

HOST SPECIFICITY OF CHEWING LICE ON POCKET GOPHERS: A POTENTIAL MECHANISM FOR COSPECIATION

DAVID L. REED AND MARK S. HAFNER

*Museum of Natural Science and Department of Zoology and Physiology,
Louisiana State University, Baton Rouge, LA 70803*

Pocket gophers (Rodentia: Geomyidae) and their ectoparasitic chewing lice (Phthiraptera Trichodectidae) have congruent phylogenies and show evidence of cospeciation. We examined a potential mechanism that could generate the observed pattern of cospeciation by testing the ability of lice to survive and reproduce on hosts other than their own. Our tests were conducted at the subspecific, specific, and generic levels relative to the natural host. Although lice established successful colonies at each level, colonization of new hosts diminished with increasing phylogenetic distance from the natural host of each louse. We suggest that the pattern of cospeciation results primarily from lack of opportunity for lice to colonize new hosts. However, in rare cases where lice disperse to new hosts, survival may be difficult on hosts that are not closely related to the natural host, which would reinforce the pattern of cospeciation.

Key words: pocket gophers, chewing lice, host specificity, cospeciation, Geomyidae, Trichodectidae

Pocket gophers (Rodentia: Geomyidae) are a taxonomically diverse lineage comprised of six genera, 35 species, and >400 recognized subspecies (Hall, 1981; Wilson and Reeder, 1993). All extant taxa are members of the subfamily Geomyinae, which consists of the tribe Geomyini (containing the genera *Geomys*, *Pappogeomys*, *Cratogeomys*, *Orthogeomys*, and *Zygogeomys*) and the tribe Thomomyini (*Thomomys*). Sympatry among species of pocket gophers is rare, but many pocket gophers have narrow zones of parapatry with other species of geomyids. Gophers are solitary and defend their burrow systems from other individuals, except during the breeding season. Wight (1930) removed adult males, adult females, and several young from each of several burrow systems, which suggests that individuals of opposite sex may spend considerable time in a single burrow during the reproductive season (Reichman et al., 1982).

Chewing lice of the genera *Geomydoecus* and *Thomomydoecus* (family Trichodecti-

dae) are external parasites restricted to pocket gophers. The entire life cycle of the chewing louse occurs on the host, and lice are dependent on the pocket gopher for food and warmth. Chewing lice are obligate parasites because they typically die upon removal from their host (Kellogg, 1913; Marshall, 1981). Because lice are wingless and live on asocial hosts that generally have allopatric distributions, their capabilities for dispersal are extremely limited (Kethley and Johnston, 1975). Dispersal typically occurs when lice are transferred from the female pocket gopher to its offspring during suckling (Rust, 1974). However, maternal transmission is insufficient to describe the current distributions of lice because closely related taxa sometimes occur on hosts that are related distantly (Hafner and Nadler, 1988).

Independent phylogenies for eight species of pocket gophers and their chewing lice were derived by Hafner and Nadler (1988) from allozymic data. The phylogenies of gophers and lice were shown to be

significantly congruent, which indicates that gophers and lice share a similar phylogenetic history (termed cospeciation). This pattern of phylogenetic congruence has been corroborated for larger taxonomic samples of gophers and lice by Hafner et al. (1994).

In this study, we attempt to elucidate the causal mechanism underlying cospeciation between gophers and lice. Clearly, long-term parallel phylogenesis requires that the parasite exhibit some specificity toward certain hosts. This specificity may result from the parasite's dependence on a particular species of host for one or more essential resources, such that the parasite cannot survive on alternative or new hosts (Kethley and Johnston, 1975). This idea commonly is termed resource tracking (Kethley, 1970). High specificity also may occur simply because the parasite has low vagility and cannot disperse to new taxa of hosts (Kethley and Johnston, 1975). These two alternative explanations for the mechanism of cospeciation were stated more succinctly by Lyal (1986), who suggested that the process of cospeciation is driven either by lack of colonization of new hosts or by lack of establishment on new hosts.

In controlled experiments, we tested whether lice could survive on new taxa of hosts and we assessed the degree to which resource tracking may drive cospeciation in this system. If lice readily survive on new hosts, then lack of opportunity for colonization of new hosts must be the primary cause of cospeciation. Alternatively, failure of lice to survive on new hosts under experimental conditions supports the idea that lice cannot establish colonies on new hosts in nature, even if the opportunity to disperse arises. This would suggest that at least one resource essential for survival of lice is lacking in the environment provided by the new host. Lice were transferred to new taxa of hosts to test a nested set of hypotheses, which stated that lice cannot survive and reproduce on new hosts of increasing phylogenetic distance (subspecies, species, and genus) from their natural host.

MATERIALS AND METHODS

We collected pocket gophers from four localities: *Thomomys bottae connectens*, $n = 6$, 2 km S of La Joya, Socorro Co., New Mexico; *T. b. opulentus*, $n = 8$, 2 km N of Escondida, Socorro Co., New Mexico; *T. talpoides*, $n = 10$, 2 km N Jemez Springs, Sandoval Co., New Mexico; *Cratogeomys castanops*, $n = 14$, 2 km N of Lubbock, state road 1264, Lubbock Co., Texas. We used traps designed by Baker and Williams (1972) to live trap gophers. We caged the gophers separately for transport to the laboratory and permanently housed the gophers individually in polycarbonate cages (29 by 53.5 by 20 cm). Each cage contained ca. 7.5 cm of untreated aspen bedding that was changed weekly. Each cage also contained a 15-cm length of polyvinyl chloride pipe (6.5 cm diameter) for shelter and gnawing material. Gophers were acclimated for 30 days in the artificial environment and kept on a cycle of 12L:12D. We fed them a daily diet of alfalfa, guinea pig chow (for vitamin B), rat chow, fresh potatoes, fresh carrots, and fresh cabbage. We measured body mass biweekly and provided veterinary care as needed.

We randomly divided the gophers into two groups, those that donated lice and those that received lice. Donors (*T. b. connectens*, $n = 2$; *T. b. opulentus*, $n = 2$; *T. talpoides*, $n = 3$; *C. castanops*, $n = 2$) provided lice for experimental transfer to other hosts. In contrast, we cleaned the receiving gophers (*T. b. connectens*, $n = 4$; *T. b. opulentus*, $n = 4$; *T. talpoides*, $n = 4$; *C. castanops*, $n = 12$) of their lice and used these gophers as recipients of new populations of lice. Treatment of recipients with a water-based pyrethrin spray (0.20% pyrethrin) killed resident populations of lice. We removed the donors from the room during this procedure to prevent accidental removal of their lice. Because the eggs of chewing lice hatch in ca. 11 days (Rust, 1974), a second treatment 15 days later removed the entire population of lice. We conducted several trials to insure that this technique was successful in removing all lice. In every case, no lice survived on hosts treated in the manner described. Treated animals remained undisturbed for 30 days post-treatment to allow for complete dissipation and degradation of the pyrethrin-based insecticide.

After the 30-day period, donors resided in the same room as recipients to insure that both groups experienced identical environmental con-

TABLE 1.—*Experimental design and results of the host-transfer experiments. Lice were transferred from their natural host (the donor) to a new host (the recipient) to test the louse's ability to survive and reproduce on the new host (n = number of replicate experiments). Yes signifies that the introduced lice survived and reproduced on the new host. No indicates that the lice died on the new host.*

Donors	Recipients			
	<i>Thomomys bottae connectens</i>	<i>Thomomys bottae opulentus</i>	<i>Thomomys talpoides</i>	<i>Cratogeomys castanops</i>
<i>Thomomys bottae connectens</i>	yes (n = 2) (control)	yes		no (n = 4)
<i>Thomomys bottae opulentus</i>	yes (n = 2)		yes (n = 1) no (n = 1)	no (n = 4)
<i>Thomomys talpoides</i>		yes (n = 2)	yes (n = 2) (control)	no (n = 4)
<i>Cratogeomys castanops</i>		yes (n = 1) no (n = 1)		

ditions. We harvested lice from the donors by anesthetizing the gopher and using forceps to remove a sample of lice ($n = 15$). Anesthetization involved the use of isoflurane delivered with an inhalation machine fitted with a vaporizer. We placed the gophers in air-tight acrylic chambers and subjected them to a mixture of 70% isoflurane and 30% oxygen. After ca. 2 min, we transferred the anesthetized animal to a delivery system that used a fitted mask containing the same mixture of isoflurane and oxygen. We intermittently administered isoflurane through the mask as needed. In each case, duration of anesthesia was ≤ 20 min. Because we administered most of the isoflurane directly into the gopher's nose via the fitted mask, the lice were unaffected. We briefly observed the lice to insure that they were uninjured during removal.

We also anesthetized the recipients as described previously, and we transferred lice to the recipients within 15 min of their removal from the donor. We released the lice just behind the head of the recipient, where grooming is difficult (Rust, 1974). To insure that the transfer of lice from donors to recipients was adequate, we transferred two samples ($n = 15$ each) 7 days apart. Thus, each recipient received two samples of lice from one donor. Tests at the subspecific and specific levels included controls, wherein we removed lice from a donor and introduced them onto a recipient of the same taxon.

Thirty days after the final transfer of lice (and every 30 days thereafter), we anesthetized recipients and examined them to verify presence or absence of lice. The inspection required ca. 10 min and consisted of a qualitative assessment of the

density of lice. The small size of the lice, density of the fur of pocket gophers, and danger of prolonged anesthesia precluded quantitative sampling of populations of lice. We concluded the experiment after 150 days (about four generations of lice—Rust, 1974).

Because it is difficult to maintain certain species of geomyids in captivity, the number of recipients used in our study was small, and we were unable to conduct all possible transfer experiments. Nevertheless, survival of even one population of lice on a single recipient constituted sufficient evidence to falsify the hypotheses tested in this study. Similarly, a successful transfer of lice from one species of host (species a) to another (species b) showed that lice could live on a new host of a different species; thus, the reciprocal transfer (from species b to species a) was largely redundant. All controls were successful (i.e., lice survived and reproduced when transferred from one individual of their natural host to another), which indicated that unsuccessful transfers unlikely resulted from residual insecticide, injury to the lice, or other flaws in our technique.

RESULTS AND DISCUSSION

Lice transferred from *T. b. opulentus* to *T. b. connectens* increased steadily in number throughout the duration of the experiment (Table 1). The reciprocal transfer (from *T. b. connectens* to *T. b. opulentus*) was not tested in our study because lice from *T. b. connectens* are known to survive and reproduce naturally on *T. b. opulentus*

at a zone of contact between these two taxa of gophers in central New Mexico (Demastes, 1990). *T. b. opulentus* and *T. b. connectens* represent two of the most divergent genetic subgroups within *T. bottae* (Patton and Smith, 1990). Although lice from these gophers belong to different species (*Geomydoecus centralis* and *G. aurei*, respectively) and are highly divergent genetically (Demastes, 1990), these lice appear to live equally well on both taxa of hosts. This suggests that differentiation of the host at the subspecific level presents little or no barrier to colonization of new taxa of hosts by lice.

In the transfers between the hosts *T. bottae* and *T. talpoides* (involving the lice *G. centralis* and *G. thomomys*, respectively), three of four tests were successful (Table 1). In the single unsuccessful transfer (involving lice from *T. b. opulentus* transferred to *T. talpoides*) all lice died within the first 30 days of the experiment. These results demonstrate that lice are able to survive and reproduce on hosts that differ at the specific level from their natural host. Considering that these hosts represent two of the most divergent species of *Thomomys* (Patton and Smith, 1981), these results may be broadly applicable to gophers, in general. However, the one unsuccessful transfer suggests a low level of natural resistance to specific-level transfers by chewing lice. Unfortunately, we were unable to conduct experiments involving lice from *T. talpoides* and *T. bottae connectens*, which may have provided additional insight into the level of natural resistance against specific-level transfers.

Only one of the 14 generic-level transfers was successful (Table 1). This involved the louse *G. expansus* (hosted by *C. castanops*), which survived and reproduced on the host *T. b. opulentus* in one of two experimental replicates. All attempts to transfer lice from donors of the genus *Thomomys* to recipients of *C. castanops* ($n = 12$) failed. These results suggest that lice may face considerable natural resistance to transfers at the generic level.

The ability of lice to survive on new hosts

appears to diminish with increasing phylogenetic distance from the natural host. Although our samples are small, we had 100% success of transfers at the subspecific level, 75% success at the specific level, but only 7% success at the generic level (Table 1). Because previous studies have documented phylogenetic congruence between gophers and lice (e.g., Hafner et al., 1994), it is natural to assume that distantly related gophers will host distantly related lice. However, examination of relationships among the taxa of gophers and lice used in this study reveals phylogenetic discordance between the trees for hosts and parasites (Fig. 1). This phylogenetic information may help explain why *G. expansus* (hosted naturally by *Cratogeomys*) survived in one of two experimental transfers to *T. b. opulentus* (Table 1). *G. expansus* may survive on *T. bottae* simply because its ancestors were hosted by *T. bottae* (Fig. 1), and it has retained the ability to live on this ancestral host. Future research examining the specificity of hosts by chewing lice should be careful to interpret experimental results in light of the phylogenetic relationships of the taxa studied.

In our experiments, all taxa of lice examined survived and reproduced on *T. bottae*, *T. talpoides*, or both (Table 1). In contrast, no taxon of louse experimentally transferred to *C. castanops* survived, which suggests that *Thomomys* may provide a generalized habitat that is sufficient to support many species of lice, whereas *Cratogeomys* offers a more restricted habitat that may be suitable only for its natural louse, *G. expansus*. *Thomomys* is the only genus of geomyids known to host lice of two genera (*Geomydoecus* and *Thomomydoecus*) on a single individual host (Hellenthal and Price, 1991, 1994).

The ability of lice to survive and reproduce on inappropriate hosts provides insight into the mechanism of cospeciation in this assemblage. Our study suggests that cospeciation in this system is the combined result of at least three factors. First, the

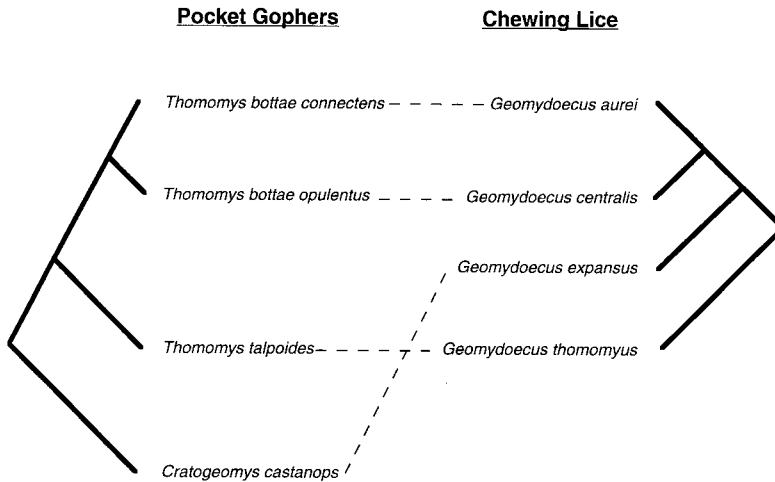


FIG. 1.—The phylogeny of pocket gophers (left) is corroborated by both morphological and molecular data (Hafner, 1982; Honeycutt and Williams, 1982; Patton and Smith, 1981, 1990). The phylogeny of chewing lice (right) is based on morphological evidence (Page et al., 1995), and the structure of the tree is consistent with allozymic data (Demastes, 1990). Dashed lines connect hosts with their natural parasites.

largely allopatric distribution of taxa of hosts (Hall, 1981) means the opportunity for transfer of lice is rare (Demastes and Hafner, 1993). Second, the poor dispersal ability of these wingless parasites means that lice may be slow to take advantage of those rare opportunities when they do occur. Finally, factors that restrict dispersal of lice are reinforced by some level of specificity, wherein lice find it difficult to survive and reproduce on hosts that are distantly related to their natural host. The cause of this specificity is unknown, but it could be physiological, ecological, behavioral, or a combination of these factors. Regardless, the biological properties of this system (including distribution of the hosts, limited dispersal ability of the lice, and some degree of specificity by the lice) means that lineages of chewing lice essentially are stranded on lineages of pocket gophers. Over evolutionary time, bifurcations in the host lineage would necessarily result in bifurcations of the parasite lineage, leading ultimately to the pattern of cospeciation that has been observed in this assemblage (e.g., Hafner and Nadler, 1990; Hafner et al., 1994; Page, 1990).

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