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Comparative body size relationships in pocket gophers and their chewing lice

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In this paper, we use the method of independent contrasts to study body size relationships between pocket gophers and their chewing lice, a host-parasite system in which both host and parasite phylogenies are well studied. The evolution of body size of chewing lice appears to be dependent only on the body size of their hosts, which confirms the 1991 findings of Harvey and Keymer. We show that there is a positive relationship between body size and hair-shaft diameter in pocket gophers, and that there is also a positive relationship between body size and head-groove width in chewing lice. Finally, we show a positive relationship between gopher hair-shaft diameter and louse head-groove width. We postulate that changes in body size of chewing lice are driven by a mechanical relationship between the parasite's head-groove dimension and the diameter of the hairs of its host. Louse species living on larger host species may be larger simply because their hosts have thicker hairs, which requires that the lice have a wider head groove. Our study of gopher hair-shaft diameter and louse head-groove dimensions suggest that there is a 'lock-and-key' relationship between these two anatomical features.

ADDITIONAL KEY WORDS:—comparative analysis – body size – independent contrasts.

CONTENTS

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INTRODUCTION

Host-parasite systems provide useful models to test evolutionary hypotheses because it is possible to obtain historical information on the relationship between changes in environmental conditions (the host) and changes in traits of the target organism (the parasite). Changes in body size related to evolution towards parasitism follow diverse trends depending on the parasite group considered. For example, an increase in body size appears to have accompanied evolution towards parasitism in nematodes (Kirchner *et al.*, 1980; Morand & Sorci, 1998), whereas a decrease in body size has occurred in isopods (Poulin, 1995). Harvey & Keymer (1991) showed, for the first time, that the evolution of increased body size in a lineage of parasites is associated with the evolution of increased size of their hosts. They showed two examples, one involving pocket gophers (Rodentia: Geomyidae) and their lice (Phthiraptera: Trichodectidae), the other involving primates and their pinworms. In the case of parasitic nematodes, increased body size is associated with delayed maturity and increased fecundity (Harvey & Keymer, 1991; Skorping *et al.*, 1991; Morand, 1996; Sorci *et al.*, 1997). It is also possible that larger hosts provide more energy for use by parasites, thus resulting in larger parasites (Morand & Sorci, 1998).

In this paper we examine the relationship between body size in pocket gophers and their chewing lice, which is one of the few host-parasite systems in which both host and parasite phylogenies are well established (Hafner *et al.*, 1994; Hafner & Page, 1995). Because chewing lice of mammals grasp the hair of the host in a semi-circular head groove (Fig. 1), the head groove appears to be critically important to the louse's survival. We hypothesize that the observed correlation between louse body size and gopher body size (reported in this study and by Harvey & Keymer, 1991) may reflect a relationship between gopher hair-shaft diameter and louse head-groove dimensions, suggesting that there is a 'lock-and-key' relationship between these two anatomical features.

Because cross-species comparisons performed using species values as data points may be confounded by phylogenetic relationships among the species analysed (Felsenstein, 1985; Harvey & Pagel, 1991), the method of the independent contrasts is used to obtain independent data points and to control for the effect of phylogeny (Felsentein, 1989).

MATERIAL AND METHODS

Host and parasite phylogenies

Recently, Hafner *et al.* (1994) provided phylogenies of pocket gophers and their chewing lice based on nucleotide sequences of the mitochondrial cytochrome oxidase I gene (Fig. 2). The host phylogeny in Figure 2 is supported by independent phylogenetic studies based on morphology, allozymes, and immunological data

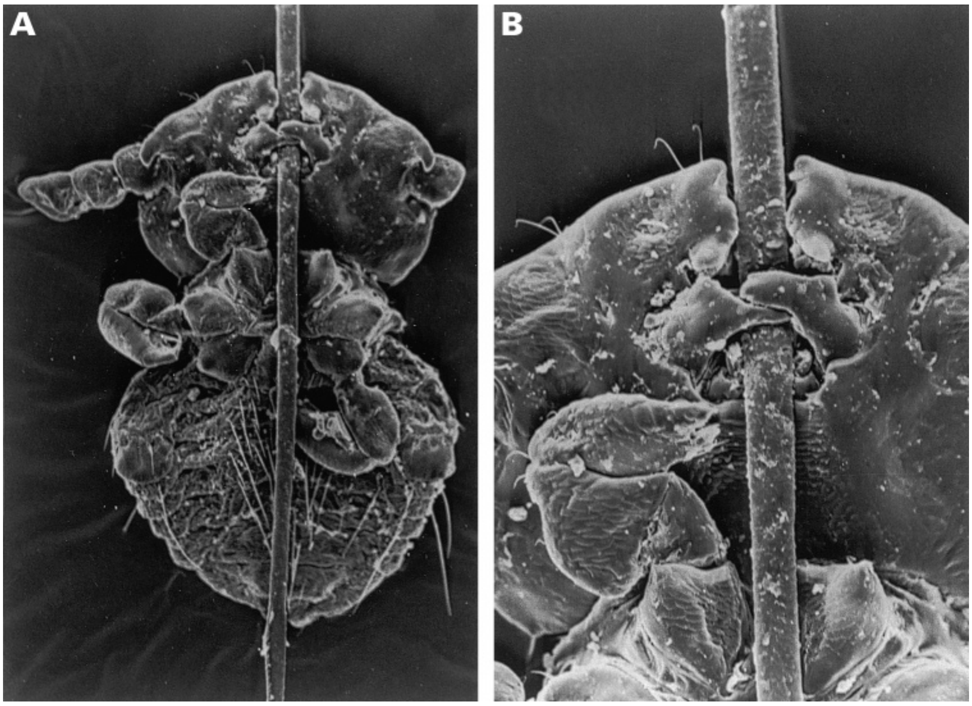

Figure 1. A, scanning-electron photomicrograph of a chewing louse (*Geomydoecus texanus*) grasping the hair of its host (*Geomys breviceps*). B, detail of the head groove of the chewing louse.

(Russell, 1968; Hafner, 1982; Honeycutt & Williams, 1982). The parasite phylogeny in Figure 2 also is supported by a cladistic analysis of morphological characters (Page *et al.*, 1995). The biology of pocket gophers and chewing lice suggests a high level of cospeciation in this host-parasite assemblage, and this expectation has been verified by statistical comparison of the host and parasite phylogenies (Hafner & Nadler, 1988; Hafner & Page, 1995).

Data collection

Data were obtained from direct measurement of preserved specimens from the collections of the Natural History Museum (London). The louse measurements (body length, temple width and groove width) were taken from slides. Temple width seems the most reliable index of louse body size because the head capsule of a louse is rigid, whereas total length includes the abdomen, which can be distorted when the louse is mounted on a slide. All gopher specimens used in the analysis were judged to be adult and, where possible, only females were used in the analysis to control for sex variation. Hairs were sampled from the mid-dorsal region of museum study skins (this region of the gopher is known to be densely populated by lice; Rust, 1974). Hair diameter ($\bar{X} \pm$ SE) was measured to the nearest 0.001 mm using a light microscope fitted with a micrometer scale. It should be noted that the 17 louse species sampled represent a small fraction of the 122 species of lice known from pocket gophers (Page *et al.*, 1995).

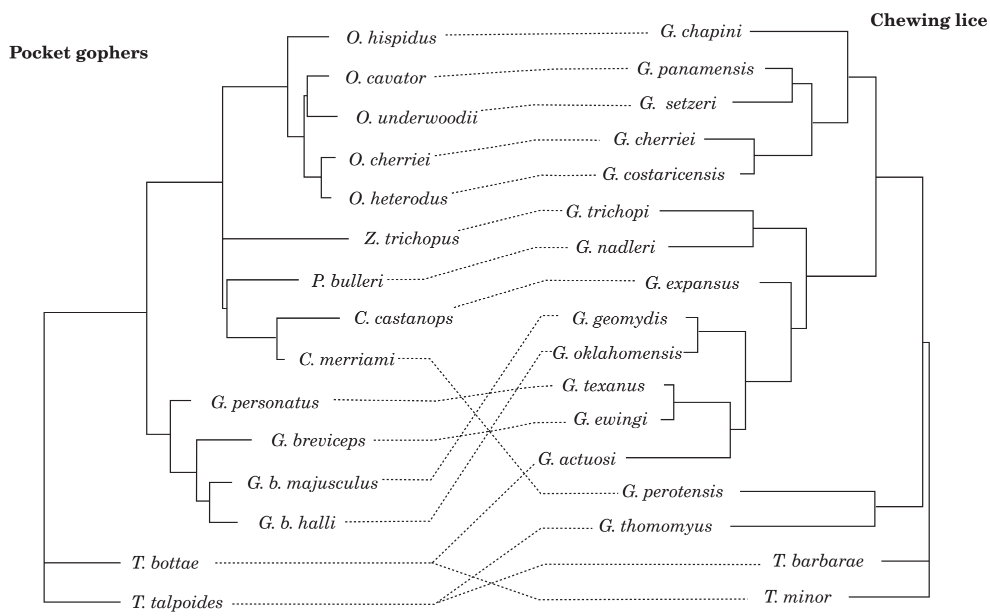

Figure 2. Phylogenies for pocket gophers and their lice based on nucleotide sequence data analysed by Hafner *et al.* (1994). Branch lengths are proportional to expected numbers of substitutions at the third codon position in the COI gene. Coexisting hosts and parasites are connected by dashed lines (redrawn from Hafner & Page, 1995). Congruent portions of phylogenies for pocket gophers and chewing lice were used in the analysis of independent contrasts (Fig. 4).

Statistical analysis

Closely related species of hosts (or parasites) may have similar body sizes simply because of their common phylogenetic origin, and not because of common selective forces. Thus, body size data for closely related species cannot be treated as statistically independent points (Harvey & Pagel, 1991).

To control for the effects of phylogeny, we used the method of independent contrasts (Felsenstein, 1985; Burt, 1991; Pagel, 1992). We used the CAIC program (Comparative Analysis using Independent Comparisons) to obtain independent values for gopher and louse body sizes (Purvis & Rambaut, 1995). However, because the independent contrasts method compares the nodes of a phylogeny, it was necessary that the host and parasite phylogenies being compared be topologically identical. Accordingly, we restricted the analysis to the congruent portions of the gopher and louse phylogenies (Fig. 2).

Pairs of sister branches that diverged long ago are likely to give greater contrasts than pairs of sister branches that diverged recently. It is thus necessary to standardize each contrast by dividing it by its standard deviation, where the standard deviation of a contrast is the square root of the sum of its branch lengths (Garland *et al.*, 1992). When investigating the relationship between louse body size (dependent variable) and gopher body size (independent variable), we used branch lengths of the parasite phylogeny. Correlation coefficients were computed through the origin to assess the relationship between changes in parasite body size and changes in host body size. To verify that contrasts were properly standardized, we performed a

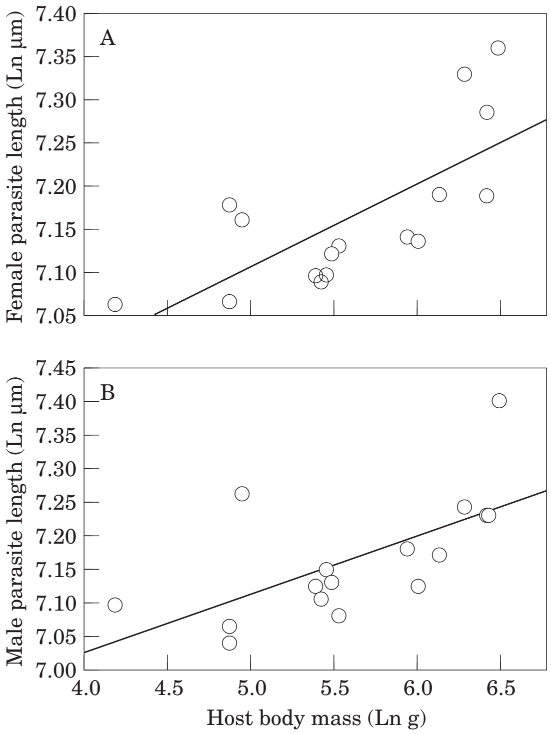

Figure 3. Major-axis regressions performed on cross-species data a) female parasite body size (μm in Ln) versus host body mass (g in Ln); b) male parasite body size (μm in Ln) versus host body mass (g in Ln).

regression of the absolute values of standardized contrasts versus their standard deviations (Garland *et al.*, 1992).

We used Model II regression analysis (major axis method) to estimate the functional relationship between gopher body size and louse body size. This regression model is appropriate for studies in which the variables compared lack statistical independence and where both variables are measured with error.

RESULTS

Cross-species correlations were conducted using structural regressions (major axis method) (Fig. 3), yielding the following regressions:

Male parasite body length (in In) = 0.11 host weight (in In) + 6.55
(confidence interval of the slope: 0.07–0.15)
Female parasite body length (in ln) = 0.09 host weight (in In) + 6.68
(confidence interval of the slope: 0.03–0.14)

TABLE 1. Body mass and diameter of guard hairs ($n = 20$ for each species) in representative specimens of pocket gophers of the family Geomyidae. All specimens are housed in the Museum of Natural Science, Louisiana State University (LSUMZ)

	Body mass (g)	Mean diameter of guard hair (μm)	SE	Specimen number and sex
Thomomys bulbivorus	334	35.01	1.84	LSUMZ 31310 F
Thomomys bottae	130	35.13	0.89	LSUMZ 29295 F
Thomomys talpoides	65	31.47	1.65	LSUMZ 34376 F
Cratogeomys castanops	240	28.30	1.61	LSUMZ 29324 F
Cratogeomys gymnurus	630	53.19	1.41	LSUMZ 34339 M
Cratogeomys merriami	605	38.55	2.62	LSUMZ 34343 M
Pappogeomys bulleri	225	37.57	1.97	LSUMZ 34338 M
Orthogeomys cavator	650	62.71	2.84	LSUMZ 29491 F
Orthogeomys heterodus	615	52.46	2.54	LSUMZ 29498 F
Orthogeomys underwoodi	250	51.48	2.76	LSUMZ 29488 F
Geomys bursarius	215	38.31	2.35	LSUMZ 29286 F
Geomys breviceps	140	37.09	2.25	LSUMZ 30717 F
Geomys personatus	232	43.81	1.18	LSUMZ 31461 F
Zygogeomys trichopus	380	40.38	3.39	LSUMZ 25099 F

The independent-contrasts methods could be used only when host and parasite phylogenies are congruent (Fig. 2). The following regressions (ordinary least squares through the origin) were found:

Male parasite body length (in In) = 0.19 host weight (in ln)
($R^2 = 0.765$, $P = 0.0009$; confidence interval of the slope: 0.014–0.24)
Female parasite body length (in ln) = 0.15 host weight (in ln)
($R^2 = 0.808$, $P = 0.0004$; confidence interval of the slope: 0.012–0.83)

No significant differences were found between slopes given by major axis regressions on cross-species data and ordinary least squares regressions on independent contrasts.

Pocket gopher body mass and hair diameter data are presented in Table 1. The analysis of gopher hair diameter revealed a significant positive relationship between gopher body mass and diameter of their guard hairs ($P = 0.023$, Fig. 4). Least-square regressions (through the origin) performed on independent contrasts shows significant relationship between gopher body size and diameter of guard hairs ($P < 0.002$). This relationship between gopher body size and hair diameter also is observed within individual gopher species and among age groups within a single species (Reed and Hafner, unpublished data). A positive relationship was found between width of the louse temple region and width of the head groove ($P = 0.0001$, Fig. 5; least-square regressions, through the origin, performed on independent contrasts shows significant relationship between louse body size and width of the head groove, $P < 0.02$). Finally, a significant positive relationship was found between louse head-groove width and gopher hair-diameter (Fig. 6).

Cross-species correlation was conducted, yielding the following regression:

Groove width (μm) = 1.2 hair diameter (μm) + 12.8 ($R^2 = 0.678$; $P = 0.0069$)

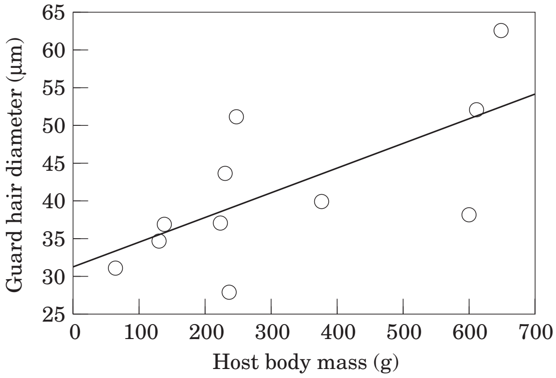

Figure 4. Relationship between body size in pocket gophers (body mass in g) and maximum diameter of their guard hairs (in μm). The cross-species relationship is highly significant ($P=0.0007$). A similar relationship is evident when wool hair ('underfur') is analysed separately ($P=0.0082$). Pocket gopher specimens included in the analysis are listed in Table 1.

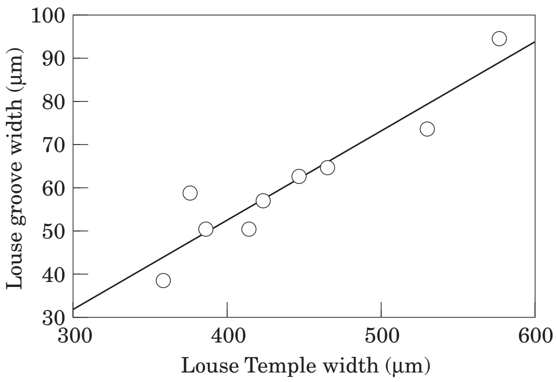

Figure 5. Relationship between body size in lice (width of the temple region of the head) and width of the head groove. The cross-species relationship is highly significant ($P<0.0001$). Included in the analysis are males and females representing 42 species of lice of the genus *Geomydoecus*.

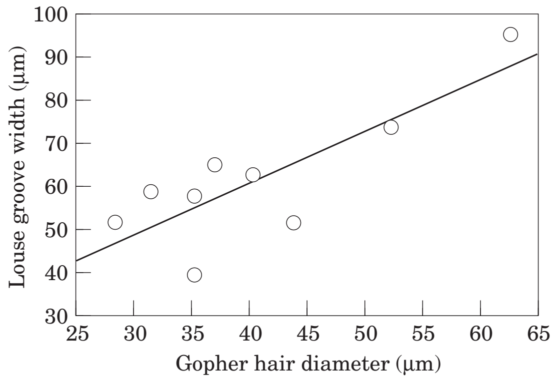

Figure 6. Relationship between louse groove width and gopher hair diameter. Cross-species relationship is significant ($P=0.006$).

TABLE 2. Results of stepwise linear regressions performed on independent contrasts for selecting an optimal subset of explanatory variables for louse head-groove width.

		slope	F	R^2	P	Degree of freedom
Variables in the model	Hair diameter	0.734	4.412			
	Louse body length (temple width)	60.78	5.118			
			8.135	0.701	0.0196	8
Variable removed from the model	Host body mass	–	–	–	0.2100	

The following regression (ordinary least squares through the origin) on independent contrasts was found:

$$\text{Groove width } (\mu\text{m}) = 1.6 \text{ hair diameter } (\mu\text{m}) \ (R^2 = 0.501;\ P = 0.033)$$

Finally, a stepwise linear regression on independent contrasts was conducted to explain the variation in louse groove width, with hair diameter, louse body size and gopher weight as independent variables. A significant relationship was found between louse groove width and both louse body size and gopher hair diameter ($R^2 = 0.701$; $P = 0.020$) (Table 2). Gopher weight was eliminated from the model ($P = 0.210$).

DISCUSSION

Our analysis confirms the findings of Harvey & Keymer (1991) and shows that larger species of gophers also support larger individual lice. This significant, positive association between gopher body size and louse body size is evident whether analysed using species values or independent contrasts.

It is not known whether body size in chewing lice is determined primarily by genetic or environmental factors. Plasticity in parasite growth and size at maturity may be influenced by environmental quality and anti-parasitic behaviour of the hosts. Size of the host, which is a component of the parasite's environmental quality, can vary with host age, social status, and health. Thus, these factors may affect the eventual size of the adult parasite. Hosts also may find it easier to remove larger parasites from their fur, which may place an upper limit on parasite body size.

Little is known about the relationships among size, age at maturity, and size-related fecundity in lice. If, as in other arthropods, louse body size is positively correlated with fecundity, and age at maturity is positively correlated with adult body size, then a gain in fecundity can be associated with delayed maturity (as in helminth parasites, see Morand & Sorci, 1998; Trouvé *et al.*, 1998; Trouvé & Morand, 1998). Nevertheless, more research is needed to explore both the evolution of life-history traits and the heritability of body size in chewing lice.

Although environmental factors, such as host longevity and resource availability, may influence louse body size in a variety of ways (Harvey & Keymer, 1991), it appears that there is also a strong genetic component to body size in chewing lice.

For example, the head region of juvenile lice is already adult size as early as the first-instar stage (R.D. Price, pers. comm.). Also, large species of lice are large regardless of whether they live on juvenile or adult hosts of the same species. This canalization of body size within louse species, coupled with the early attainment of adult body size by juvenile lice, suggests that strong, stabilizing selection constrains body size in lice. We postulate that the optimal body size for a given species of louse may be determined by a simple relationship between the louse's body size and the diameter of the hairs of its host.

Chewing lice of mammals grasp the hair of the host in a semi-circular groove located at the apex of the louse's head (Fig. 1). The hair shaft passes through this groove as the louse moves up and down the hair while feeding and depositing eggs. The head groove also can be clamped tightly around the hair to prevent dislocation of the louse during grooming by the host. Thus, the head groove appears to be critically important to the louse's survival, and a louse with a head groove that is too small or too large to grasp the host's hair may be unable to feed efficiently and may be easily dislodged during grooming by the host. Our preliminary studies of gopher hair-shaft diameter and louse head-groove dimensions suggest that there is a 'lock-and-key' relationship between these two anatomical features. Although our sample sizes are small, our data suggest that the louse head groove is consistently 20–30% wider than the hair shaft of its natural host.

The postulated lock-and-key relationship between gopher hair-shaft diameter and louse head-groove width may explain the observed correlation between gopher body size and louse body size reported in this study and by Harvey & Keymer (1991). There is a strong, positive relationship between body size and hair-shaft diameter in pocket gophers (Fig. 4). There is also a strong, positive relationship between body size and head-groove width in chewing lice (Fig. 5). Thus, louse species that live on larger species of pocket gophers may be larger simply because their hosts have thicker hairs, which requires that the lice have a wider head groove. This is confirmed by the positive relationship between louse head-groove width and gopher hair diameter (Fig. 6), independently of gopher body size (Table 2).

It is possible that a similar lock-and-key relationship exists between the gonopods of lice (appendages used to clasp hairs while attaching eggs) and hair diameter of their hosts (Murray, 1957,1987). For example, Murray (1957) showed experimentally that lice would not lay eggs unless they could grasp the hair securely between their abdomen and gonopods. Thus, laboratory colonies of lice living exclusively on large-diameter hairs (or glass fibres used to mimic hairs) laid few or no eggs. According to Murray (1987), this relationship between hair diameter and gonopod size explains why the eggs of a small species of biting louse (*Damalinia*) are found only on the body hairs of its natural host, whereas those of a larger species of haematopinid louse are found also on the coarse hairs of the mane and tail. We have yet to examine the relationship between gonopod size and body size in gopher lice of the genus *Geomydoecus*, but we predict that gonopod size will be correlated with overall body size as was shown for head-groove size (Fig. 5).

The size relationship between gopher hair diameter and louse head-groove width (and, possibly, gonopod length) also may explain why certain species of lice appear unable to survive on certain species of hosts in laboratory transfer experiments. For example, experiments by Reed & Hafner (1997) show that lice transferred among host species of similar body size often are able to establish successful breeding colonies on foreign (non-native) hosts. Also, lice that naturally occur on a large species of host occasionally are able to survive on a smaller host species, but the reverse is not true. This suggests that the head grooves of lice from the smaller hosts may be too narrow (or the gonopod too short) to grasp the thick hairs of the larger host species. This possibility is currently being investigated. A similar study of body size relationships between bird lice and their hosts has shown that feather size is a crucial factor in determining the success of lice experimentally introduced onto new hosts (D. Clayton, pers. comm.).

Parasitic animals, whether endoparasites or ectoparasites, invariably will face size constraints dictated by some physical dimension of their habitat, whether it be overall size of the space occupied or the size and position of available attachment sites, such as the hairs of mammals. Usually, these constraints will set only an upper limit to the parasite's body size. However, in other cases, the physical dimension of the habitat may dictate both upper and lower boundaries to the parasite's body size. This appears to be the case for chewing lice on pocket gophers, in which case the lice must be sufficiently large to grasp the host's hair, but sufficiently small to grasp it firmly. Although louse body size is almost certainly influenced by a variety of other factors, including competition, predation, age at first reproduction, fecundity, host longevity, and resource availability, it is perhaps most parsimonious to conclude that the overarching determinant of a louse's body size is a simple physical constraint, namely, hair diameter of its host.

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