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GENETIC DIFFERENTIATION AMONG CHEWING LOUSE POPULATIONS (MALLOPHAGA: TRICHODECTIDAE) IN A POCKET GOPHER CONTACT ZONE (RODENTIA: GEOMYIDAE)

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Abstract.—Genetic variation among populations of chewing lice (*Geomydoecus actuosi*) was examined in relation to chromosomal and electrophoretic variation among populations of their hosts (*Thomomys bottae*) at a contact zone. Louse demes were characterized by low levels of genetic heterozygosity ($\bar{H} = 0.039$) that may result from founder effects during primary infestation of hosts, compounded by seasonal reductions in louse population size. Louse populations sampled from different hosts showed high levels of genetic structuring both within and among host localities. Microgeographic differentiation of louse populations is high (mean $F_{ST} = 0.092$) suggesting that properties of this host–parasite system promote differentiation of louse populations living on different individual hosts. Among-population differentiation in lice ($F_{ST} = 0.240$) was similar to that measured among host populations ($F_{ST} = 0.236$), suggesting a close association between gene flow in pocket gophers and gene flow in their lice.

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Mallophagan lice of the genera *Geomydoecus* and *Thomomydoecus* (Trichodectidae) are wingless ectoparasitic insects that live exclusively on pocket gophers of the rodent family Geomyidae (Marshall, 1981; Hellenthal and Price, 1984). Most previous studies of chewing lice from pocket gophers have focused on louse distribution and alpha-level taxonomy (Price and Hellenthal, 1980; Timm and Price, 1980; Hellenthal and Price, 1984), and the genetic structure of louse populations has been investigated only recently (Nadler and Hafner, 1989).

A biochemical-systematic study of pocket gophers and their chewing lice (Hafner and Nadler, 1988, in press) revealed that the evolutionary histories of these rodents and their parasites appear to be linked via cospeciation. That is, the phylogenies of the two groups are remarkably similar, and in most cases investigated by Hafner and Nadler (1988), speciation events in the chewing louse assemblage appear to have been roughly contemporaneous with speciation events in the host assemblage. Thus, intrinsic or extrinsic barriers that restricted or prevented gene flow between pocket gopher populations also appear to have constrained or stopped gene flow between their louse populations. This evolutionary association between chewing lice and pocket gophers was demonstrated on a finer scale by Patton et al. (1984), who showed that the distribution of two host-specific louse species across a pocket gopher contact zone reflected closely the degree of gene flow between the host populations.

It is not surprising that pocket gophers and their chewing lice show a history of cospeciation, especially if one considers the natural histories of the organisms involved. The entire life cycle of chewing lice occurs on the host; lice, having limited intrinsic

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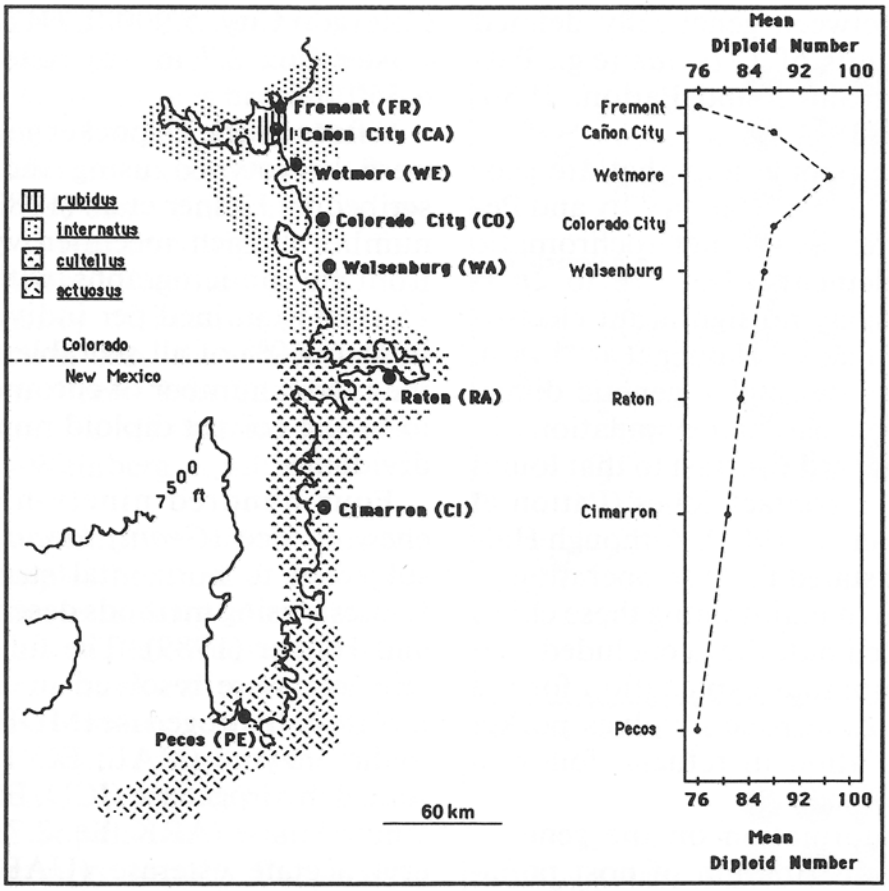

FIG. 1. Distribution of *T. bottae* subspecies across the Sangre de Cristo contact zone. Mean pocket gopher diploid number is indicated for each locality (data from this study and Hafner et al., 1983). Locality abbreviations are in parentheses.

vagility, depend on interhost contact for dispersal (Timm, 1983). Thus, the behavior and population structure of pocket gophers should be major determinants of the genetic structure of their louse populations. It follows that populations of lice should show high levels of genetic substructuring because of the asocial behavior of their hosts (Hall, 1981) and the patchy distribution of host populations (Patton and Feder, 1981). Indeed, populations of chewing lice on different individuals of a host species at a single locality have been shown to have island-like populations structuring (Nadler and Hafner, 1989).

In this study, we explore further the evolutionary linkage between chewing lice and their hosts by analyzing the population genetics of chewing lice (*Geomydoecus actuosi*) collected from pocket gophers (*Thomomys bottae*) that inhabit the eastern front of the Sangre de Cristo Mountains in northern New Mexico and southern Colorado. We interpret our genetic data for louse populations in view of previous knowledge of their host populations based on studies of electrophoretic, chromosomal, and morphological variation (Hafner et al., 1983).

Genetic Structure of Host Populations

Populations of pocket gophers (*Thomomys bottae*) in northern New Mexico and southern Colorado comprise four subspecies described on the basis of external and cranial morphology: *T. b. actuosus, T. b. cultellus, T. b. rubidus,* and *T. b. internatus* (Fig. 1). In this region, *T. bottae* has a narrow, peninsular distribution along the eastern slopes of the Sangre de Cristo Mountains; the major area of *T. bottae* distribution lies to the south and southwest. Hafner et al. (1983) showed that populations of pocket gophers along a transect between Cañon City, Colorado and Pecos, New Mexico show three concordant panzonal clines: character gradients in mean diploid number, pelage brightness, and mean morphometric coefficient of variation were found across the zone. These clines define a zone that is much wider (approximately 200 km) than other

contact zones between genetically defined geographic subunits of *T. bottae* (e.g., Patton et al., 1979; Smith and Patton, 1980; Smith et al., 1983).

Pocket gopher populations that are geographically distant (e.g., Cañon City and Pecos, Fig. 1) differ by 12 heterochromatic chromosomal elements ($2n = 76$ to $2n = 88$), yet they display no significant electromorphic differentiation (Hafner et al., 1983). This low level of detectable genetic differentiation between parental populations in this zone is in marked contrast to that found in other *T. bottae* contact zones (Patton et al., 1979; Smith et al., 1983). Although Hafner et al. (1983) stated that the operation of natural selection in maintaining these clines could not be ruled out, they concluded that the most parsimonious explanation for the establishment of the zone involves pocket gopher differentiation in refugia, followed by secondary contact.

Given this information on the genetics and geographic distribution of host populations in the Sangre de Cristo contact zone (Hafner et al., 1983), and given that pocket gophers and their chewing lice are known to show parallel patterns of speciation (Hafner and Nadler, 1988), we addressed the question of whether pocket gophers and chewing lice also exhibit parallel patterns of genetic differentiation when compared at the level of the population.

Materials and Methods

Twenty-eight specimens of *Thomomys bottae* were collected from eight localities spanning the length of the Sangre de Cristo contact zone (Fig. 1). Samples of lice were brushed from the pelage of individual pocket gophers, transferred to cryotubes, frozen in liquid nitrogen, and stored at −70°C. Pocket gophers skin-plus-skeleton voucher specimens were deposited in the Moore Laboratory of Zoology, Occidental College, Los Angeles, and the Museum of Natural Science, Louisiana State University, Baton Rouge. Voucher specimens of lice were deposited in the Entomology Collection of the University of Minnesota, St. Paul. Collecting localities were listed in Hafner et al. (1983), with the following additions: Colorado: (*Fremont* locality) Fremont Co., 8.0 mi (by road); N Cañon City, 6,100 ft; (*Colorado City* locality) Pueblo Co., 1.0 mi, SW Colorado City, 5,900 ft; (*Wetmore* locality) Custer Co., 2.7 mi (by road), S Wetmore, 6,550 ft.

Fifteen of the 28 pocket gophers collected were karyotyped using the methods described by Hafner et al. (1983). The diploid number of each specimen was determined from photomicrographs, with an average of 15 cells examined per individual. Approximately 60% of all scorable cells possessed the modal number of chromosomes judged to be the correct diploid number for an individual.

Four hundred ninety-nine individual chewing lice (*Geomydoecus actuosi*) were subjected to horizontal starch-gel electrophoresis using methods described by Nadler and Hafner (1989). The following 14 protein loci were resolved in individual lice: malate dehydrogenase (MDH, EC 1.1.1.37), malic enzyme (MAE, EC 1.1.1.40), isocitrate dehydrogenase (ICD, EC 1.1.1.42), arginine kinase (ARK, EC 2.7.3.3), umbelliferyl acetate esterase (UAE, EC 3.1.1.1), α-naphthyl acetate esterase (EST, EC 3.1.1.1), peptidases A and C (PEPA, PEPC, EC 3.4.11), phosphoglucose isomerase (PGI, EC 5.3.1.9), fumarate hydratase (FUM, EC 4.2.1.2), superoxide dismutase (SOD-1, SOD-2, EC 1.15.1.1), adenosine deaminase (ADA, EC 3.5.4.4), and xanthine dehydrogenase (XDH, EC 1.1.1.204). Methods of enzyme staining and allele designation were as in Nadler and Hafner (1989).

The BIOSYS-1 computer program (Swofford and Selander, 1981) was used to analyze louse electromorphic data. Chi-square goodness-of-fit and exact-probability tests were performed to determine if samples of lice conformed to Hardy–Weinberg equilibrium expectations at polymorphic loci. Genetic differentiation among samples of lice was analyzed using F statistics (Nei, 1977). Rogers' (1972) coefficient of genetic similarity was calculated between each pair of louse populations. Correlation tests were performed using Pearson's rank correlation coefficient.

Results

Genetic Variation in the Parasites

Intrapopulation Variation.—Levels of direct-count heterozygosity in louse populations taken from single hosts ranged from

zero to 0.068 (Table 1). Chi-square significance tests revealed six cases in which protein loci in *G. actuosi* samples brushed from individual hosts deviated from Hardy–Weinberg equilibrium expectations ($P < 0.05$). Four of these cases (indicated by asterisks in Table 1) remained significant following exact-probability tests, and all showed a deficiency of heterozygotes (inbreeding coefficient less than zero). One louse population, Pecos-4 in Table 1, had two loci (EST and FUM) that did not conform to Hardy–Weinberg equilibrium expectations.

Genetic Differentiation within Localities.—Louse samples brushed from different hosts at a single locality often showed marked differences in allele frequencies (Table 1; Fig. 2), and intralocality variance in allele frequencies, summarized by mean F_{ST} values (Table 2), ranged from 0.039 to 0.162 (unweighted mean $F_{ST} = 0.092$). For example, the louse populations brushed from hosts at the Wetmore locality (hosts were trapped no more than 200 m apart) showed substantial differences in allele frequencies at the esterase locus, and these differences were not significantly correlated with distance between capture sites of the hosts. High positive mean F_{IT} values at several localities indicated a deficiency of heterozygotes when data for louse populations were pooled ("Wahlund effect"; Wahlund, 1928).

Differentiation between Localities.—The esterase locus was polymorphic at all localities, but not in all louse populations at each locality (Fig. 2). Phosphoglucose isomerase was polymorphic at five of nine localities, and the PGI "c" allele was found exclusively in populations of lice from the Cañon City and Wetmore localities (Fig. 2).

Analysis of standardized variance in allele frequencies (F_{ST} values) revealed substantial macrogeographic variation among louse populations across the zone. Mean F statistics (Nei, 1977) for all variable loci were $\bar{F}_{IS} = 0.069$, $\bar{F}_{IT} = 0.293$, and $\bar{F}_{ST} = 0.240$. Rogers' genetic similarity values calculated between louse populations from the zone ranged from 0.898 (between Cimarron population 1 and Cañon City population 2) to 1.00 (several cases). Most of this genetic differentiation resulted from the presence of rare and unique alleles or allele frequency differences among the louse populations.

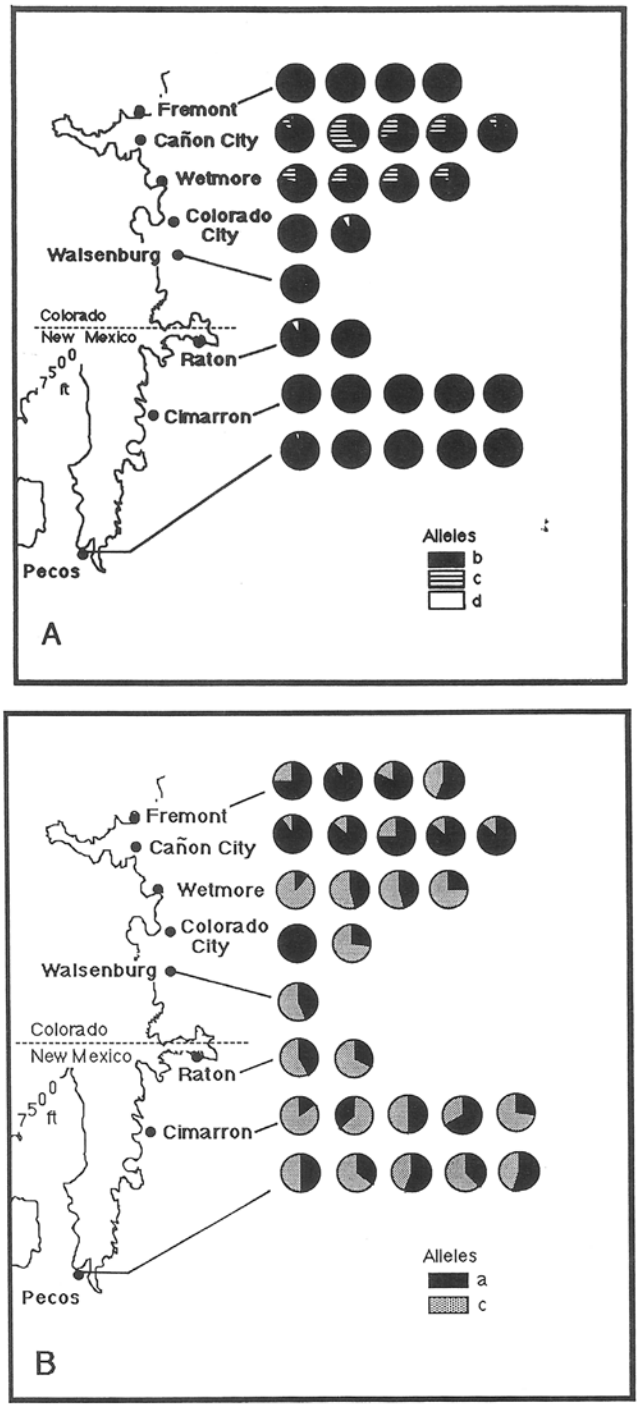

FIG. 2. Geographic variation of *Geomydoecus actuosi* allele frequencies in two polymorphic loci: (A) phosphoglucose isomerase; (B) general esterase. Each pie diagram represents a louse population from an individual host at the locality indicated.

Chromosomal Variation in the Hosts

Diploid numbers of the pocket gophers karyotyped in this study ranged from $2n = 76$ to $2n = 100$. Geographic variation in diploid number (Fig. 1) generally followed the clinal trend reported by Hafner et al. (1983), except that this study revealed diploid numbers exceeding $2n = 88$ and showed a reversal in the cline at the northern end

TABLE 1. Allele frequencies and genetic variability at five polymorphic loci in 28 populations of *G. actuosi* from individual hosts. A = mean number of alleles per locus; $\bar{H}$ = mean proportion of 14 loci heterozygous per individual; $\bar{H}_{exp}$ = expected mean heterozygosity; P = proportion of 14 loci polymorphic per population (0.95 criterion). Numbers in parentheses are louse sample sizes. Asterisks indicate deviation from Hardy–Weinberg equilibrium (exact probability test, $P < 0.05$).

	Fremont locality				Cañon City locality					Wetmore locality			
	Host 1 (6)	Host 2 (7)	Host 3 (11)	Host 4 (13)	Host 1 (48)	Host 2 (27)	Host 3 (26)	Host 4 (26)	Host 5 (32)	Host 1 (10)	Host 2 (11)	Host 3 (17)	Host 4 (11)
Locus/allele													
EST a	0.75	0.92	0.82	0.56	0.90	0.86	0.75	0.86	0.86	0.11	0.46	0.45	0.25
c	0.25	0.08	0.18	0.44	0.10	0.14	0.25	0.14	0.14	0.89	0.54	0.55	0.75
MAE a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91
c													0.09*
PGI b	1.00	1.00	1.00	1.00	0.88	0.39	0.69	0.73	0.89	0.78	0.75	0.75	0.80
c					0.11	0.61	0.31	0.27	0.11	0.22	0.25	0.25	0.20
d					0.01								
ICD c	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
d													
FUM a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
b													
c													
A	1.07	1.07	1.07	1.07	1.21	1.14	1.14	1.14	1.14	1.14	1.14	1.14	1.21
$\bar{H}$	0.036	0.012	0.026	0.048	0.028	0.049	0.063	0.047	0.032	0.032	0.060	0.045	0.046
$\bar{H}_{exp}$	0.029	0.012	0.022	0.037	0.029	0.052	0.058	0.046	0.032	0.041	0.065	0.065	0.066
P	7.14	7.14	7.14	7.14	14.29	14.29	14.29	14.29	14.29	14.29	14.29	14.29	21.43

TABLE 1. Extended.

	Colorado City locality		Walsenburg locality	Raton locality		Cimarron locality					Pecos locality				
	Host 1 (10)	Host 2 (19)	Host 1 (9)	Host 1 (32)	Host 2 (17)	Host 1 (10)	Host 2 (12)	Host 3 (9)	Host 4 (10)	Host 5 (16)	Host 1 (21)	Host 2 (18)	Host 3 (17)	Host 4 (26)	Host 5 (28)
Locus/allele															
EST a	1.00	0.27	0.44	0.42	0.32	0.15	0.64	0.50	0.67	0.27	0.50	0.35	0.56	0.38	0.55
c		0.73	0.56	0.58	0.68	0.85	0.36	0.50	0.33	0.73	0.50	0.65	0.44	0.62*	0.45
MAE a	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
c		0.05*													
PGI b	1.00	0.96	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00
c															
d		0.04		0.04							0.02				
ICD c	1.00	1.00	1.00	0.87	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
d				0.13											
FUM a	1.00	1.00	1.00	0.91	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.84	1.00
b				0.09		0.10								0.12*	
c														0.04	
A	1.00	1.21	1.07	1.29	1.07	1.14	1.07	1.07	1.07	1.07	1.14	1.07	1.07	1.21	1.07
$\bar{H}$	0.00	0.044	0.048	0.068	0.038	0.021	0.039	0.024	0.032	0.019	0.034	0.042	0.027	0.018	0.038
$\bar{H}_{exp}$	0.00	0.042	0.037	0.069	0.032	0.033	0.035	0.038	0.034	0.029	0.040	0.034	0.036	0.054	0.036
P	0.00	14.29	7.14	21.43	7.14	14.29	7.14	7.14	7.14	7.14	7.14	7.14	7.14	14.29	7.14

TABLE 2. Mean intralocality F statistics for 23 louse populations. Numbers in parentheses indicate number of louse populations surveyed per locality.

Locality	$\bar{F}_{IS}$	$\bar{F}_{IT}$	$\bar{F}_{ST}$
Fremont (4)	−0.286	−0.163	0.096
Cañon City (5)	−0.027	0.083	0.107
Wetmore (4)	0.182	0.227	0.055
Cimarron (5)	0.154	0.291	0.162
Pecos (5)	0.187	0.219	0.039

of the transect. Two pocket gophers with diploid numbers of $2n = 94$ and $2n = 100$ were collected at the Wetmore locality (Fig. 1). In addition, a single individual karyotyped from the Fremont locality (northern extreme of the zone) possessed 76 chromosomes; this represents an abrupt and unexpected reduction in diploid number in the north (Fig. 1). The pattern of diploid number variation over geography, as it is now understood, shows a peak of $2n = 100$ in the vicinity of the Wetmore locality with a decreasing gradient to $2n = 76$ to the south, and an abrupt reduction to $2n = 76$ to the north.

DISCUSSION

These genetic data support previous evidence (Nadler and Hafner, 1989) indicating that chewing lice on pocket gophers show high levels of population substructuring. The patchy distribution of pocket gopher populations (Patton and Feder, 1981) and the asocial nature of individuals within a population apparently restrict opportunities for louse transfer between hosts. Populations of *Thomomys bottae* in the Sangre de Cristo region (which is on the northeastern periphery of the species' distribution) are generally small and patchy in distribution (Hafner et al., 1983). Because chewing lice on pocket gophers require interhost contact for dispersal (Timm, 1983), it is not surprising that the distribution, population structure, and behavior of host populations in the Sangre de Cristo contact zone have profound effects on louse population structure.

Genetic differentiation among louse populations is also promoted by the low inherent vagility of the chewing lice; these insects are wingless and their entire life cycle occurs on the host. Variation in allele frequencies among louse populations from different hosts at the same locality (Table 1) suggests that stochastic processes, such as founder effects and genetic drift, contribute heavily to interpopulation differentiation (unless we postulate different selection regimes on hosts living only meters apart). The potential for founder effects in chewing lice may be unusually large because primary infection of individual pocket gophers is believed to occur by transmission of a relatively small number of lice from a female host to her offspring (Rust, 1974).

Although the frequency of alleles at the esterase locus varied among localities and among populations at each locality (Fig. 2), there was no significant correlation between esterase allele frequencies in louse populations and linear distance between trap sites at a locality or linear distance between localities. We recognize that distance between trap sites is only a crude estimate of the relative positioning of the home ranges of individual pocket gophers. Even so, the isolation-by-distance model may not be appropriate for within-locality analyses because the linear distance between pocket gopher burrow systems may not directly influence the dispersal of lice, unlike, for example, flying insects that colonize habitat islands. If louse transmission occurs mainly through intimate interindividual contact, such as female host to offspring, then we might predict special genetic relationships between louse populations on kindred hosts. If most louse transmission follows maternal lineages of the hosts, we expect that future studies will reveal parallel patterns between louse population markers and mitochondrial-DNA lineages of their hosts. Unfortunately, we lack information on intralocality genealogy of the pocket gophers, so we are currently unable to test this hypothesis.

Estimates of genetic heterozygosity in *G. actuosi* are at the lower range of values reported for other sexually reproducing insects (Graur, 1985). This low level of genetic diversity is further evidence that lice undergo periodic genetic bottlenecks. If such bottlenecks occur frequently, perhaps seasonally (Rust, 1974) or with each infection of a new host, there may be reduced opportunity for the accumulation of allelic variation. This

same phenomenon (frequent genetic bottlenecks) had been invoked to explain the low genetic heterozygosity reported for pocket gopher populations in the Sangre de Cristo region (Hafner et al., 1983) and in Mexico (Hafner et al., 1987).

Generally high, positive values for mean F_{IT} (Table 2) revealed a deficiency of heterozygous individuals when allelic data were pooled for louse populations from all hosts at a single locality. In contrast, polymorphic loci analyzed in samples of lice from individual pocket gophers rarely departed from Hardy–Weinberg equilibrium expectations. Such heterozygote deficiencies are expected when two heterogeneous subsamples (differentiated demes) are pooled and analyzed genetically (Wahlund, 1928). Thus, the genetic data for louse populations support previous evidence (Nadler and Hafner, 1989) that lice on each individual host represent a genetic deme.

Levels of microgeographic (within-locality) differentiation among louse populations varied by locality (Table 2), but the unweighted mean variance in allelic frequencies ($F_{ST} = 0.092$) is among the largest reported for insects over a small geographic scale, and exceeds that measured across the entire geographic range of many other insect species (McCauley and Eanes, 1987). This high level of microgeographic population substructuring is consistent with the island-like distribution of the hosts, compounded by the reduced dispersal abilities of the lice. As expected, microgeographic differentiation among louse demes is greater than that measured among populations of host-specific phytophagous insects possessing greater dispersal abilities. For example, populations of milkweed beetles inhabiting patches of host plants separated by a few kilometers have F_{ST} values ranging from 0.03 to 0.06 (McCauley and Eanes, 1987). Likewise, F_{ST} values measured among microgeographic populations of *Collops georgianus,* a bettle restricted to the island-like habitat of granitic rock outcrops, were also relatively low (mean $F_{ST} = 0.012$; King, 1987). Finally, microgeographic genetic differentiation among treehoppers (Homoptera) of the *Enchenopa binotata* species complex ranged from $F_{ST} = 0.013$ to 0.036, even though the dispersal rate of these host-specific treehoppers among individual trees was relatively low (Guttman et al., 1989).

Levels of F_{ST} for the 28 louse populations collected from throughout the study area were also high by typical insect standards (McCauley and Eanes, 1987). An average of 24% of the overall variance in allelic frequencies resulted from genetic differences among populations of lice from different individual hosts. This evidence confirms other indications of high levels of genetic differentiation among populations of *G. actuosi* living on different individuals of the host species (Nadler and Hafner, 1989). Moderate to high F_{ST} levels have been reported for spatially subdivided insect species (King, 1987; McCauley and Eanes, 1987; Liebherr, 1988; Guttman and Weigt, 1989), and this macrogeographic differentiation has been attributed to habitat patchiness. For treehoppers, *Enchenopa,* F_{ST} levels appear to be correlated with vagility (Guttman and Weigt, 1989); however, for carabid ground beetles, *Agonum* and *Platynus,* there appears to be no simple relationship between flight-wing development and genetic heterogeneity (Liebherr, 1988). It appears that dispersal ability and habitat patchiness interact to determine gene-flow levels in carabid beetles (Liebherr, 1988).

Although our estimates of genetic variation in louse populations are rather crude (based on only 14 loci), they are roughly similar to estimates of genetic variation measured in populations of their hosts (data for hosts from Hafner et al., 1983). For example, average (unweighted) polymorphism was low in both the parasites and their hosts (10.7% for 28 louse populations, and 8.6% for 10 pocket gopher populations), and average heterozygosity values were also low in both groups (3.9% in the chewing lice, and 1.6% in their hosts). We interpret these similarities as support for our contention that both pocket gopher and chewing louse populations in this region are subject to periodic population bottlenecks that depress levels of genetic variation. It is important to emphasize, however, that population bottlenecks in the hosts probably occur independently of those in the parasites. For example, a dramatic reduction in pocket gopher population density (even to as few as two breeding individuals) does not

require a concomitant reduction in louse density because each host may harbor hundreds of breeding lice. Similarly, the extreme, seasonal reductions observed in louse populations seem to cycle independently of pocket gopher population density (Rust, 1974; pers. observation). Finally, the chewing lice may pass through genetic bottlenecks at each initial infection of a host individual; if so, occurrence of this latter type of bottleneck should be universal in louse populations and, again, should be unrelated to host density.

If depressed levels of genetic variation in pocket gopher and chewing louse populations in the Sangre de Cristo region are the result of similar populational phenomena (bottlenecks) that occur independently in the hosts and parasites, we predict that future studies involving pocket gopher populations with higher levels of genetic variation will find no relationship between levels of genetic variation in the hosts and their parasites. Moreover, if chewing lice are always subject to population bottlenecks at initial infection of host individuals, we predict generally low levels of genetic variation in all chewing louse populations throughout their geographic range. Our evidence to date, although limited to only a small portion of the geographic range of *Geomydoecus,* is consistent with this prediction.

In contrast to our assertions concerning levels of within-population genetic variation in these hosts and parasites (which we contend are not causally linked), we predict that future research will reveal a direct, causal linkage between levels of among-population differentiation in pocket gophers and their chewing lice. For example, in the present study, levels of genetic differentiation, as estimated by F_{ST}, were remarkably similar in the hosts and parasites (0.236 in the pocket gophers and 0.240 in the chewing lice). Such similarities are expected in a host–parasite system in which gene flow among parasite populations is closely linked to, perhaps dependent on, gene flow among their hosts. Given the natural history of these parasites, it is difficult to imagine how louse gene flow could exceed that of their hosts. It is perhaps more reasonable to expect that gene flow between louse populations should lag behind gene flow between their hosts, because successful dispersal by a pocket gopher (i.e., genetic introgression into a new population) does not guarantee successful colonization (much less, introgression) by the pocket gopher's lice. Pocket gopher mating may take place without transfer of lice, and simple transfer of lice does not ensure successful genetic introgression into the established louse population on the new host. Future studies comparing interpopulational genetic differentiation in pocket gophers and their lice will determine whether a significant relationship exists between levels of gene flow in the two groups; evidence presented thus far (this study; Patton et al., 1984) is supportive of such a relationship. Importantly, a linkage between gene flow in pocket gophers and gene flow in chewing lice could, given time, generate the pattern of cospeciation already observed in this host–parasite assemblage (Hafner and Nadler, 1988).

Although the genetic evidence from louse populations sheds little new light on the history of this pocket gopher contact zone, the data are, nevertheless, consistent with the refugium hypothesis for the origin of the zone (Hafner et al., 1983). The PGI "c" allele in the north (Fig. 2) may have originated in an isolated louse population concomitant with the origin of the high diploid number in their hosts. However, when the hosts spread southward (passing the chromosomal mutation into new gopher populations), the novel PGI allele carried by the lice failed to transfer into southern louse populations (Fig. 1). Although this scenario is untestable, it is consistent with our expectation that gene flow between louse populations may, in certain instances, lag behind gene flow between their hosts.

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