LINKING HETEROZYGOSITY, DEMOGRAPHY, AND FITNESS OF TROPICAL POPULATIONS OF *LIOMYS PICTUS*

ELLA VÁZQUEZ-DOMINGUEZ, DANIEL PIÑERO, AND GERARDO CEBALLOS

Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, Ciudad Universitaria, México, Distrito Federal 04510, México

The relationship between heterozygosity and spatial and temporal changes in population density, and between heterozygosity and body weight, were studied in four populations of the spiny pocket mouse, *Liomys pictus*, from tropical dry forests in Chamela, Jalisco, Mexico. Individuals of *L. pictus* experience profound fluctuations in populations mainly due to the strong environmental seasonality of their habitat. Nineteen presumptive gene loci were assayed with starch-gel electophoresis to estimate heterozygosity, and mean body weight was analyzed as a fitness-correlated character. Observed average heterozygosity values were high (H = 0.188–0.198), whereas average fixation values (F = 0.350–0.429) were positive, indicating a significant deficiency of heterozygotes. Changes in numbers of individuals and heterozygous loci per individual were associated with different phases of fluctuations in density of *L. pictus*. During the increase phase, persistence of individuals was higher and average heterozygosity values declined, probably due to inbreeding. During the decline of the population when food and water were scarce, heterozygosity increased, and adults, which overall showed less deficiency of heterozygotes, were significantly more abundant. Average number of heterozygous loci and body weight also showed a positive and significant correlation. These results agree with the hypothesis that changes in genetic variability may be a consequence of demographic changes, and that, consequently, traits associated with fitness could show correlations with heterozygosity.

Key words: *Liomys pictus*, heteromyid rodents, heterozygosity, population density, allozymes, fitness

Genetic attributes of natural populations may diverge as a result of factors such as differential selection, demographic variation, or dispersal (Lacy, 1987; Scribner et al., 1991; Soulé, 1976). Repeated sampling of a population may provide insights into associations between measures of genetic variability and fluctuations in populations (Mathews and Porter, 1993; Smith et al., 1975; Wolda, 1987), dispersal and reproductive performance (Krebs and Myers, 1974; Nelson, 1993; Scribner et al., 1983), and other demographic variables, considering the associated environmental factors (Boonstra et al., 1998; Charlesworth and Giesel, 1972; Mitton, 1989, 1993; Nevo et al., 1984).

Behavioral, morphological, and physiological traits might be correlated with heterozygosity when these characters directly or indirectly affect an individual's probability of survival (Bush and Smouse, 1992; Johannesson and Tatarenkov, 1997; Mitton, 1989, 1993; Oostermeijer et al., 1995). Evidence for associations between heterozygosity and morphological and physiological traits in animals also has been found by comparing levels of heterozygosity among cohorts, between juveniles and adults, or between size classes within populations (Allendorf and Leary, 1986; Mitton, 1993; Rhodes et al., 1996). Particularly in studies with mammals, a positive and significant relationship has been found between heterozygosity and features such as dispersal (Krebs et al., 1973), exploratory behavior (Garten, 1977), body weight (Garten, 1976,

1977; Kaufman and Kaufman, 1987), and metabolic processes (Teska et al., 1990).

Accordingly, because populations of mammals often exhibit age-specific and temporal genetic changes (Flowerdew, 1987; Patton and Rogers, 1993; Scribner et al., 1997; Smith et al., 1975), concurrent changes in those traits related to size of populations may be associated with temporal changes in levels of heterozygosity (Gaines and Krebs, 1971; Scribner et al., 1991; Smith et al., 1975; Zimmerman, 1988). Most of these findings have been interpreted as supporting evidence of Charlesworth and Giesel's (1972) hypothesis that in a population with overlapping generations, changes in genetic variability may be responses to changes in population density.

Significant changes in allelic frequencies, genotypic proportions, and heterozygosity have been related to changes in size of populations in microtine rodents (Gaines and Krebs, 1971; Gaines et al., 1978), oldfield mice (*Peromyscus polionotus*—Smith et al., 1975), eastern cottontails (*Sylvilagus floridanus*—Scribner et al., 1983), white-tailed deer (*Odocoileus virginianus*—Chesser et al., 1982; Scribner et al., 1985), and mule deer (*O. hemionus*—Scribner et al., 1991). Those studies showed a positive and significant correlation between genetic variability and density; moreover, fitness-correlated characters were used to explain those associations, in which the more heterozygous individuals showed a significant advantage regarding survival, reproduction, body weight, and rates of growth (Gaines and Krebs, 1971; Gaines et al., 1978; Smith et al., 1975).

Local populations of the spiny pocket mouse, *Liomys pictus*, an endemic heteromyid of western and southern Mexico (Ceballos and Miranda, 1986; Williams et al., 1993), exhibit profound seasonal fluctuations in population density in the dry tropical deciduous and semideciduous forests of Chamela, Jalisco, Mexico (Ceballos 1989, 1991; Mendoza, 1997). Populations of this species, as those of other heteromyids, are limited largely by food; thus, fluctuations in density and persistence of individuals are directly associated with temporal variation in productivity (Ceballos, 1989; French, 1993; Mendoza, 1997). Population density typically increases during favorable periods of high food supply (quantity and variety) following the rainy season and then declines during the subsequent long (usually 8-months) dry season.

The populations of *L. pictus* in Chamela, Jalisco, provide an opportunity to review associations between demographic parameters and genetic variability in a mammalian species. Our objective was to evaluate, through a 14-month study of four populations of *L. pictus*, the hypothesis that changes of individual heterozygosity could result from fluctuations in population size. The concomitant hypothesis that traits associated with survival should show correlations with genetic variability also was tested by examining the relationship between mean body weight and heterozygosity.

Materials and Methods

Study site.—The study was conducted at the Chamela Biological Station (Universidad Nacional Autónoma de México), located on the Pacific coast of Mexico in the southern part of the state of Jalisco (19°29′N, 105°01′W). Dominant vegetation types in this area are tropical deciduous forest (hereafter referred to as dry forest) and semideciduous forest (hereafter referred to as arroyo forest—Ceballos, 1989; Rzedowski, 1978). The climate is characterized by a dry-wet seasonality, with an average monthly temperature of 24.9°C and an average precipitation of 748 mm/year, 80% of which usually is concentrated in a few months (July–October—Bullock, 1986; García-Oliva et al., 1991). The rest of the year is marked by a dry season when most plants shed their leaves.

Two 0.8-ha grids were located in the dry forest (DRY1, DRY2) and two in the arroyo forest (WET1, WET2), all of which were ca. 5 km apart. Sixty-four Sherman live traps, baited with a mixture of rolled oats, peanut butter, and va-

nilla extract, were set in each plot, 8-m apart in an 8 by 8-trap-grid arrangement. Traps were opened and checked during 3 consecutive nights coinciding with the new moon. That procedure was done at 2-month intervals for 14 months from November 1994 to January 1996. Upon first capture, mice were sexed, marked by toe-clipping, and blood samples were taken in the field by a superficial cut on the caudal vein; samples were stored in liquid nitrogen. Location on grid and body weight to the nearest 0.1 g of each individual were recorded for each capture.

Electrophoretic techniques.—Horizontal starch-gel electrophoresis was performed (methods, stains, and buffers from Pasteur et al., 1988; Selander et al., 1971; Teska et al., 1990). We assayed 26 proteins and obtained resolution for 12, encoding 19 presumptive loci. Buffer systems employed and proteins studied were: 1) tris maleate, pH 7.4, 100 mA, 15 h: glucose-6-phosphate dehydrogenase, 1.1.1.49 (G6PD1, G6PD2); glucose-6-phosphate isomerase, 5.3.1.9 (GPI); malic enzyme, 1.1.1.40 (ME); 2) histidine, pH 5.6, 55 mA, 5 h: lactate dehydrogenase, 1.1.1.27 (LDH1, LDH2); malate dehydrogenase, 1.1.1.35 (MDH); 6-phosphogluconate dehydrogenase, 1.1.1.44 (6PGD); 3) lithium-borate, Ph 7.6, 55 mA, 8 h: general protein, nonspecific (GP1, GP3); leucine aminopeptidase, 3.4.11.1 (LAP); mannose-6-phosphate isomerase, 5.3.1.8 (MPI1, MPI2); esterase, 3.1.1.1 (ES1, ES2); glycyl-L-leucine, 3.4.13.11 (PEPA1, PEPA2) and L-leucylglycyl glycine peptidases, 3.4.13.11 (PEPB); peroxidase, 1.11.1.7 (PER). Reference samples were run on each gel to ensure consistent scoring.

Genetic variability within populations was calculated and expressed as mean number of alleles per locus, percentage of polymorphic loci per population (using the 95% criterion—Nei, 1973, 1987), and average proportion of heterozygous loci per individual at each locality (H, direct count estimate—Hedrick, 1985), using the BIOSYS-1 program (Swofford and Selander, 1981). The average fixation index (F—Hedrick, 1985) also was calculated for each grid.

Statistical analyses.—Differences in number of heterozygous loci per individual among grids and between sexes were analyzed with a two-way analysis of variance (ANOVA—Tabachnick and Fidell, 1989; Zar, 1984). To further explore differences in genetic structure among individuals, mice were grouped in two weight classes: juveniles $\leq$ 35.0 g and adults $\geq$ 45.0 g. That was an indirect method to asses age in this species (Ceballos, 1989). Differences in number of heterozygous loci between juveniles and adults and among the four grids were evaluated with a two-way ANOVA (Tabachnick and Fidell, 1989).

To evaluate patterns of weight of individuals, an ANOVA was performed on initial body weight among grids, between males and females, and among individuals with different number of heterozygous loci (Zar, 1984). To ascertain if an association between heterozygosity and body weight existed, a Pearson correlation-coefficient test was applied to individual values of weight and number of heterozygous loci (Zar, 1984).

Densities of populations were calculated by the direct-enumeration method, which estimated the minimum number of individuals known to be alive. This method gives a reliable estimate of size of population if the probability of capture for an average individual is >50%, avoiding unrealistic assumptions implicit in capture-recapture methods (Ceballos, 1989; Gaines et al., 1978; Mendoza, 1997). Differences in average densities of populations between grids within forests were examined with a t-test (Zar, 1984). Temporal (2-month sampling intervals) and spatial (within and between dry and arroyo forests) changes in densities of populations were tested with an ANOVA.

To test if demographic and genetic variables were related, the relationship between changes in average number of heterozygous loci and fluctuations in density during the 14-month period was investigated. That was done by calculating correlation coefficients between those two variables.

Another feature directly related to population dynamics of *L. pictus* was persistence (Ceballos, 1989; Mendoza, 1997). We estimated persistence as the percentage of individuals from a single cohort that persist through time in the sampling site; excluded from that estimation were individuals captured only once or in the last month of trapping (Ceballos, 1989; Ostfeld et al., 1985). Although traps were checked every 2 months, if an individual was found in 2 consecutive trapping periods, it was assumed that it persisted in the field during the month we did not sample. Thus, to estimate a percentage of persistence for each grid, we divided number of

TABLE 1.—*Total number of male and female* Liomys pictus *trapped in two dry forest (DRY1, DRY2) and two arroyo forest grids (WET1, WET2) during 8 trapping periods in Chamela, Jalisco, Mexico. Average weight and average number of heterozygous loci are indicated for each sex (standard errors in parentheses).*

	Number of individuals		Average body weight (g)		Average number of heterozygous loci	
Grid	Female	Male	Female	Male	Female	Male
DRY1	26	18	39.0 (6.9)	47.9 (6.9)	3.5 (0.3)	3.4 (0.5)
DRY2	27	25	42.9 (6.8)	47.4 (10.0)	3.4 (0.4)	3.8 (0.5)
WET1	26	20	39.3 (6.8)	49.5 (11.7)	4.0 (0.3)	3.0 (0.4)
WET2	18	19	39.2 (6.1)	51.5 (8.2)	3.8 (0.4)	3.9 (0.4)

individuals that persisted 2–10 months (minimum and maximum possible persistence of an individual, respectively, because we sampled during 14 months) by the total number of individuals trapped in each grid. We examined percentage differences among grids and among trapping months with a Kruskal-Wallis test (Zar, 1984). Finally, we estimated correlation coefficients to evaluate the relationship between persistence (considering number of trapping periods that every individual persisted in each grid) and number of heterozygous loci for each individual.

RESULTS

A total of 179 individuals of *L. pictus* was trapped during the 8 trapping periods (44, 52, 46, and 37 individuals in the DRY1, DRY2, WET1, and WET2 grids, respectively; Table 1). A higher number of females were trapped in three of the four grids, and they consistently weighed less than males ($P < 0.001$; Table 1).

Heterozygosity.—Analyses of genetic structure showed few differences among grids and individuals. Of the 19 loci studied, only one (ME) was monomorphic across all four grids. MDH was monomorphic in grids DRY1 and WET1, whereas LDH2 was monomorphic in grid WET2 (Appendix 1). No statistical difference was found in observed heterozygosity among grids (Kruskal-Wallis test, $P > 0.05$—Wayne, 1990). Average fixation (F) values also were positive, indicating a deficiency of heterozygotes (Table 2).

Mice were heterozygous at ≤10 loci. Number of heterozygous loci did not differ statistically between sexes ($F = 0.337$, $d.f. = 1$; $P = 0.562$) or among grids ($F = 0.319$, $d.f. = 3$; $P = 0.811$). However, when mice were grouped in age classes, differences between juveniles and adults were significant ($F = 4.107$, $d.f. = 1$; $P = 0.045$). Adults showed consistently higher average number of heterozygous loci, irrespective

TABLE 2.—*Genetic variation in 19 loci for individual* Liomys pictus *from Chamela, Jalisco, Mexico (standard errors in parentheses); dry (DRY1, DRY2) and arroyo forest (WET1, WET2) grids.*

Sites	Mean number of individuals per locus	Mean number of alleles per locus	Percentage of polymorphic loci	Observed heterozygosity	Expected heterozygosity	Fixation index
DRY1	43.2 (0.3)	2.1 (0.1)	89.5	0.183 (0.032)	0.338 (0.038)	0.429 (0.074)
DRY2	51.5 (0.2)	2.1 (0.1)	94.7	0.192 (0.025)	0.328 (0.037)	0.389 (0.054)
Total	94.6 (0.4)	2.1 (0.1)	94.7	0.188 (0.026)	0.339 (0.036)	0.429 (0.051)
WET1	45.7 (0.1)	2.1 (0.1)	89.5	0.191 (0.029)	0.314 (0.039)	0.370 (0.056)
WET2	36.4 (0.1)	2.1 (0.1)	89.5	0.207 (0.031)	0.332 (0.041)	0.329 (0.068)
Total	82.1 (0.3)	2.1 (0.1)	94.7	0.198 (0.029)	0.327 (0.039)	0.350 (0.043)

TABLE 3.—*Effect of sex, number of heterozygous loci, and forest type on initial body weight of* Liomys pictus *from Chamela, Jalisco, Mexico.*

Source of variation	*d.f.*	Sum of squares	Mean square	*F*	*P*
Type of forest	3	156.7	52.2	0.92	0.434
Sex	2	3,395.3	3,395.3	59.74	0.000
Number of heterozygous loci	10	1,484.6	148.5	2.62	0.007
Type of forest-sex	3	511.4	170.5	3.0	0.034
Type of forest-number of heterozygous loci	20	2,036.5	101.8	1.79	0.029
Sex-number of heterozygous loci	9	400.6	44.5	0.78	0.632
Forest type-sex-number of heterozygous loci	18	1,181.3	65.6	1.15	0.311
Residual	114	6,479.0	56.8		
Total	178	15,645.5	87.9		

of grid. We also evaluated adult-juvenile changes in deficiency of heterozygotes and found significantly smaller values (less deficiency) in adults (average $F = 0.338$) than juveniles (0.514—Mann-Whitney *U*-test, $P = 0.027$).

Heterozygosity and weight.—Initial body weight of individuals did not differ among grids but was significantly different between sexes (males were heavier than females) and among individuals with different number of heterozygous loci (on average, those with more heterozygous loci weighed more). The interaction between grid and number of heterozygous loci was significant, which indicated that, although body weight alone was not different among dry and arroyo forests, it differed among grids when considering weights of mice with different number of heterozygous loci (Table 3).

Because grids showed no difference in relation to number of heterozygous loci or body weight, and to examine the relationship between heterozygosity and body weight, we considered grids together as one dataset. In the resulting dataset, body weight and number of heterozygous loci showed a positive correlation ($r = 0.223$, $P < 0.01$; Fig. 1), further indicating that in-

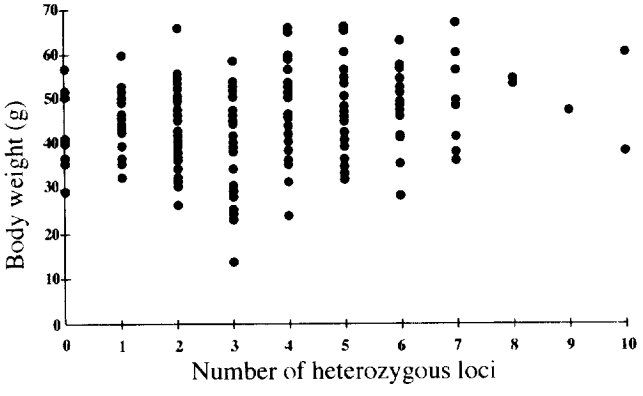

FIG. 1.—Correlation between number of heterozygous loci and initial body weight in individuals of *Liomys pictus* from Chamela, Jalisco, Mexico ($r^2 = 0.223$; $P < 0.001$; $n = 179$).

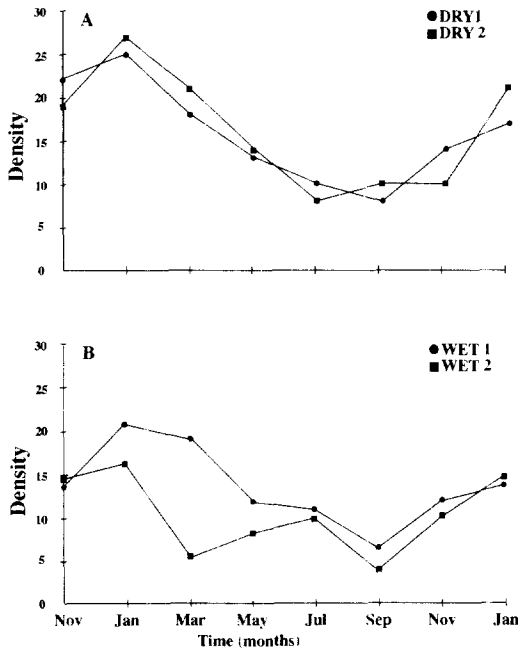

FIG. 2.—Changes in population density (MNA = minimum number of individuals known to be alive) of *Liomys pictus* in A) dry and B) arroyo forests from Chamela, Jalisco, Mexico, November 1994–January 1996.

dividuals that weighed more had more heterozygous loci.

Population density.—Average population densities on grids DRY1 and DRY2 and grids WET1 and WET2 were not significantly different; nor were average densities different when considering both grids together for each forest (20 and 16 individuals/ha in dry and arroyo populations, respectively). Average percentage of recapture of mice known to be alive during the study was 76–89% in the four grids—above the 50% required for using the direct-enumeration method for calculating density. Temporal changes in density during the 8 trapping periods showed similar patterns in the four grids studied (Fig. 2). There was an initial peak density in January 1995 followed by a decline by the end of the dry season (May–June), which continued throughout the rainy season (July–September), with a recovery period toward the beginning of the next dry season (January 1996).

Results of ANOVA for differences in average density in each trapping period (fluctuation in size of populations) among grids were not significant ($P > 0.05$). Therefore, the four grids were considered together, and results showed differences among trapping periods ($F = 8.230$, $d.f. = 7$; $P < 0.001$). Peak density observed in January 1995 was significantly different in relation to all other trapping periods; months with the lowest density (May–September 1995) also were different with respect to increase (November 1994 and November 1995–January 1996) and peak periods of population change.

Changes in average number of heterozygous loci during different phases of the fluctuations in size of populations also were evaluated with an ANOVA, and results were similar to those for fluctuations in density (Fig. 3). In relation to trapping periods, statistical differences were observed for low-density months compared with recovery months (November 1995–January 1996).

Analysis of the association between number of heterozygous loci and density for each dry and arroyo population over the study showed a positive, but nonsignificant trend (dry forest, $r = 0.344$, $P = 0.192$; arroyo forest, $r = 0.294$, $P = 0.269$). Thus, considering the four grids together, we grouped periods of increased, peak, and decreased density separately and calculated how average density and average number of heterozygous loci changed among them. Results showed a consistent pattern; the lowest average number of heterozygous loci was observed in the increase period and the highest during the decrease one, while during the peak period, the value was intermediate (3.2, 4.0, and 3.7, respectively). Density values for the same periods were 14.1, 9.6, and 23.2 individuals/ha, respectively (Fig. 4a). Average number of heterozygous loci was significantly different be-

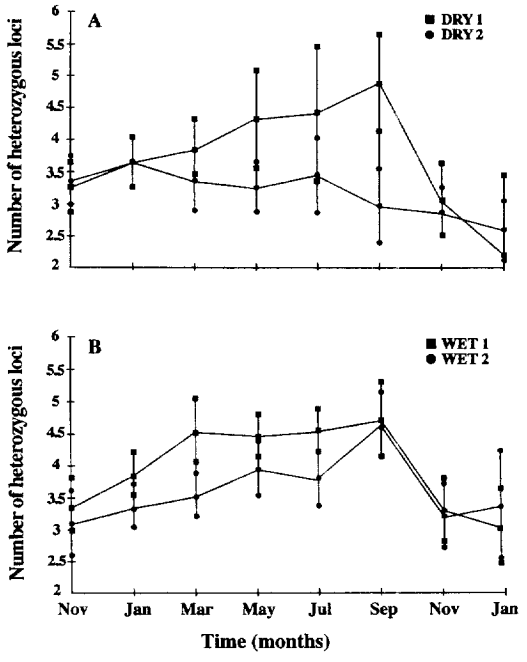

FIG. 3.—Changes in mean number of heterozygous loci of individuals of *Liomys pictus* in A) dry and B) arroyo forests from Chamela, Jalisco, Mexico, November 1994–January 1996. The bars above and below each value represent one standard error.

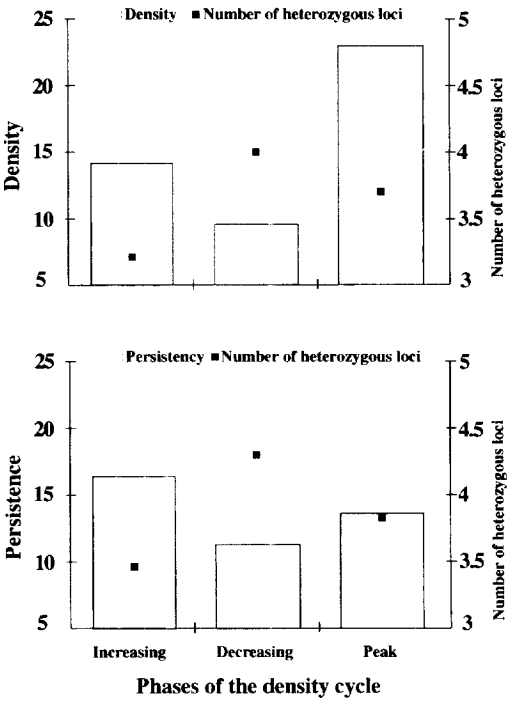

FIG. 4.—Population density and number of individuals that persisted in the study grids, during increase, decrease, and peak periods of the fluctuating population cycle of *Liomys pictus* from Chamela, Jalisco, Mexico.

tween increase and decrease periods of population change ($P < 0.01$).

Persistence.—Most individuals persisted <5 months (ANOVA; $P < 0.05$; Fig. 5), and there were no differences among grids ($P > 0.05$). The correlation between persistence of individuals and their number of heterozygous loci also was not statistically significant. For consistency with the analyses of population density, we also grouped periods of increased, peak, and decreased density across the four grids. With this, we calculated the number of individuals that persisted in each period and their number of heterozygous loci. Average number of individuals that persisted were 17.2, 11.7 and 14.3 in increase, decrease, and peak phases of population change, respectively (Fig. 4b). In relation to heterozygosity, the lowest average number of heterozygous loci was observed in the increasing period (3.5) and the highest during the decreasing period (4.4), while the peak period was intermediate (3.9; Fig. 4b).

DISCUSSION

Genetic variability.—Average observed heterozygosity values in these populations were high (dry forest, H = 0.188; arroyo forest, H = 0.198) compared with previous studies of this species (Patton and Rogers, 1993; Rogers, 1986, 1990; Rogers and Engstrom, 1992) and a recent study (Vázquez-Domínguez, 1997) of two populations of *L. pictus* in dry and arroyo forests, 20 km away from the present study sites. Vázquez-Domínguez (1997) analyzed 30 loci from tissue and blood samples of 104 individuals and reported an average observed heterozygosity of 0.089. For a better comparison, we reanalyzed data from that study

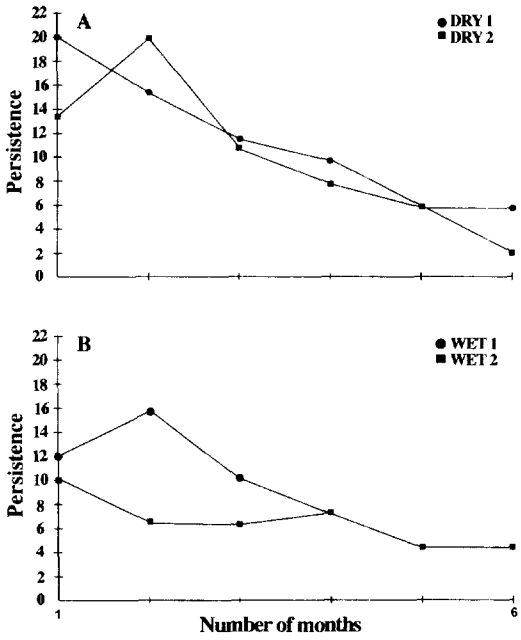

FIG. 5.—Number of individuals of *Liomys pictus* in A) dry and B) arroyo forests from Chamela, Jalisco, Mexico, that persisted in the study site, November 1994–January 1996.

for the same 19 blood proteins used in the present work, and average heterozygosity maintained a similar value (H = 0.097). Thus, accounting for caveats inherent to estimates of heterozygosity from electromorphic analyses (e.g., interlocus and intralocus sampling variance and errors—Lewontin, 1985; Nei and Roychourdhuri, 1974), we found different heterozygosity values in ecologically similar populations studied 1 year apart. Nevertheless, expected heterozygosity values were similar in both cases (average values were 0.331 for the previous study, and 0.333 for the present one).

Heterozygosity can change in a natural population in various ways. Number of polymorphic loci, number of alleles, and allelic frequencies determine heterozygosity values (Carson, 1990; Nevo et al., 1984; Selander, 1976); however, all these parameters were similar in populations from both studies (Vázquez-Domínguez, 1997; present study). Temporal, spatial, or biological subdivision of populations also have an effect on heterozygosity (Harrison and Hastings, 1996; Smith et al., 1975; Soulé, 1976). Rogers and Engstrom (1992) found extensive differentiation among 12 populations of *L. pictus* distributed from northern to the extreme southern Mexico. Age structure and allelic frequencies also are intimately related, and a change in one may lead to a change in the other (Endler, 1992).

Liomys pictus in Chamela, Jalisco, experiences drastic fluctuations in size of populations mainly due to the strong environmental seasonality of its habitat, characterized by severe droughts and long periods of scarcity of food (Ceballos, 1989, 1991; Mendoza, 1997). This kind of fluctuating population structure suggests events of inbreeding, as does extreme levels of partitioning among populations (Rogers and Engstrom, 1992). Likewise, our previous (Vázquez-Domínguez, 1997) and present results indicate that populations of *L. pictus* studied are characterized by a significant deficiency of heterozygotes, which indicates inbreeding (Hartl, 1980).

Inbreeding, among other factors, may underlie age-specific and temporal changes in genetic characteristics of populations (Scribner et al., 1991; Thornhill, 1993). The marked fluctuations in size of populations in these populations of *L. pictus* may result in a high rate of turnover and fluctuations in the young-adult age structure, and cumulative recruitment of offspring that differ in genotypic composition from their parents. All of the above enhance the potential for short-term changes in genetic composition (Harrison and Hastings, 1996). Likewise, dispersal and social structure are important factors that may result in genetic differences, even over short distances and time intervals (Harrison and Hastings, 1996; Nelson, 1993; Scribner et al., 1991; Vázquez-Domínguez, 1997).

Heterozygosity, weight, and age.—We found a positive and significant correlation between number of heterozygous loci and

weight, indicating that individuals that weighed more had more heterozygous loci. In studies comparing individuals of *P. polionotus* from overlapping generations, body weight was correlated positively with heterozygosity and was important in determining response of other characteristics such as social dominance, competitive ability, reproduction, and exploratory behavior (Garten 1976, 1977; Kaufman and Kaufman, 1987). These associations also could be found in *L. pictus*, but they remain to be tested.

It has been reported for some animal species that higher heterozygosity is found in older rather than younger age cohorts (Allendorf and Leary, 1986; Dobson et al., 1998; Mitton, 1993). We found that adult individuals had a higher number of heterozygous loci (i.e., higher genetic variation) than juveniles. We also found less deficiency of heterozygotes in adults than juveniles. These characteristics also are related to density parameters, as is explained next.

Heterozygosity and population density.—Our results support the hypothesis of Charlesworth and Giesel (1972) in that genetic equilibrium apparently is dependent upon demographic characteristics. We also agree with Scribner et al. (1983) who stated that fluctuations in age structure of populations due to characteristics that may be nonspecific with respect to genotype (e.g., changes in mortality or fecundity) can result in significant changes in genetic variability in the population as a whole.

Observed fluctuation patterns in density and temporal changes in heterozygosity were significantly related, involving both changes in size of populations and number of heterozygous loci. These significant changes in heterozygosity agree with studies of fluctuations in size of populations and genetic changes in several species of small mammals (Boonstra et al., 1998; Briese and Smith, 1974; Scribner et al., 1983; Smith et al., 1975). Such studies have shown that during early parts of the increase phase when densities are low, mice do not disperse and observed heterozygosity declines due to inbreeding (*P. polionotus*—Briese and Smith, 1974). In the peak phase of population change, dispersal occurs and the population becomes more outbred. During the declining phase, heterozygosity increases probably due to selection pressures against the relatively homozygous animals and superior fitness of heterozygous individuals (*P. polionotus*—Smith et al., 1975; *Microtus pennsylvanicus*—Krebs et al., 1973; *S. floridanus*—Scribner et al., 1983).

Accordingly, during the increase phase of population change when individuals do not disperse (Briese and Smith, 1974), we found the greatest number of individuals that persisted in the study area and low heterozygosity values. During the declining phase, which encompassed the dry-season months when supply of food was scarce, fewer individuals persisted, and heterozygosity values increased. These changes in number of heterozygous loci that accompany fluctuations (increase and decrease phases) in size of populations agree with the prediction that genetic variation in a population is inextricably tied to fluctuations in size of populations (Charlesworth and Giesel, 1972; Mathews and Porter, 1993). It is important to notice that these results represent a 14-month survey; thus, it will be worthwhile to follow these populations for several years and explore if these results hold constant.

Smith et al. (1975) suggested that changes in heterozygosity could be a mechanism linking demography and genetics in populations of small mammals. Evidence for this comes from studies evaluating the correlation between heterozygosity and characteristics of individuals and populations. In such cases, behavioral, morphological, and physiological traits have shown correlations with genic heterozygosity (Mitton, 1993). We also found a significant correlation between heterozygosity and body weight (morphological trait), likely a phenotypic effect which could affect fitness. Similarly, water metabolization (physiolog-

ical trait) was correlated with heterozygosity in a previous study in which we observed that the more heterozygous individuals of *L. pictus* were better able to conserve water and energy (Vázquez-Domínguez et al., 1998). Adults had a significantly greater number of heterozygous loci and a smaller deficiency of heterozygotes, supporting the pattern that the increase in observed heterozygosity during the decline phase of population change is probably due to the superior fitness of the more heterozygous individuals (Briese and Smith, 1974; Krebs et al., 1973; Scribner et al., 1983, 1991).

Our studies (Vázquez-Domínguez, 1997; Vázquez-Domínguez et al., 1998) represent the first evidence of these associations between genetic variability and different traits of populations and species that have been observed in a tropical species from a seasonal environment. This suggests similar patterns of heterozygosity and its relation to such characteristics in both tropical and temperate ecosystems.

Resumen

Se estudió la relación entre heterocigosidad y cambios espaciales y temporales de la densidad poblacional, además de la relación entre heterocigosidad y masa corporal, en cuatro poblaciones del ratón espinoso, *Liomys pictus*, de la selvas tropicales secas de Chamela, Jalisco, Mexico. *Liomys pictus* presenta fluctuaciones poblacionales extremas debido principalmente a la marcada estacionalidad de su hábitat. Para estimar la heterocigosidad, se analizaron 18 loci utilizando electroforesis en gel de almidón; el peso promedio se consideró un componente de adecuación. Los valores promedio de heterocigosidad observada fueron marcadamente altos (H = 0.188–0.198), mientras que las poblaciones presentaron una deficiencia significativa de heterocigotos (F = 0.350–0.429). Se encontró una relación significativa del número de individuos y el número de loci heterócigos por individuo con las diferentes fases de las fluctuaciones en el tamaño poblacional de *L. pictus*: durante la fase de incremento, la persistencia de los individuos fue mayor y la heterocigosidad promedio disminuyó, probablemente debido a eventos de endogamia. Durante el periodo de decremento de la densidad, cuando el alimento y el agua fueron escazos, la heterocigosidad aumentó y los individuos adultos, que presentaron menor deficiencia de heterócigos, fueron los más abundantes. El número promedio de loci heterócigos y el peso individual también presentaron una correlación positiva y significativa. Estos resultados apoyan la hipótesis de que los cambios en la variabilidad genética pueden ser efecto de cambios demográficos y que, consecuentemente, los caracteres asociados a la adecuación de los individuos pueden mostrar correlación con la heterocigosidad.

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APPENDIX I

Allelic frequencies for 19 loci in populations of Liomys pictus *from dry and arroyo forests in Chamela, Jalisco, Mexico. Sample sizes are in parentheses.*

Locus	Allele	Dry Forest-1 (44)	Dry Forest-2 (52)	Arroyo Forest-1 (46)	Arroyo Forest-2 (37)
ES1	1	0.273	0.413	0.435	0.365
	2	0.727	0.587	0.565	0.635
ES2	1	0.659	0.769	0.772	0.689
	2	0.341	0.231	0.228	0.311
GP1	1	0.182	0.212	0.207	0.459
	2	0.818	0.788	0.793	0.541
GP3	1	0.318	0.394	0.322	0.459
	2	0.682	0.606	0.678	0.541
GPI	1	0.440	0.594	0.278	0.439
	2	0.560	0.406	0.722	0.561
G6PD1	1	0.523	0.404	0.389	0.417
	2	0.443	0.481	0.533	0.528
	3	0.034	0.115	0.078	0.056
G6PD2	1	0.570	0.673	0.500	0.431
	2	0.430	0.327	0.500	0.569
LAP1	1	0.489	0.245	0.337	0.311
	2	0.477	0.725	0.652	0.608
	3	0.034	0.029	0.011	0.081
LDH1	1	0.300	0.096	0.076	0.106
	2	0.700	0.904	0.924	0.894
LDH2	1	0.837	0.865	0.880	0.957
	2	0.162	0.135	0.120	0.043
MDH1	1	0.034	0.106	0.044	0.135
	2	0.966	0.894	0.956	0.865
ME1	1	1.000	1.000	1.000	1.000
MPI1	1	0.058	0.098	0.076	0.081
	2	0.942	0.902	0.924	0.919
MPI2	1	0.849	0.931	0.924	0.824
	2	0.151	0.069	0.076	0.176
PEP1	1	0.744	0.817	0.761	0.905
	2	0.256	0.183	0.239	0.095
PEP2	1	0.267	0.422	0.391	0.297
	2	0.733	0.578	0.609	0.703
PEP3	1	0.795	0.856	0.880	0.946
	2	0.205	0.144	0.120	0.054
PER1	1	0.386	0.520	0.444	0.432
	2	0.614	0.480	0.556	0.568
6PGD1	1	0.942	0.875	0.902	0.865
	2	0.058	0.125	0.098	0.135