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SPATIAL PARTITIONING OF HOST HABITAT BY CHEWING LICE OF THE GENERA *GEOMYDOECUS* AND *THOMOMYDOECUS* (PHTHIRAPTERA: TRICHODECTIDAE)

David L. Reed, Mark S. Hafner, Shannon K. Allen, and Melanie B. Smith
Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana 70803

ABSTRACT: Chewing lice, *Geomydoecus* and *Thomomydoecus,* coexist on pocket gophers, *Thomomys* spp. We investigated the spatial distribution of the 2 genera on their hosts and explored possible mechanisms of resource partitioning by chewing lice. Chewing lice appear to partition available host resources spatially, with *Geomydoecus* occurring primarily on the lateral and dorsal regions of the host, and *Thomomydoecus* occurring primarily on the lateral and ventral regions. Although spatial partitioning of the host habitat is evident, it does not appear to be explained by hair diameter. Spatial partitioning of the host's body could be the result of some other factor, possibly temperature or humidity gradients of the host's body.

Ectoparasitic chewing lice, *Geomydoecus* and *Thomomydoecus* spp. (Phthiraptera: Trichodectidae), live their entire lives exclusively on pocket gophers of the rodent family Geomyidae (Marshall, 1981; Hellenthal and Price, 1984). Chewing lice are wingless, obligate parasites that can survive only a short time when removed from their host (Kellogg, 1913; Marshall, 1981). One species of louse often is confined to a single species of host (Emerson and Price, 1981), which suggests a long-term, perhaps obligate, association between each host–parasite pair. In many instances, this long-term association has resulted in parallel cladogenesis between the pocket gopher and chewing louse lineages. This pattern, termed ''cophylogeny,'' is well documented for certain lineages of pocket gophers and their associated chewing lice (Hafner and Nadler, 1988; Demastes and Hafner, 1993; Hafner et al., 1994).

Although most individual pocket gophers host populations of a single species of louse, 3 species within *Thomomys* host representatives of 2 genera of chewing lice (*Geomydoecus* and *Thomomydoecus*; Hellenthal and Price, 1984), with species of both genera usually coexisting on an individual host. Given the principle of competitive exclusion (Gause, 1934), stable coexistence of 2 species of lice on an individual host suggests that the lice partition some aspect of the resources provided by the host (Durden, 1987).

During our initial studies of chewing louse distribution on pocket gophers, we noticed that guard hair diameter seems to vary predictably with body region, perhaps providing a mechanism for resource partitioning by chewing lice. Lice attach to gopher hairs by means of a head groove located on the rostrum (Fig. 1). Secure attachment is necessary for survival of the parasite because of the louse's absolute dependence on the host. Reed et al. (in press) showed a significant positive relation between hair diameter in several genera of pocket gophers and rostral groove width of their chewing lice, and also demonstrated that the head groove of a louse was of the appropriate size to grip tightly onto the hair shaft of its natural host.

In the present study, we investigate hair diameter as a potential mechanism for resource partitioning that may result in stable coexistence between 2 species of chewing lice on an individual pocket gopher. Specifically, we test the hypothesis that louse species of *Geomydoecus* and *Thomomydoecus* are able to coexist by partitioning the host's resources spatially on the basis of hair diameter.

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MATERIALS AND METHODS

Three specimens of *Thomomys bottae connectens* were trapped on 17 March 1997 in Albuquerque, Bernadillo County, New Mexico. Two males and 1 female were collected using traps designed by Baker and Williams (1972). We used pocket gophers collected on a single day from a single locality to limit variation in louse population density caused by weather patterns, reproductive condition of the host, or other seasonal or geographic factors.

Each gopher was killed by placing it in an airtight container saturated with chloroform. This process also immediately immobilized and killed the resident louse population of each gopher. The gopher was then incised medially along the abdomen, and the entire skin was removed and pinned to a piece of cardboard, fur side down. Unnecessary movement of the skin was avoided to reduce accidental displacement of the lice. The skin was frozen on a block of dry ice, then pressed between 2 pieces of cardboard, wrapped tightly in aluminum foil, and frozen in an ultracold freezer (−75 C).

While frozen, the gopher skin was cut into 10 regions (Fig. 2): anterior ventral, cheek, dorsal head, lateral nape, lateral, nape, posterior dorsal, posterior ventral, rump, and ventral head. Samples from the right and left sides of the body were pooled for each region, and each region was placed individually in a plastic bag to avoid loss of lice and contamination by lice from other regions. Each section of the gopher pelt was brushed vigorously, and lice were collected in a 1.5-ml cryotube. Adult lice were then identified as either *Geomydoecus aurei* or *Thomomydoecus minor* using a dissection microscope. Only adults were used in this analysis because visual identification of juvenile lice is problematic. Each pelage region was measured (in cm^2) so that the number of lice per region could be standardized (lice/cm^2). The total surface area (the 10 regions combined) and overall louse density (lice/cm^2) were calculated for each of the 3 gopher specimens. Assuming a null model of even louse distribution, the expected number of *Geomydoecus* and *Thomomydoecus* for each region on the basis of the size of the region and the mean density for that particular gopher was determined. Chi-square analyses were used to test whether the observed numbers of lice were significantly different from expected numbers on the basis of an even distribution.

Ten guard hairs were taken from each of the 10 regions from all 3 gophers (chewing lice normally grasp guard hairs rather than underfur; personal observation). The hairs were mounted on microscope slides, and the mid-point diameter of each hair was measured (in μm) using a light microscope fitted with an ocular micrometer. Analysis of variance (ANOVA) and a Duncan post-ANOVA test (SAS Institute, 1994) were used to detect significant differences in mean hair diameter among the 10 regions. Specimens are deposited in the New Mexico Museum of Natural History (NMMNH 2378, 2379, and 2380).

RESULTS

Mean hair diameter (pooled data for the 3 hosts) varied from 33.61 ± 1.75 μm in the rump region to 45.22 ± 1.53 μm in the lateral-nape region (Table I). The Duncan post-ANOVA test identified 5 groups of regions within which mean hair diameter was not significantly different (Table I). In general, pocket go-

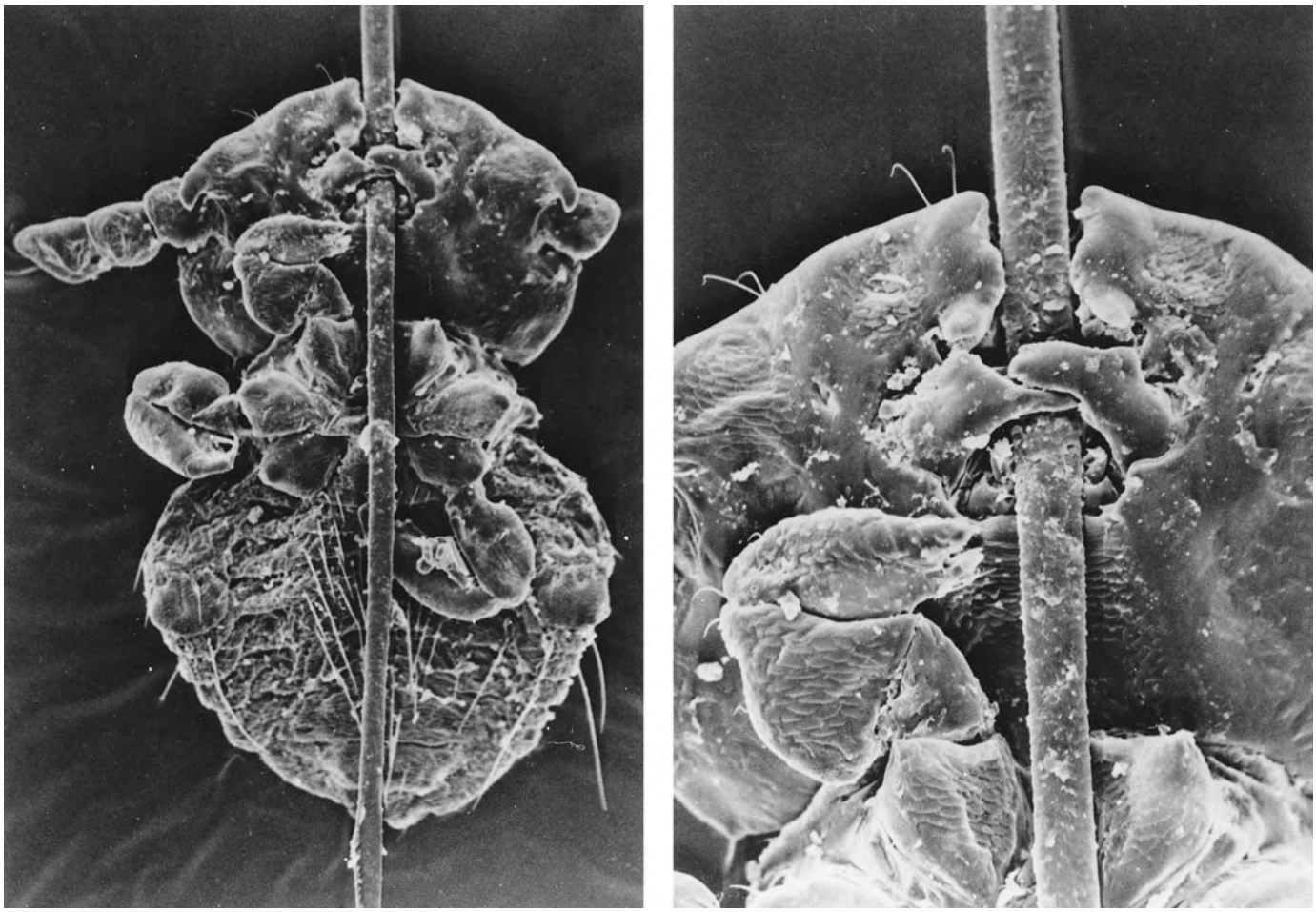

FIGURE 1. Electron micrograph of a chewing louse (*Geomydoecus aurei*) attached to a pocket gopher (*Thomomys bottae*) hair shaft (left). Magnified view of rostral groove and hair shaft (right).

pher hair was smaller in diameter on the dorsal surfaces and larger in diameter on lateral and ventral surfaces.

The overall mean density of *G. aurei* (pooled data for all 3 hosts; Table II) was 0.34 lice/cm^2 (range 0.28–0.50 lice/cm^2), and overall mean density for *T. minor* was 0.94 lice/cm^2 (range 0.28–1.38 lice/cm^2). Chi-square analysis of louse distribution revealed that none of the populations of either species was distributed evenly over the gopher pelage (all chi-square values exceeded the critical value of 27.88, $P < 0.001$, df = 9; Table II).

Individuals of *G. aurei* were found in all 10 regions of the gopher pelage, although some regions contained very few individuals (see pooled data, Table II). Likewise, at least 1 individual of *T. minor* occurred in all regions except the dorsal-head region. *G. aurei* occurred in greater abundance than expected on dorsal and lateral surfaces of the hosts (Fig. 2a), whereas *T. minor* was found in greater abundance than expected on lateral and ventral surfaces (Fig. 2b). For *Geomydoecus,* the regions of high abundance (shaded regions in Fig. 2a) comprised only 34% of the total surface area of the gopher yet contained 78% of all *Geomydoecus* individuals (Table II). In contrast, the regions of high abundance for *Thomomydoecus* (shaded regions in Fig. 2b), which also comprised 34% of the total surface area of the gopher, contained only 55% of all *Thomomydoecus* individuals. Therefore, there are large differences in both density and distribution of the 2 louse taxa (Fig. 3).

DISCUSSION

G. aurei and *T. minor* are not evenly distributed throughout the pelage of their host (*T. bottae*) and show a tendency to subdivide the available habitat dorsoventrally (Figs. 2, 3). Future studies will determine whether this pattern changes geographically, seasonally, or with the age or reproductive condition of the host. Considering that lice showed the same distributional pattern on the male and female hosts examined in this study (Table II), gender of the host does not appear to influence louse distribution, at least for nonreproductive hosts (as in this study).

Given that both genera of lice were found throughout the gopher pelage (with the single exception of the absence of *Thomomydoecus* in the dorsal-head region; Table II), it is clear that the taxa are interactive (as defined by Brooks, 1980) and are able to transit, if not forage and reproduce in, regions of pelage with hairs of different diameters. In fact, regions of high abundance for *G. aurei* encompass almost the entire range of hair diameters (from 34.32 to 45.22 μm, Table I). In contrast,

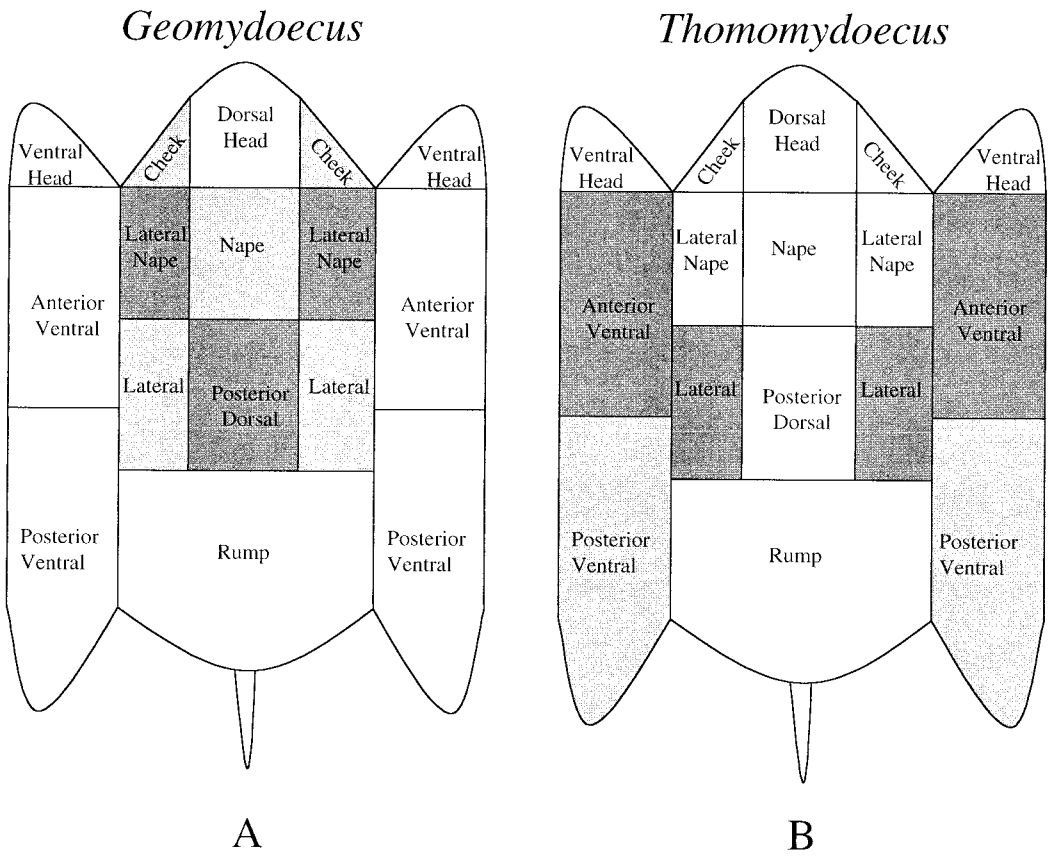

FIGURE 2. Diagrammatic view of the external surface of a pocket gopher showing the distribution of *Geomydoecus* (**A**) and *Thomomydoecus* (**B**) lice. Darkly shaded regions contained more lice than expected in all 3 pocket gopher specimens examined (Table I). Lightly shaded regions contained more lice than expected in 2 of the 3 pocket gopher specimens examined. Unshaded regions contained fewer lice than expected in at least 2 of the pocket gopher specimens examined.

regions of high abundance for *T. minor* include only regions with hairs of intermediate diameter (from 39.53 to 42.66 μm, Table I).

Despite the general dorsoventral trend in hair diameter (Table I) and a similar dorsoventral trend in louse distribution (Table II, Fig. 2), the broad overlap in hair diameters used by the 2 species (Table I) suggests that hair diameter, alone, is insufficient to explain habitat partitioning in this louse community. It is possible, however, that *Thomomydoecus* lice are less efficient than their competitors at grasping hairs of extremely large or small diameter, yet are superior competitors in regions of intermediate hair diameter. It is also possible that the 2 louse species differ in their ability to evade grooming pressure from the host, which may vary dorsoventrally. Waage (1979) suggests that areas of overlap in the distribution of co-occurring ectoparasites may receive greater grooming pressure from the

TABLE I. Mean guard hair diameter (μm) for each of the 10 body regions in the 3 pocket gopher specimens examined. The Duncan post-ANOVA test reveals 5 groups (designated A–E) within which mean hair diameter was not significantly different. For each region, louse taxa found in greater abundance than expected (Fig. 2) are indicated.

Region	Mean hair diameter (μm)	Duncan grouping	Greater abundance than expected
Lateral nape	45.22 ± 1.53	A	*Geomydoecus aurei*
Cheek	44.90 ± 1.76	A	*Geomydoecus aurei*
Posterior ventral	42.66 ± 1.28	A B	*Thomomydoecus minor*
Anterior ventral	41.40 ± 1.60	A B	*Thomomydoecus minor*
Lateral	39.53 ± 1.83	B	Both species
Ventral head	38.72 ± 1.51	B C	Neither species
Dorsal head	38.31 ± 1.54	B C D	Neither species
Nape	35.23 ± 1.53	C D E	*Geomydoecus aurei*
Posterior dorsal	34.32 ± 1.67	D E	*Geomydoecus aurei*
Rump	33.61 ± 1.75	E	Neither species

TABLE II. Total surface area (cm^2) of each pelage region (Fig. 2) and number of observed and expected lice per region for the 2 coexisting species of chewing lice. Data are pooled for the 3 hosts examined.

		Thomomydoecus minor		*Geomydoecus aurei*	
Region	Area (cm^2)	Observed	Expected	Observed	Expected
Anterior ventral	58.89	80	59	11	20
Cheek	40.38	2	37	12	14
Dorsal head	35.63	0	35	6	14
Lateral nape	33.01	21	26	29	11
Lateral	56.01	128	50	26	18
Nape	30.01	16	29	14	10
Posterior dorsal	35.25	28	35	62	13
Posterior ventral	67.00	71	62	12	21
Rump	165.75	153	151	4	54
Ventral head	27.88	17	32	9	10
Total	549.78	516	516	185	185

host because of higher overall density of parasites. Waage contends that removal of parasites from these areas of overlap (by grooming) would reinforce spatial partitioning of the ectoparasites by removing the ability of parasites to cross corridors between areas of exclusive habitation. However, our observations of captive pocket gophers suggest that they groom only infrequently, and we think it is more likely that the habitat partitioning observed in this study results from differential responses on the part of the 2 louse species to other microhabitat features such as temperature or humidity gradients or location and density of sebaceous glands of the host (Murray, 1957). It seems reasonable to postulate that the dorsal and ventral surfaces of a pocket gopher constitute very different microhabitats, and this hypothesis will be examined in future studies. In addition, future studies of *T. bottae* populations that host only 1 of these 2 species will reveal the extent to which competition

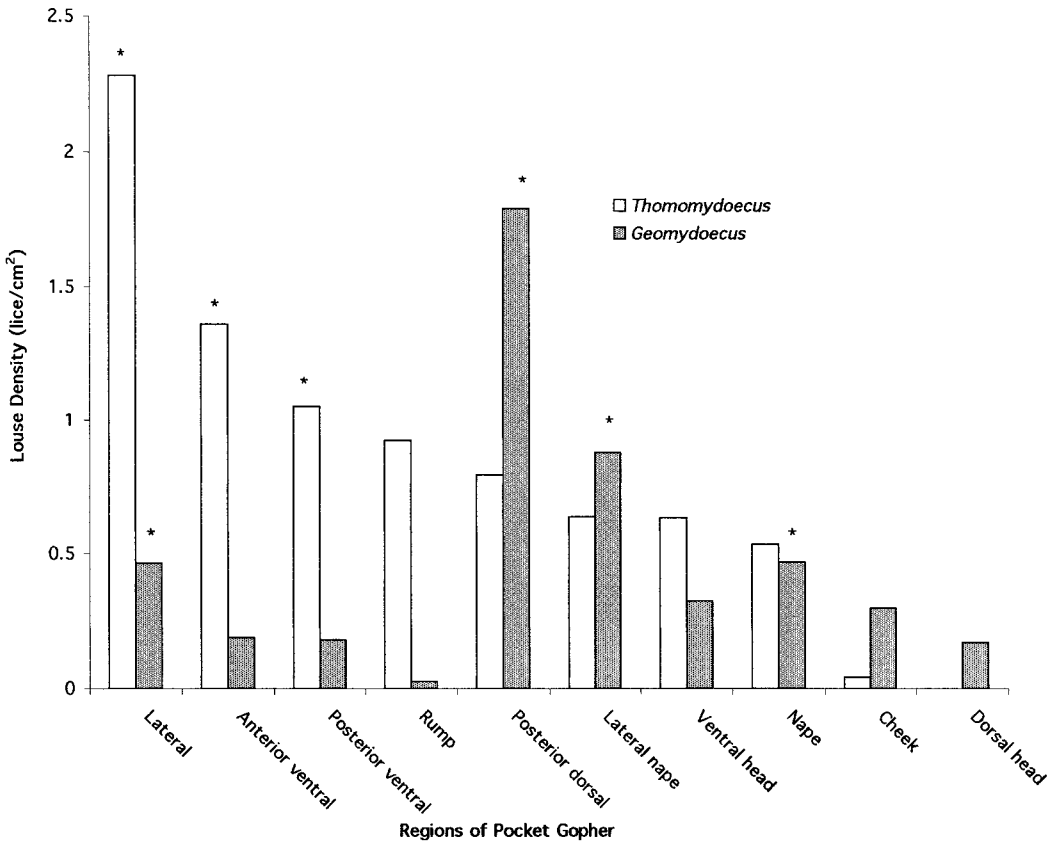

FIGURE 3. Comparative density of *Thomomydoecus* and *Geomydoecus* lice in the 10 regions of pocket gopher pelage. Asterisks indicate regions that contained more lice than expected in all 3 pocket gopher specimens examined (Table I, Fig. 2). Regions are arranged left to right in order of decreasing abundance of *Thomomydoecus minor*.

may be influencing the distribution of these species when they coexist.

The fact that hair diameter may have little or no influence on louse distribution at the level of the individual host does not automatically falsify the hypothesis that hair diameter may be an important causal factor influencing louse distribution at higher phylogenetic levels, e.g., among different species and genera of hosts (Reed, 1994; Page and Hafner, 1996). For example, Morand et al. (in press) and Reed et al. (in press) have shown dramatic differences in hair diameter among different genera of pocket gophers and have documented a close relation between hair diameter in the hosts and rostral groove dimensions of their chewing lice. Artificial transfer studies by Reed and Hafner (1997) suggest that lice that normally parasitize species of pocket gophers with narrow hairs may be unable to grasp the wider hairs of larger species of pocket gophers. Finally, studies by Murray (1957) show that hair diameter in sheep may influence ovipositing in their chewing lice. Together, these studies suggest that hair diameter may be a course-grained determinant of chewing louse distribution, wherein lice are unable to transfer between hosts with large differences in hair diameter (e.g., Reed and Hafner, 1997), but are tolerant of lower levels of variation, such as those observed at the individual and infraspecific host levels. It follows that some other as yet unknown environmental parameter, perhaps temperature or humidity, may be the fine-grained determinant of louse distribution at the individual and infraspecific host levels. If so, differential responses to these factors by different species of lice may enable stable coexistence of multiple species on a single host individual.

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