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# Heterozygosity patterning and its relation to fitness components in experimental populations of *Liomys pictus* from tropical forests in western Mexico

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We investigated the relationship between individual heterozygosity and the utilization of food and water in experimental populations of *Liomys pictus* from the markedly seasonal tropical dry deciduous and semideciduous forests of Chamela, Jalisco, in western Mexico. Thirty presumptive gene loci were analysed using starch-gel electrophoresis to estimate levels of heterozygosity. Mean body weight was used as a direct measure of the performance of individuals under food and water stressful conditions. *L. pictus* individuals subjected to a sequentially decreasing food treatment showed high feeding efficiency, with a ratio of food absorbed/food consumed of almost one. The association between food utilization and heterozygosity was not statistically significant, despite the pattern observed that the more heterozygous individuals maintained their weight better during the food treatment. Water utilization was positively associated with heterozygosity. When deprived of water, the more heterozygous individuals lost less weight than the less heterozygous ones. The ability of the more heterozygous individuals to better conserve water and energy may contribute to their adaptation to the extreme seasonality of the Chamela forests.



ADDITIONAL KEY WORDS:—heterozygosity – fitness components – heteromyids – *Liomys pictus* – tropical forests – allozymes – Mexico.

CONTENTS



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## INTRODUCTION

Correlations between heterozygosity and fitness components have been extensively documented, leading to the consensus that fitness is enhanced by heterozygosity and that any decrease in genetic variation will be paralleled by a decrease in fitness (Allendorf & Leary, 1986; Quattro & Vrijenhoek, 1989; Bush & Smouse, 1992; Mitton, 1993; Oostermeijer *et al.*, 1995; Johannesson & Tatarenkov, 1997), although there are important exceptions (McAndrew, Ward & Beardmore, 1982; Booth, Woodruff & Gould, 1990; Whitlock, 1993).

Variables related to metabolic processes such as body size, body weight, growth, energy storage, and reproduction have been found to be strongly correlated to fitness in vertebrates (Cothran *et al.*, 1983; Mitton & Grant, 1984; Allendorf & Leary, 1986; Pemberton *et al.*, 1988; Teska, Smith & Novak, 1990; Mitton, 1993). For example, in the oldfield mice *Peromyscus polionotus*, body weight was positively correlated with heterozygosity and was important in determining the response of other characteristics directly related with survival, such as social dominance, competitive ability, reproduction, and exploratory behaviour (Garten, 1976, 1977; Kaufman & Kaufman, 1987).

It has been hypothesized that the relationship between heterozygosity and fitness-correlated characters is more likely to result in an advantage during stress than during optimal environmental conditions (Mitton & Grant, 1984; Mitton, 1993) and that heterozygosity broadens the range of physiological tolerance and function relative to homozygosity (Samollow & Soulé, 1983). Accordingly, in experimental conditions in which individuals of the American oyster, *Crassostrea virginica*, were exposed to stressful conditions regarding temperatures, the more heterozygous individuals maintained weight better than the less heterozygous ones (Rodhouse & Gaffney, 1984). More heterozygous individuals of *Peromyscus polionotus* subjected to varying degrees of dietary stress, utilized food and maintained body weight better than their less heterozygous counterparts (Teska *et al.*, 1990; see Mitton, 1993 for an ample review). In this case, small changes in certain components of the energy budget, such as food assimilation, resulted in large changes in secondary productivity (e.g. energy for growth and reproduction), which influences fitness (Teska *et al.*, 1990).

Heteromyid rodents are known for their low rates of basal metabolism and low rates of energy use (French, 1993). They have acquired specialized behavioural, morphological, and physiological characteristics in their adaptive radiation to colonize seasonal environments (i.e. granivorous diet, cheek pouches to carry seeds, a seed hoarding behaviour, and an ability to survive for weeks on a diet of dry seeds with no water available; Fleming, 1977; MacMillan, 1983; French, 1993; Randall, 1993). The characteristics of the Heteromyidae reflect the adaptations required by these species for frugal use of available energy and water (McNab, 1979; MacMillan,

1983; French, 1993). These adaptations may affect characters influenced by metabolic processes and secondary productivity.

The spiny pocket mice *Liomys pictus*, an endemic heteromyid species of western and southern Mexico (Ceballos & Miranda, 1986; Williams, Genoways & Braun, 1993), is present in the tropical dry deciduous and semideciduous forests of Chamela, Jalisco, Mexico (Ceballos, 1989; Mendoza, 1997). Although *L. pictus* shares the habitat with several other rodent species, it is the dominant species in the deciduous forest, especially throughout the dry season, when it relies on seeds as its primary source of energy and water (Ceballos, 1989; French, 1993; Mendoza, 1997). Because of the strong environmental seasonality of its habitat, characterized by periods of food scarcity and long droughts, food utilization and water conservation capacities are of primary importance for individual survival (Fleming, 1977; French, 1993) and, in turn, may be important determinants of fitness.

The main objective of our study was to examine the hypothesis of greater advantage of heterozygosity during stress than during optimal environmental conditions. We evaluated the relationship between individual isozyme heterozygosity and the utilization of food and conservation of water, under varying degrees of stress, in experimental populations of *Liomys pictus* from Chamela, Jalisco, Mexico.

## MATERIAL AND METHODS

### *Study site*

Rodents were trapped at the Chamela-Cuixmala Biosphere Reserve, located on the southern portion of the State of Jalisco, on Mexico's western coast (19°25′N and 105°00′W). The site is characterized by a marked climatic seasonality, with an average monthly temperature of 24.9°C and a mean precipitation of 748 mm/year (Bullock, 1986). The rainy season lasts from July to October, concentrating 80% of the total precipitation, while the rest of the year represents a severe dry season, when most plants shed their leaves (Bullock, 1986; García-Oliva, Ezcurra & Galicia, 1991). The vegetation is predominantly tropical deciduous forest (hereafter dry forest) and semideciduous forest (hereafter arroyo forest; Rzedowski, 1978; Ceballos, 1989).

Individuals of *L. pictus* were collected in dry and arroyo forests for a total of 52 individuals per forest. Trapping areas were approximately 5 km apart. Mice were trapped using Sherman live-traps, sexed, and weighed to the nearest 0.1 g. Pregnant females were discarded. All animals were transported to the laboratory, housed individually in a photoperiodically-controlled animal room, and separated at random into two groups of 32 and 20 animals from each forest, for the food and water treatments, respectively.

### *Food treatment*

In order to have a reference value for the experimental food treatment, we initially measured the quantity of sunflower and oat seeds consumed by the animals that allowed them to maintain a relatively steady weight. Then, after a 2-week acclimation

period, each mouse was sequentially fed high, medium, and low diets, corresponding to 100, 50, and 25% of the reference value, respectively. Mice were fed each diet for a 6-day treatment period, and water was given ad libitum (Teska *et al.*, 1990). We measured the initial body weight of individuals at the start of each period, and body weight, amount of food eaten, and faeces produced midway through and at the end of each 6-day period. The change in body weight was considered a measure of their performance under stress. For each individual, faeces produced and seeds not consumed were dried and weighed. Amount of food absorbed was calculated by subtraction of egested from ingested amounts of dry matter and the feeding efficiency was measured as the ratio of food absorbed to food consumed.

### *Water treatment*

The animals in the water experiment had no food restriction, but had no water available. Changes in body weight were measured every 2 days for a total of 12 days. Water conservation capacity (i.e. weight maintenance throughout the experiment) was measured as the average weight loss. At the end of the treatment, mice were given water and their increment in weight was measured every 2 days during the following 10 days, which we called the recovery period.

### *Isozyme analyses*

Upon completion of both treatments, blood and tissue samples of all individuals were used to assay 34 proteins with horizontal starch-gel electrophoresis. We obtained good resolution for 19 proteins encoding 30 presumptive loci. Stains and buffers were used as described by Selander *et al.* (1971), Pasteur *et al.* (1988), and Teska *et al.* (1990). Buffer systems employed and proteins studied are summarized in the Appendix.

Of the 30 loci examined for each individual, 23 were polymorphic, with an average number of alleles per locus of 2.0 and 2.1, and an average heterozygosity value of 0.085 and 0.094, for dry and arroyo forests respectively. Detailed information about genetic variability of these populations is presented elsewhere (Vázquez-Domínguez, 1997). The average number of heterozygous loci per individual in the dry and arroyo populations was 2.1 and 3.1, respectively, but differences were not statistically significant ($P>0.05$).

Mice were assigned to one of three allozyme heterozygosity categories for data analyses: low for individuals with 0 or 1 heterozygous loci, medium for values from 2 to 4 heterozygous loci, and high for values of 5 or more. Because levels of heterozygosity were determined after the experimental treatments, an unequal number of individuals were included within each category. To avoid such disproportional grouping, we also performed our analyses considering only two categories: low (from 0 to 2 heterozygous loci) and high (3 or more). Because the statistical analyses did not differ between both groupings, we present the results using only two categories in order to have even groups for comparisons.

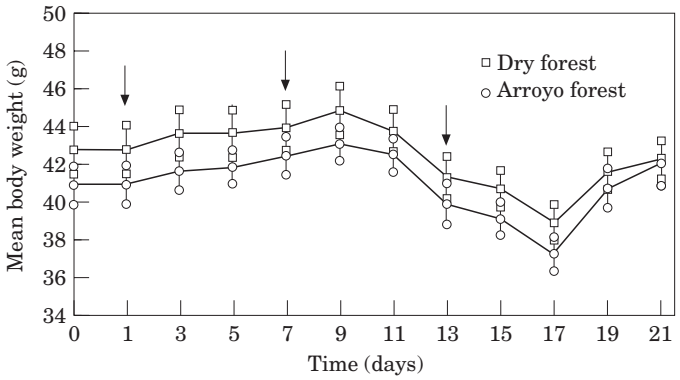


Figure 1. Mean body weight change during the decreasing food treatment for the experimental populations of *Liomys pictus* from Chamela, Jalisco, Mexico. Commencement of high, medium, and low food quantity periods are indicated by arrows. The bars above and below each value represent one standard error.

### *Statistical analyses*

Differences in initial body weight of individuals between dry and arroyo populations were tested by means of a *t*-test for each food and water treatment (Zar, 1984). To avoid sex biased results, we tested for differences in the number of heterozygous loci (heterozygosity category) between males and females with a *G* test for contingency tables (Wayne, 1990).

To evaluate whether the ability of individuals to maintain body weight was related to their heterozygosity, we analysed the data from the food and water treatments with a repeated measures analysis of covariance (Zar, 1984; Tabachnick & Fidell, 1989). In the food treatment, the dependent variables were body weight change, food absorbed, and feeding efficiency. Initial body weight, as recorded at the start of each 6-day period, was used as a covariate and the heterozygosity category as a classification variable. Post-hoc comparisons were performed with a Tukey test with unequal replication (Tabachnick & Fidell, 1989) to evaluate each interaction for heterozygosity category and food quantity separately.

For the water treatment, the dependent variables were final body weight (at the end of the 12-day treatment and at the end of the recovery period), average weight lost, and average weight recovered. The same covariate and classification variable were used in this analysis.

## RESULTS

### *Food treatment*

Initial mean body weight of animals in the dry forest was higher but not statistically different from that in the arroyo forest population ($42.8 \pm 7.4$ and $40.9 \pm 5.6$, respectively; Fig. 1). Body weight decreased during the dietary experiment for all mice, reaching values of $38.8 \pm 5.1$ and $37.0 \pm 5.3$, in dry and arroyo populations, respectively (Fig. 1).

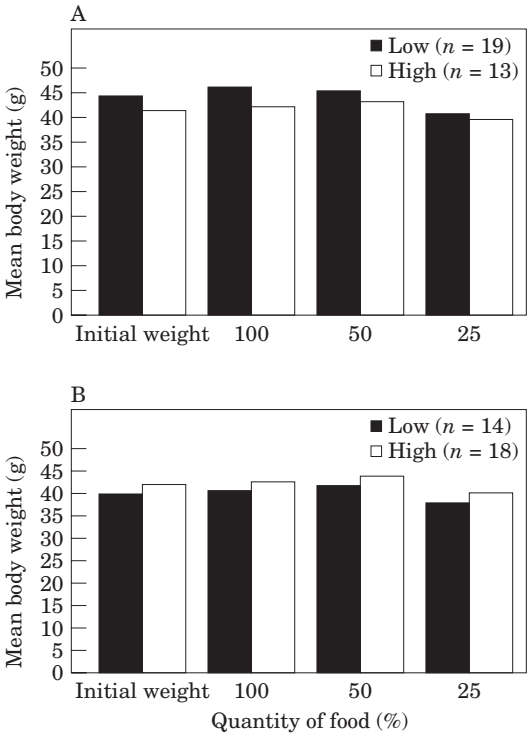


Figure 2. Least square means for initial body weight and weight change in each high, medium, and low food quantity periods, for *Liomys pictus* in (A) dry and (B) arroyo experimental populations from Chamela, Jalisco, Mexico. Low (0 to 2 heterozygous loci) and high (3 or more) heterozygosity categories and number of individuals in each category (n) are indicated in the upper right corner. Standard errors are too small to be shown clearly (range 0.7–1.5 g).

Mice were heterozygous at as many as eight loci and the number of heterozygous loci did not differ statistically between sexes ($G$ test; $P>0.05$), so covariance analyses were performed with both female and male individuals together. Considering the body weights recorded for each individual within each dietary experiment (each 6-day period), least square means were computed for the two heterozygosity categories (Fig. 2A, B).

In both the dry and arroyo forest populations, mice within the high heterozygosity category maintained their weight better than their less heterozygous counterparts as the quantity of food decreased. By the end of the food treatment (low quantity diet), the animals lost 6.4 and 5.6% of their initial mean weights in the low and high heterozygosity categories, respectively (Fig. 2A).

Results from the covariance analysis for the dietary treatment showed that variation in body weight was not statistically different between dry and arroyo forests (Table 1). In this analysis, food quantity was a highly significant source of variation. Contrary to what might be expected, heterozygosity category and the interaction of population × heterozygosity were not significant (Table 1). In the post-hoc comparisons, the interaction of the variables heterozygosity category and middle and low quantity diet are statistically significant ($P<0.001$), but not the interaction with high quantity diet. This suggests that individuals in the two heterozygosity categories

TABLE 1. Covariance analysis results for variation in body weight in the experimental dry and arroyo populations of *Liomys pictus* from Chamela, Jalisco, Mexico, during the sequentially food decreasing treatment. The initial body weight recorded at the beginning of each quantity diet was used as a covariate and heterozygosity category as a classification variable

| Source | df | SS | F | P |
|---|---|---|---|---|
| Population | 1 | 5.546 | 2.230 | 0.131 |
| Treatment | 2 | 229.430 | 95.113 | 0.000 |
| Heterozygosity category | 1 | 0.021 | 0.008 | 0.925 |
| Time[a] | 1 | 69.225 | 72.006 | 0.000 |
| Pop [b]*Trmt[c] | 2 | 0.086 | 0.035 | 0.965 |
| Pop*Hcat[d] | 1 | 1.350 | 0.560 | 0.455 |
| Trmt*Hcat | 2 | 1.557 | 0.645 | 0.526 |
| Pop*Time | 1 | 0.980 | 1.019 | 0.314 |
| Trmt*Time | 2 | 32.570 | 33.879 | 0.000 |
| Hcat*Time | 1 | 0.094 | 0.097 | 0.755 |
| Pop*Trmt*Hcat | 2 | 0.767 | 0.318 | 0.728 |
| Pop*Trmt*Time | 2 | 0.847 | 0.881 | 0.416 |
| Pop*Hcat*Time | 1 | 0.253 | 0.245 | 0.621 |
| Trmt*Hcat*Time | 2 | 0.386 | 0.401 | 0.670 |
| Pop*Trmt*Hcat*Time | 2 | 0.696 | 0.724 | 0.486 |

[a] Time refers to weight measured midway and at the end of each 6-day period (repeated measures).

[b] Pop (Population) refers to dry and arroyo forest populations.

[c] Trmt (Treatment) are the three dietary quantities: high (100%), medium (50%), and low (25%). See text for details.

[d] Hcat (Heterozygosity category) is low and high allozyme heterozygosity classification (see Material and methods).

TABLE 2. Percentages of feeding efficiency in each high, medium, and low food quantity diet for the food treatment, in the experimental dry and arroyo populations of *Liomys pictus* from Chamela, Jalisco, Mexico. Low and high heterozygosity categories are explained in text

| | Heterozygosity category | |
|---|---|---|
| Population/food quantity | Low | High |
| *Dry forest* | | |
| high (100%) | 96.7 (0.2)[a] | 97.1 (0.1) |
| medium (50%) | 96.4 (0.3) | 96.1 (0.5) |
| low (25%) | 96.3 (0.5) | 97.6 (0.5) |
| *Arroyo forest* | | |
| high (100%) | 96.5 (0.2) | 96.6 (0.4) |
| medium (50%) | 96.8 (0.4) | 96.5 (0.3) |
| low (25%) | 97.1 (0.6) | 97.7 (0.3) |

[a] Values in parenthesis represent one standard error.

responded significantly different when given less food (50 and 25% of the initial food quantity), and the more heterozygous mice tended to maintain their weight better under those conditions than the more homozygous mice (Fig. 2A,B).

Feeding efficiency was markedly high for dry and arroyo populations (Table 2). Covariance analyses for feeding efficiency were similar to the food treatment results

TABLE 3. Changes in mean body weight during the water treatment, in the experimental dry and arroyo populations of *Liomys pictus* from Chamela, Jalisco, Mexico

| | Mean body weight | | |
|---|---|---|---|
| Population | initial | final | recovery |
| Dry forest | 40.0±4.5 | 26.4±3.3 | 39.3±4.3 |
| Arroyo forest | 39.9±5.2 | 27.5±3.9 | 38.8±4.9 |

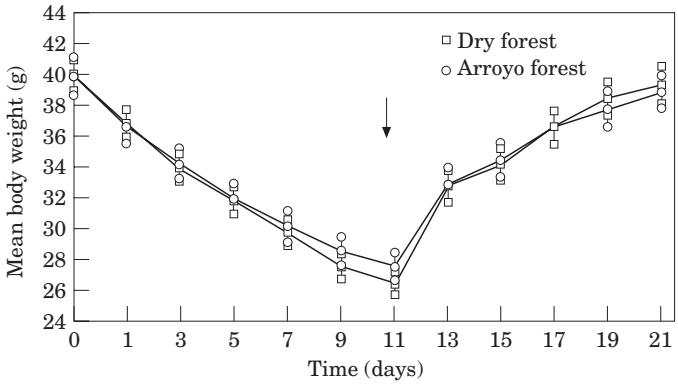


Figure 3. Mean body weight change during the water deprivation treatment for the experimental populations of *Liomys pictus* from Chamela, Jalisco, Mexico. The arrow indicates the recovery period starting point. The bars above and below each value represent one standard error.

in both populations, with dietary quantity (treatment) having a highly significant effect ($P<0.001$) and heterozygosity category and the interaction not significant.

### *Water treatment*

Initial body weight of animals was not significantly different between dry and arroyo forests (Table 3; $P>0.05$). Mean body weight of mice decreased during the 12-day water experiment in both the dry and arroyo forest populations (Fig. 3; Table 3). On average, individuals from the dry forest lost a greater percentage of their initial weight than those from the arroyo forest (2.8 versus 2.6% per day), but recovered a greater percentage of the lost weight (4.9 versus 4.1%).

As change in weight is partitioned among the two heterozygosity categories, some patterns can be appreciated (Fig. 4). Individuals from the dry forest within the low and high categories lost about the same percentage of their initial body weight. For the recovery period, mice within the high heterozygosity category recovered a greater percentage (99%) of their lost weight than those in the low category (87%; Fig. 4A). In the arroyo population, weight lost is also similar in the two heterozygosity categories, but individuals in the high category recovered less weight (86%) than those in the low category (95%; Fig. 4B).

TABLE 4. Covariance analysis results for mean weight lost and weight recovered, during the 12-day water deprivation treatment, in the experimental dry and arroyo populations of *Liomys pictus* from Chamela, Jalisco, Mexico. The initial body weight recorded at the beginning of the treatment was used as a covariate and heterozygosity category as a classification variable

| | | Weight lost | | | Weight recovered | | |
|---|---|---|---|---|---|---|---|
| Source | df | SS | F | P | SS | F | P |
| Population | 1 | 25.5 | 4.0 | 0.052 | 2090.8 | 2.3 | 0.134 |
| Heterozygosity category | 1 | 4.8 | 0.8 | 0.389 | 109.8 | 0.1 | 0.727 |
| Time[a] | 5 | 544.9 | 958.5 | 0.000 | 179.1 | 94.2 | 0.000 |
| Pop[b]*Hcat[c] | 1 | 37.9 | 6.0 | 0.019 | 2463.6 | 2.7 | 0.105 |
| Pop*Time | 5 | 2.5 | 4.3 | 0.001 | 1.2 | 0.6 | 0.638 |
| Hcat*Time | 5 | 0.2 | 0.3 | 0.919 | 0.2 | 0.1 | 0.049 |

[a] Time refers to weight measured every two days during the 12-day treatment for weight lost, and the 10 days recovery period (repeated measures).
[b] and [c] Abbreviations as in Table 1.

The covariance analysis showed significant differences between dry and arroyo populations for individual weight lost during the 12-day period with no water available (Table 4). Individuals from the arroyo population lost, on average, less weight than those from the dry population (Fig. 4) and the former individuals within the high heterozygosity category also showed the least weight loss for both populations (Fig. 4). Likewise, the interaction of population × heterozygosity category was significant for weight lost (Table 4), further indicating that individuals with different levels of heterozygosity, in each population, performed significantly different. Finally, none of the factors or interactions had a significant effect during the recovery period (Table 4).

## DISCUSSION

### *Heterozygosity and food utilization*

The family Heteromyidae is mainly distributed, with the exception of the genus *Heteromys*, from seasonally-dry tropical forests to extremely dry desert habitats. In these environments, high summer temperatures, unpredictable precipitation, and ephemeral primary productivity enhance the animals' extreme physiological adaptations for water and energy conservation (McNab, 1979; French, 1993).

Under such environmental conditions, food as a limiting factor has been documented for many heteromyid species, including *Liomys pictus* (Ceballos, 1989; Brown & Harney, 1993; Mendoza, 1997), and also for non-heteromyid species living in seasonal environments (*Peromyscus polionotus*; Smith, 1971). Teska *et al.* (1990) found feeding efficiency to be positively correlated with heterozygosity in *P. polionotus* when experimentally stressed by limited availability of food. Their results indicate that more heterozygous mice utilized food and maintained body weight better (assimilated food more efficiently) than more homozygous individuals.

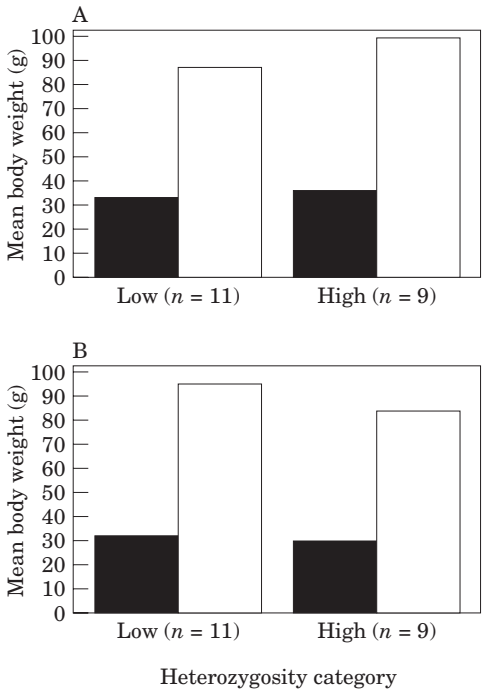


Figure 4. Percentage of weight lost (■) and recovered (□) during the water deprivation treatment, for individuals of *Liomys pictus* in (A) dry and (B) arroyo experimental populations from Chamela, Jalisco, Mexico. Heterozygosity categories refer to: low (0 to 2 heterozygous loci) and high (3 or more). Standard errors are too small to be shown clearly (range 0.4–1.7 g).

In the present study, the association between food utilization and heterozygosity was not statistically significant, despite the pattern observed that the more heterozygous individuals weighed more and/or maintained their body weight better as dietary stress increased, in both dry and arroyo populations. The post-hoc comparisons, while having fewer degrees of freedom, do indicate significant interactions between the heterozygosity category and middle and low quantity diet. This may suggest that, when given less food, individuals in the two heterozygosity categories responded significantly different and the more heterozygous mice maintained their weight better.

Although the loci studied might not be indicative of the level of heterozygosity and/or the traits under consideration might not be affected by the loci studied (Mitton & Pierce, 1980; Booth *et al.*, 1990), we think these considerations do not explain the present results. We screened a higher number of loci compared to many studies showing the relationship between heterozygosity and fitness components in small mammals (Garten, 1976, 1977; Cothran *et al.*, 1983) and in other organisms (see Mitton, 1993, for a review). As Johnson (1978) emphasized, most of the loci scored routinely in electrophoretic studies of enzyme polymorphisms code for enzymes involved in intermediary metabolism (i.e. in the processing and utilizing of energy), such as food utilization. We also need to consider that the experimental conditions might not have induced a physiological response dependent on the level of heterozygosity of individuals.

Although feeding efficiency was not statistically associated with heterozygosity, it is important to mention that *L. pictus* showed rather high values of efficiency (average of 95 to 97% for all three dietary quantities), absorbing almost all of the food they consumed. Efficient utilization of food has been found to be a critical factor during unfavourable times when food declines in quality and abundance (Teska *et al.*, 1990), and could have masked the effects of the dietary stress.

### *Heterozygosity and water metabolization*

Water conservation (metabolization) was an important source of variation. Differences in weight lost between populations, as well as the population × heterozygosity category interaction were statistically significant. Consistently, individuals with a low number of heterozygous loci lost more weight than those with more heterozygous loci.

The fact that analysis of covariance results of weight recovered were not statistically significant might indicate that, although individuals within high and low heterozygosity categories had a different ability to maintain weight during water stress, this is not necessarily reflected in their capacity to recover the weight they lose.

The differences found between dry and arroyo populations regarding weight recovered could be related to their particular environmental characteristics. The arroyo forest is a relatively more mesic environment where not all plants shed their leaves in the dry season (Bullock, 1986; Ceballos, 1989). Thus, a certain amount of food and water (free water in the food and metabolic water) is available year round, unlike the dry forest where food is scarce during drought months. Consequently, individuals in the dry forest commonly confront a more severe dietary and water stress than those in the arroyo forest. This could explain the fact that, although mice in the dry forest lost on average more weight when deprived of water, they were capable of recovering a higher percentage of the lost weight compared to the arroyo population. Nevertheless, this remains to be tested.

From our results, it is evident that individuals of *L. pictus* from Chamela, if deprived from consuming water, are able to tolerate a great weight reduction before becoming seriously weakened. *Liomys salvini*, which lives in a Costa Rican environment as seasonal as Chamela, lasted 7 days without consuming water and lost 3.4% of its initial weight per day (20% in total; Fleming, 1977). Another example is *L. salvini* from Nicaragua, which can live for at least 24 days in the absence of water, losing 17% of its weight (Hudson & Rummel, 1966). In the present study, *L. pictus* lasted 12 days and lost about 3% of its initial weight per day (31–34% in total). Like other heteromyid species, it is able to survive on a dry diet because it has enhanced physiological and behavioural abilities to reduce losses when water stressed (Hinds & MacMillen, 1985; French, 1993).

It has been suggested that the rigours of unpredictable environmental conditions or resources that vary in time, space and severity are precisely the sort of challenges against which heterozygotes, by virtue of their predicted greater physiological flexibility, would be superiorly buffered (Samollow & Soulé, 1983). Our results support the prediction that, under stressful conditions, *L. pictus* individuals that are genetically more variable conserve (metabolize) water better than their less variable counterparts.

There is much to be understood about the relationship between genetic variability

and population structure in natural populations of this species. In light of the present results, the relationship between heterozygosity patterns and fitness components in *L. pictus* from Chamela is not detected when mice are decreasingly deprived of food, probably because of their high feeding efficiency, but this association is clearly seen when they are water stressed. *Liomys pictus* individuals with higher heterozygosity, and corresponding capabilities for better water and energy conservation, may have greater flexibility in dealing with the seasonal environmental conditions of their habitat. This characteristic should contribute to their ability to maintain abundant populations in the physically severe, unpredictably semiarid dry and arroyo forests of Chamela, Jalisco, Mexico.

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## APPENDIX

Protein loci and electrophoretic conditions for *Liomys pictus* (1) Tris maleate, pH 7.4, 100 mA, 15 h; (2) Histidine, pH 5.6, 55 mA, 5 h; (3) Lithium-Borate, pH 7.6, 55 mA, 8 h; (4) Tris-Citrate, pH 8.0, 120 V, 7 h; (5) Lithium, pH 8.0, 100 V, 7 h; (6) Tris-Citrate, pH 6.3, 120 V, 5 h.

| Protein | E.C. | Locus | Buffer |
|---|---|---|---|
| Acid phosphatase | 3.1.3.2 | ACP | 4 |
| Aconitase | 4.2.1.3 | ACO | 6 |
| Adelinate kinase | 2.7.4.3 | AK | 6 |
| Aspartate aminotransferase | 2.6.1.1 | AAT | 4 |
| Esterase | 3.1.1.1 | ES1, ES2 | 3 |
| Esterase | 3.1.1.1 | ES3 | 5 |
| General protein (nonspecific) | | GP1, GP2 | 3 |
| General protein (nonspecific) | | GP3, GP4 | 3 |
| Glucose-6-phosphate dehydrogenase | 1.1.1.49 | G6PD1, G6PD2 | 1 |
| Glucose-6-phosphate isomerase | 5.3.1.9 | GPI | 1 |
| Glutamate dehydrogenase | 1.4.1.2 | GLD | 4 |
| Glycerophosphate-3- dehydrogenase | 1.1.1.8 | G3PDH | 4 |
| Lactate dehydrogenase | 1.1.1.27 | LDH1, LDH2 | 2 |
| Leucine aminopeptidase | 3.4.11.1 | LAP | 3 |
| Malate dehydrogenase | 1.1.1.35 | MDH | 2 |
| Malic enzyme | 1.1.1.40 | ME | 1 |
| Mannose-6-phosphate isomerase | 5.3.1.8 | MPI1, MPI | 3 |
| Menadione reductase | 1.6.99.2 | MNR1, MNR2 | 5 |
| Peptidases glycyl-L-leucine | 3.4.13.11 | PEPA1, PEPA2 | 3 |
| L-leucylglycyl glycine | 3.4.13.11 | PEPB | 3 |
| Peroxidase | 1.11.1.7 | PER | 4 |
| 6-phosphogluconate dehydrogenase | 1.1.1.44 | 6PGD | 2 |