizes on captive birds after 6 weeks at different humidities (fig. 2). In the low-humidity treatment, mean humidity ( $\pm$  SE) was  $42.6\% \pm 4.3\%$  RH and the mean temperature was  $19.4^\circ \pm 3.6^\circ\text{C}$ . In the high-humidity treatment, mean humidity was  $67.7\% \pm 9.4\%$  RH and the mean temperature was  $18.3^\circ \pm 5.2^\circ\text{C}$ . Nymphs were observed in all treatments, indicating that reproduction had occurred. Louse populations were normalized with a  $\log(\text{population size} + 1)$  transformation before analysis. *Columbicola baculoides* population sizes were not significantly different in the high- and low-humidity treatments (fig. 2; paired  $t_5 = 0.296$ ,  $P = .780$ ). In contrast, *C. macrourae*3 populations were significantly smaller at low humidity compared with at high humidity (paired  $t_5 = 2.913$ ,  $P = .033$ ).

We also compared the populations of both species of lice when they were alone with when they co-occurred on hosts (fig. 3). *Columbicola baculoides* adult populations were significantly smaller in the presence of *C. macrourae*3 than when they were alone (paired  $t_{10} = -2.937$ ,  $P = .015$ ). *Columbicola baculoides* nymphs showed the same trend, but the difference was not significant (paired  $t_{10} = -1.677$ ,  $P = .125$ ; fig. 3). Overall, *C. baculoides* populations (adults and nymphs) were smaller in the presence of *C. macrourae*3 than when they were alone (Fisher’s combined probability:  $\chi_4^2 = 12.56$ ,  $P = .014$ ).

In contrast, *C. macrourae*3 populations were unaffected by *C. baculoides* (fig. 3; for *C. macrourae*3 adults: paired  $t_{10} = 1.515$ ,  $P = .161$ ; for *C. macrourae*3 nymphs: paired

$t_{10} = 0.942$ ,  $P = .368$ ). Combined analysis of adults and nymphs also revealed *C. macrourae*3 population size to be independent of the presence of *C. baculoides* (Fisher’s combined probability:  $\chi_4^2 = 5.67$ ,  $P = .225$ ).

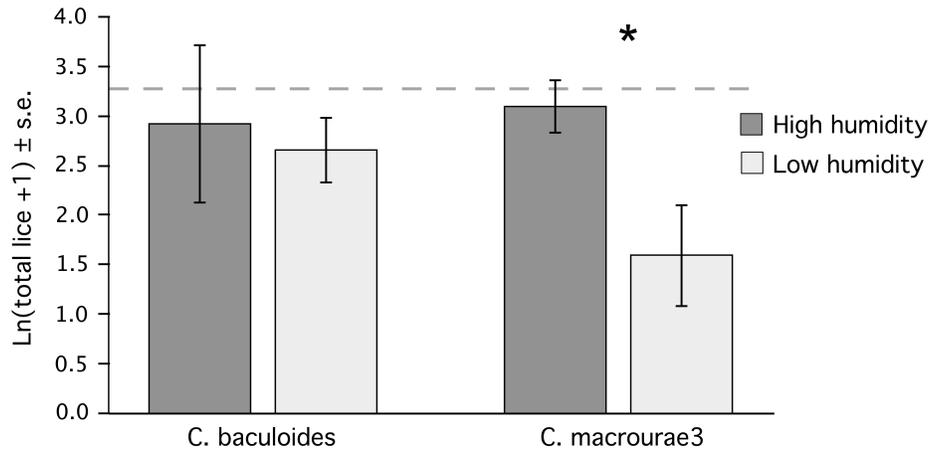
#### Louse Fitness Comparisons across Humidity Levels

Humidity had a significant effect on the survival and reproduction of both species of lice in the incubator (fig. 4). The number of surviving adults dropped with reduced humidity, but there was no overall difference in the strength of that relationship between the two louse species (fig. 4A; for humidity:  $F_{3,181} = 12.06$ ,  $P < .0001$ ; for louse species:  $F_{1,181} = 0.26$ ,  $P = .61$ ; no significant interaction term). However, a post hoc analysis of the interval between 70% and 60% RH showed a significant reduction in *C. macrourae*3 adult survival (fig. 4A;  $t_{98} = 2.31$ ,  $P < .05$ ). In contrast, *C. baculoides* adult survival increased slightly at 60% RH, although the increase was not statistically significant ( $t_{101} = -0.45$ ,  $P = .65$ ). We were particularly interested in the 60%–70% RH interval because it approximates the mean annual RH across the zone of overlap between *C. baculoides* and *C. macrourae*3 in nature (fig. 1).

The number of surviving nymphs (per female) was also significantly reduced by humidity, but again there was no overall difference in the strength of the relationship between the two louse species (fig. 4B; for humidity:  $F_{3,181} = 6.77$ ,  $P < .001$ ; for louse species:  $F_{1,181} = 0.01$ ,  $P = .91$ ; no significant interaction). However, if the analysis was again restricted post hoc to the interval between 70% and 60% RH, there was no significant change in the survival of *C. macrourae*3 nymphs ( $t_{90} = 1.56$ ,  $P = .12$ ) but there was a significant increase in the survival of *C. baculoides* ( $t_{91} = -2.1$ ,  $P < .05$ ).

The number of eggs (per female) was also significantly reduced by humidity; in this case, the impact differed significantly between *C. baculoides* and *C. macrourae*3 and there was a significant interaction between humidity and louse species (fig. 4C; for humidity:  $F_{3,181} = 13.28$ ,  $P < .001$ ; for louse species:  $F_{1,181} = 5.32$ ,  $P < .05$ ; for humidity  $\times$  louse species:  $F_{3,181} = 2.94$ ,  $P < .05$ ). Post hoc tests revealed this effect to be due to a significant difference between *C. baculoides* and *C. macrourae*3 at the 60% level (fig. 4C;  $t_{46} = 2.79$ ,  $P < .01$ ).

We used mass loss as a proxy for water vapor loss by adult *C. baculoides* and *C. macrourae*3. Over the course of 8 h at sublethal low humidity, *C. baculoides* maintained body mass better than *C. macrourae*3 (fig. 5). The mean mass lost by groups of 10 *C. baculoides* was 0.087 mg (11.8% of total mass) compared with 0.123 mg (18.4% of total mass) by *C. macrourae*3. There was a significant effect of louse species and incubator treatment on mass loss, as



**Figure 2:** *Columbicola baculoides* and *Columbicola macrouae3* (i.e., the *C. macrouae* lineage found on mourning doves) populations following 6 weeks' exposure to high-humidity (~65% relative humidity) and low-humidity (~45% relative humidity) conditions. Each bar is the mean of louse populations from six birds. The dotted line represents the size of the experimentally transferred populations ( $n = 25$  lice). *Columbicola baculoides* populations were not significantly affected by humidity, whereas *C. macrouae3* populations were significantly smaller at low humidity. Asterisk indicates significant difference ( $P < .05$ ).

well as a significant interaction (louse species:  $F_{1,52} = 18.83$ ,  $P < .0001$ ; incubator treatment:  $F_{1,52} = 496.0$ ,  $P < .0001$ ; louse species  $\times$  incubator treatment:  $F_{1,52} = 15.27$ ,  $P < .001$ ).

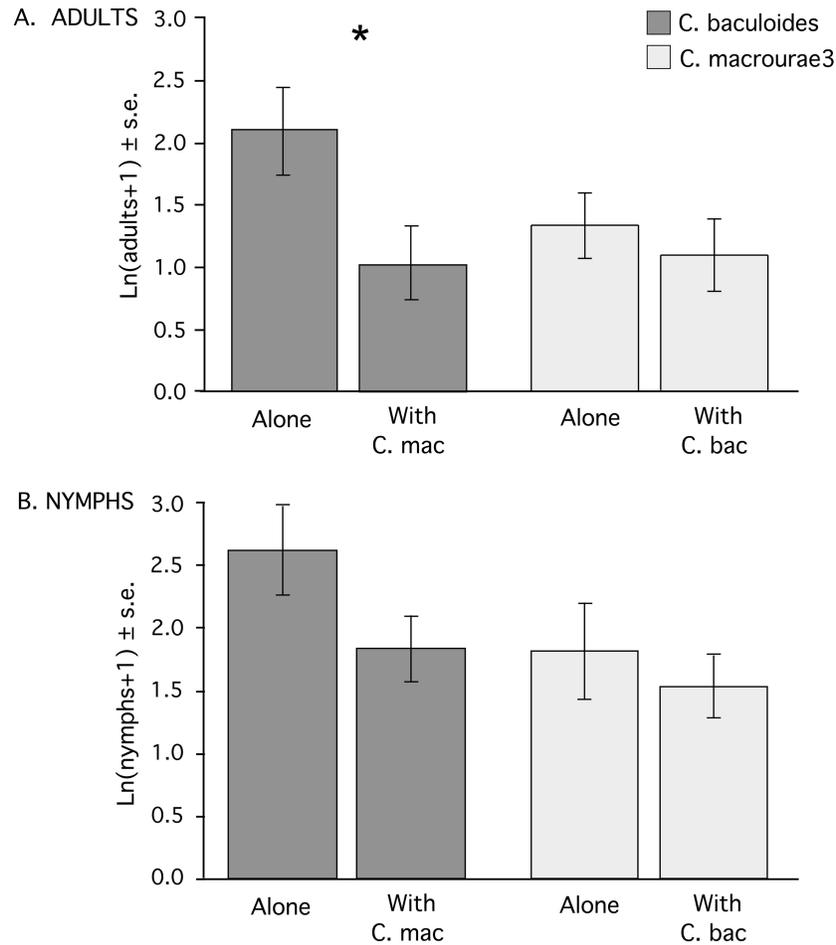
### Discussion

Our primary goal was to test the hypothesis that condition-specific competition may govern the geographic distribution and diversity of parasites. We used two species of feather lice and their widespread mourning dove hosts to test whether interspecific competition and abiotic conditions play a role in parasite diversity. We plotted the distribution of mourning dove lice onto a map of mean annual RH across the United States. The resulting pattern revealed that *Columbicola baculoides* is found primarily in the western part of the country, where the humidity is relatively low, while *Columbicola macrouae3* is found primarily in the more humid eastern half of the country (fig. 1). These patterns suggest that *C. baculoides* is adapted to arid conditions that *C. macrouae3* cannot withstand.

The relationship between distribution and humidity in the United States is mirrored in South America by close relatives of *C. baculoides* and *C. macrouae3*. The spotted dove (*Patagoenas maculosa*) also hosts two *Columbicola* species, *Columbicola triangularis* and *Columbicola adamsi*. The range of the spotted dove extends from humid rainforest in Brazil to the drier steppes of Argentina. *Columbicola triangularis*, which is the sister species of *C. baculoides*, is found on birds in the arid region, while *C.*

*adamsi*, which is a close relative of *C. macrouae3*, is found only on birds in humid regions (Johnson et al. 2007; K. P. Johnson, personal communication). This replicated pattern of geographic specificity, correlated with ambient humidity, suggests that the trait(s) allowing sister species *C. baculoides* and *C. triangularis* to survive in arid habitats may reflect an adaptation derived from their common ancestor.

Our survey of the distribution of *C. baculoides* and *C. macrouae3* included seven cases in which the two species were found at the same locality. Most of these cases were distributed along a humidity isocline separating 56%–65% and 66%–75% mean annual RH (fig. 1). The two species occasionally share individual hosts. Taxonomists working on lice normally mount specimens from different host individuals on different microscope slides. Most of the cases in table 1 of *C. baculoides* and *C. macrouae3* from the same locality on the same day include at least one case in which specimens of the two species are mounted on a single slide, indicating that they came from the same host individual. Our own collecting efforts confirm that the two species co-occur on single host individuals. We removed and identified lice from five mourning doves collected in Lawrence, Kansas, which lies in the transition zone. Two of the five doves had *Columbicola*; each of these birds had both *C. baculoides* and *C. macrouae3*. In addition, Galloway and Palma (2008) collected and identified lice from 117 mourning doves in Manitoba, Canada. They reported 32 individuals with *C. baculoides*, 22 individuals with *C. macrouae3*, and nine individuals with both *C.*



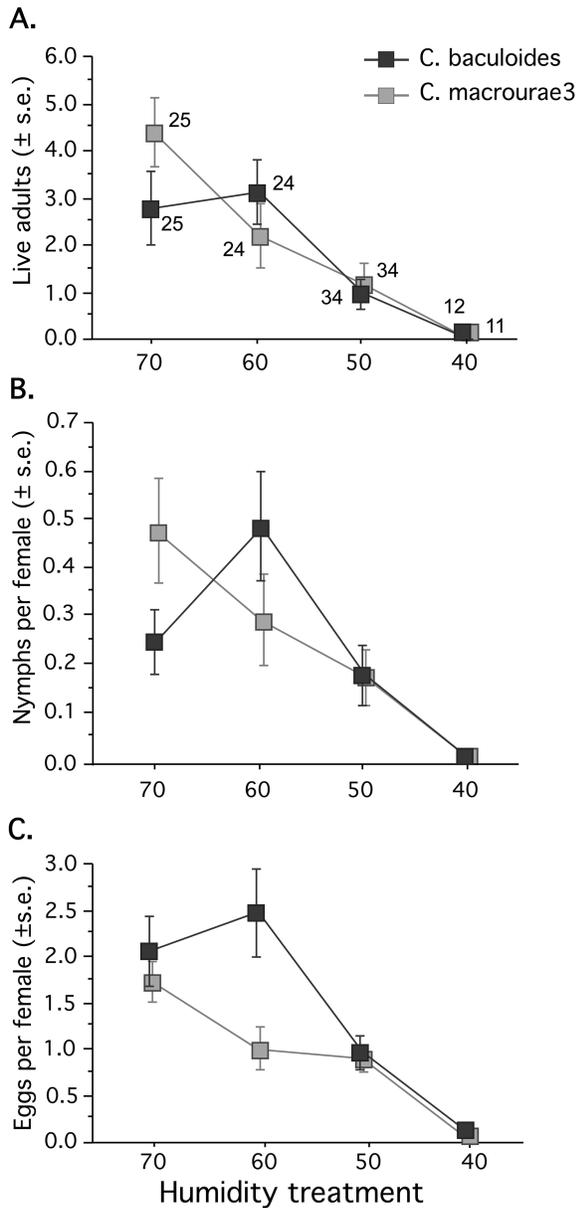
**Figure 3:** Population sizes of *Columbicola baculoides* and *Columbicola macrourae3* (i.e., the *C. macrourae* lineage found on mourning doves) when alone on a host compared with mixed-species infestations. Each bar is the mean of louse populations from 11 birds. A, Adult *C. baculoides* populations were significantly larger when alone on hosts compared with when sharing a host with *C. macrourae3*; asterisk indicates significant difference ( $P < .05$ ). B, *Columbicola baculoides* nymphs showed the same trend, but the difference was not significant. Combined analysis of adults and nymphs also showed that *C. baculoides* populations were significantly larger when alone on hosts compared with when they were sharing a host with *C. macrourae3* (see text).

*baculoides* and *C. macrourae3*. Although we have not examined Canadian humidity data, Manitoba is directly north of our U.S. transition zone, and these humidity trends are known to persist into Canada.

The distribution of *C. baculoides* and *C. macrourae3* is broadly congruent with the distribution of two subspecies of mourning doves, *Zenaidura macroura carolinensis* and *Zenaidura macroura marginella*, which have a wide zone of overlap in the central United States (Mirarchi and Baskett 1994). The rough concordance of these host subspecies with *C. baculoides* and *C. macrourae3* is consistent with the possibility that the lice have simply speciated on closely related host taxa (Page 2003; Clayton et al. 2004). This is not the case, however, because *C. macrourae3* and *C. bac-*

*uloides* are not sister groups but distantly related lineages from different sections of the *Columbicola* phylogeny (Johnson et al. 2007). Furthermore, the zone of overlap between *C. baculoides* and *C. macrourae3* (fig. 1) is west of the overlap between the mourning dove subspecies, which runs from Michigan to eastern Texas (Mirarchi and Baskett 1994).

An interesting exception to the east/west distributions of *C. macrourae3* and *C. baculoides* is that some of the mourning doves we collected in northern Utah had both species of lice (fig. 1). Of 15 birds collected in northern Utah in May 2005, 14 (93%) had *C. baculoides*, as expected (mean = 23 *C. baculoides* per bird). Interestingly, though, three of the birds (20%) also had *C. macrourae3* (mean =

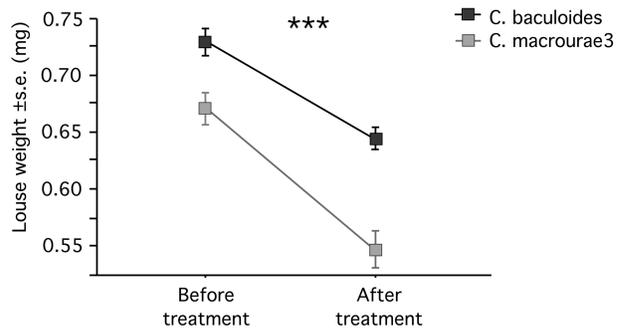


**Figure 4:** Relative sizes of *Columbicola baculoides* and *Columbicola macrourae3* (i.e., the *C. macrourae* lineage found on mourning doves) populations at different ambient humidities. Numbers next to the symbols in A show the number of replicate vials for A, B, and C; each vial started with 10 lice. A, Mean number of adults ( $\pm$ SE) surviving per vial after 2 weeks at the indicated humidity; B, mean number of live nymphs ( $\pm$ SE) per adult female after 2 weeks; C, mean number of eggs per female after 2 weeks.

4 *C. macrourae3* per bird). These records suggest that the geographic specificity of the two species of lice may break down on the host's wintering grounds. The Yucatán Peninsula is a major overwintering destination for mourning

doves from both sides of the humidity transition (Mirarchi and Baskett 1994). Thus, it is conceivable that western birds can become infested at the wintering grounds with *C. macrourae3* from eastern birds, possibly as a result of phoretic dispersal on hippoboscid flies, which is common in *Columbicola* (Harbison et al. 2008). If our humidity hypothesis is correct, however, *C. macrourae3* on western birds should not be able to survive for long on the host's arid breeding grounds. To test this hypothesis, we collected additional mourning doves from northern Utah in August and early September of 2007 ( $n = 4$ ) and 2008 ( $n = 10$ ). Although only five of these birds had *Columbicola* (mean = 5.8 lice per bird), as predicted, all of the lice ( $n = 29$ ) were *C. baculoides*. The prevalence of *C. baculoides* on mourning doves in Utah also dropped at the end of summer (from 93% to 36%). Summers in Utah are hot and dry, and 2007 was the hottest summer on record for the state (<http://www.noaanews.noaa.gov/stories2007/s2917.htm>). Perhaps even *C. baculoides* has difficulty thriving in the low humidity associated with such high temperatures.

A reciprocal scenario, of sorts, may explain the single *C. baculoides* record from Ohio. This specimen was collected in April 1932 from a host that may have just returned from the wintering grounds. If *C. baculoides* infest a mourning dove with no competing *C. macrourae3*, we would predict that *C. baculoides* could survive unimpeded in the humid east, but only in single-species infestations. More sampling of eastern birds would allow us to test this prediction. Indeed, more sampling from many of the localities is needed. Taken together, these records show a strong geographic pattern (fig. 1); however, the small num-



**Figure 5:** Mass loss by *Columbicola baculoides* and *Columbicola macrourae3* (i.e., the *C. macrourae* lineage found on mourning doves) over an 8-h treatment at relatively low humidity in an incubator. Values are the combined mass of 10 individual lice. *Columbicola macrourae3* lost significantly more mass than did *C. baculoides*, although both species lost mass at low humidity. Asterisks show significant difference ( $P < .001$ ).

ber of specimens collected from most locations makes it difficult to be sure that a particular species is absent from any given locality.

Our captive bird transfer experiments showed that *C. baculoides* does equally well in humid or arid conditions, while *C. macrourae* suffers in arid conditions. Our in vitro results suggest that the difference between *C. baculoides* and *C. macrourae* sensitivity is most pronounced at ~60% RH. At 60% RH in the incubator, *C. macrourae* had lower survival of adults and nymphs, as well as lower egg production, than *C. baculoides*. These patterns may reflect a difference in the level of stress experienced by *C. macrourae* and *C. baculoides* as the RH drops. Interestingly, the geographic transition between the distributions of *C. macrourae* and *C. baculoides* occurs close to the 60% mean annual RH zone (fig. 1). The humidity data we report does not represent the full range of daily or seasonal variation found in nature. Daily fluctuations in humidity could conceivably provide a buffer allowing *C. macrourae* to persist in some regions. Therefore, it is not surprising to see some variation in species distributions, especially within regions of moderate humidity.

The persistence of *C. baculoides* in arid conditions may be due to the ability of this species to maintain body water content at low humidity. Feather lice do not drink fluid; rather, they actively remove water vapor from the atmosphere, a strategy that has been documented in many different arthropod groups (Wright and Machin 1993). Our mass-loss experiment was performed at 40% RH, which was an intentionally stressful condition (Rudolph 1983). It was therefore not surprising that *C. baculoides* and *C. macrourae* both experienced significant reductions in body mass. However *C. baculoides* fared better than *C. macrourae* did (fig. 5), indicating that it is more resistant to arid conditions.

Although adaptation to arid conditions can explain the presence of *C. baculoides* in the arid western United States, it does not explain why it is restricted to the West. We therefore explored the hypothesis that this restriction might be due to condition-specific competition with *C. macrourae*. The data from our competition experiments suggests that this is indeed the case: *C. baculoides* is competitively inferior to *C. macrourae* (fig. 3). However, these data do not identify the limiting resource underlying competition between *C. baculoides* and *C. macrourae*. It is unlikely that the two species were competing for food because the average number of lice per bird in this experiment, regardless of treatment, was only 24.9 ( $\pm 6.9$ ). Bitted mourning doves used for culturing lice (see "Material and Methods") can support louse populations that are 10–20 times larger than these populations for much longer than the 6 weeks (J. R. Malenke, unpublished data).

Hence, mourning dove feathers provide sufficient food to support much larger louse populations.

*Columbicola baculoides* and *C. macrourae* may be competing indirectly for enemy-free space. Mourning doves in our experiments were allowed to preen normally, which is the primary defense of most birds against ectoparasites like lice (Clayton et al. 2005). Bush and Malenke (2008) recently reported evidence for competition for enemy-free space between species of feather lice parasitizing rock pigeons (*Columba livia*). As in the current study, the poorer competitor experienced competitive release when alone on the host. The authors concluded that limited refuges from preening are at least partly responsible for competition. In the rock pigeon experiment, the two competing lice were from different genera with different morphotypes and different strategies for escaping host defenses. *Columbicola baculoides* and *C. macrourae* are much more similar, so we would predict greater overlap in refuge use and thus stronger competition. Indeed, the effects of competition between *C. baculoides* and *C. macrourae* are detectable at smaller population sizes than is the case for rock pigeon lice. A test of our hypothesis that enemy-free space is the limiting resource in competition between *C. baculoides* and *C. macrourae* could be performed by repeating our competition experiment with bitted birds with impaired preening. Under such conditions, we would predict an increase in both species of lice and for the disparity between *C. baculoides* populations alone and co-occurring with *C. macrourae* to disappear because, without the enemy (preening) present, there would be no need for refugia.

The effect of competition is also dependent on life stage. *Columbicola baculoides* nymphs did not respond as strongly as *C. baculoides* adults to competitive release (fig. 3). One reason for this could be the much larger variation in nymphal populations than adults. Such variation can swamp biologically significant patterns. Another possibility is that nymphs do not experience competition as strongly as adults do. First- and second-instar nymphal lice are tiny, which may enable them to escape host preening more easily. If small size helps to protect them from host defense, then the availability of refugia may be less critical for the survival of nymphs. *Columbicola* nymphs also tend to congregate on the host's head, a region that is impossible for the host to preen (Nelson and Murray 1971; Bush et al. 2010).

The ability of *C. baculoides* to withstand the arid conditions of the western United States may prove advantageous in the face of climate change. All else being equal, RH drops with increasing temperature. The International Panel on Climate Change (IPCC 2007) projects an increase in global temperature of 1.1°–6.4°C in the next century. Such an increase in temperature would result in a corresponding drop in RH of 4%–23% ( $\Delta RH = -0.03 -$

$3.586 \times \Delta T$ ; Labajo et al. 1991). Our results suggest that a 20% change in mean RH would be sufficient to drive *C. macrourae* out of large portions of the central and eastern United States, thus allowing *C. baculoides* to spread onto birds in those regions. Hence, condition-specific competition is subject to change as environmental conditions change. This expansion of *C. baculoides*'s range could happen even if the distribution of mourning doves is unaffected, effectively reducing the diversity of *Columbicola* on U.S. mourning doves from two species to one.

Changes in global climate may lead to reductions in parasite diversity in a variety of systems as refuges from competition are lost. With more than 20,000 described species of terrestrial ectoparasites (Poulin 2006) and many more undescribed species, the effect on biodiversity could be significant. Conditionality in species interactions is by no means restricted to ectoparasites, and other systems may suffer similar consequences. For example, the relationship between mycorrhizal fungi and their plant hosts fluctuates along the mutualism/parasitism continuum. Mycorrhizae are more likely to be mutualistic in moist conditions and parasitic in dry conditions (Johnson et al. 1997). Climate change could have important effects on crop success and global plant biodiversity if it results in a shift of mycorrhizae toward parasitic interactions. On the other hand, the effects of climate change could be moderated by context-dependent interactions. In Israeli shrublands, facilitation between shrubs and grasses maintains biodiversity in xeric communities. In humid environments, the presence of shrubs reduces the species richness of co-occurring annual grasses, possibly due to competition. The reverse occurs in xeric habitat, where shrubs seem to offer an environmental refuge from harsh desert conditions, maintaining diversity where grasses alone would not survive (Holzapfel et al. 2006).

In summary, ecologists have often failed to fully appreciate the context dependency of interspecific interactions (Agrawal et al. 2007). The strength and direction of these interactions often depends on biotic and abiotic features of the environment (Holland and DeAngelis 2009; Juliano 2009; Maestre et al. 2009). Our data suggest that one result of this context dependency is that small changes in the environment may lead to significant changes in the diversity of seemingly stable communities. This study demonstrates the impact of context dependency—in the form of condition-specific competition—on the geographic distribution and diversity of avian ectoparasites. Context dependency may well play a significant role in the distribution and diversity of other types of parasite communities.

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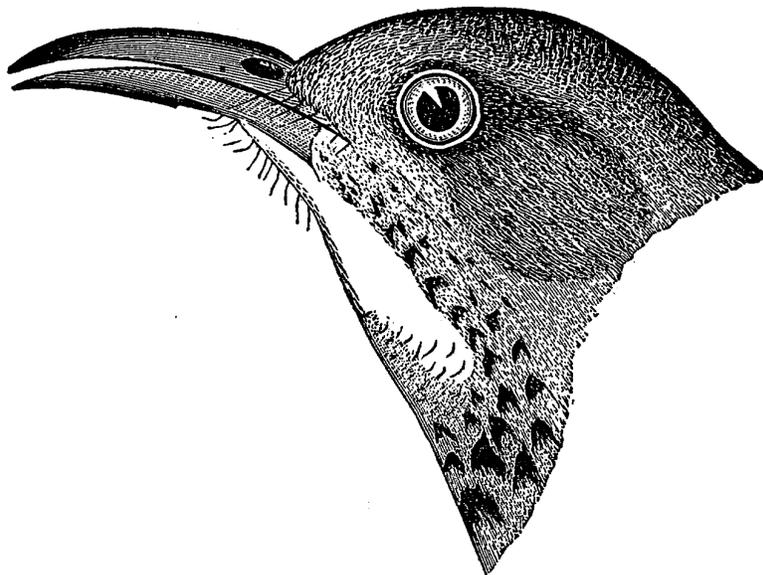
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