UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO

INSTITUTO DE ECOLOGIA

PATRONES DE HETEROCIGOSIDAD Y SU RELACION CON COMPONENTES DE ADECUACION DEL ROEDOR *Liomys pictus* EN CHAMELA, JALISCO

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TESIS DE DOCTORADO

1997

Contigo atraparé los sueños que fueron clandestinos,
aquellos que aún no tienen dueño, acaso el torbellino...
Y mantendremos el empeño de combatir molinos,
que la razón, sin el ensueño
produce desatinos...

"Arrebato" Luis Eduardo Auté

...que rendirse es morir de pena, y que luchar por ser
es alegría que saca agudo filo a la esperanza.

Subcomandante Marcos, enero 1997

... me siento a su lado
le abrazo bien fuerte
y le digo te quiero.
Voltea, me mira y me da una sonrisa.
-viejo amigo mio,
lindo viejo padre.

Flaco,

por esa eternidad

prometida...

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RESUMEN

Se estudió la estructura genética del roedor heterómido, *Liomys pictus*, en las selvas tropicales de Chamela, Jalisco, México, para evaluar cuatro preguntas particulares. Conocer en detalle los niveles de variación genética de la especie en esta zona. De acuerdo a las hipótesis que establecen una relación positiva entre niveles de heterocigosidad y la heterogeneidad ambiental y entre éstos y los componentes de adecuación, examinar si existían diferencias en la variación genética como resultado de la estacionalidad y heterogeneidad de dos ambientes contrastantes, la selva caducifolia y la selva subcaducifolia. Y, si había una relación positiva entre los niveles de heterocigosidad individual y ciertas características consideradas componentes de adecuación, como son la masa corporal y la utilización eficiente del alimento y la conservación del agua. Por último, con base en la hipótesis que establece que cambios en la variación genética pueden ser efecto de cambios demográficos, evaluar si las fluctuaciones de la densidad poblacional estaban asociadas a cambios en la variación genética.

Se analizaron 30 loci isoenzimáticos por medio de electroforesis en gel de almidón. Se encontró que las poblaciones de *L. pictus* en Chamela, Jalisco, presentan niveles de variación genética (P = 73.3 a 94.7; H = 0.089 a 0.198) marcadamente mayores que los reportados anteriormente para la especie, además de un exceso significativo de homocigotos, lo cual indica una fuerte endogamia. No se encontraron diferencias entre poblaciones asociadas a la estacionalidad contrastante de las dos selvas. En relación a los componentes de adecuación considerados, se observó una correlación positiva y significativa entre el número de loci heterócigos y la masa corporal. La conservación eficiente del agua también presentó una correlación positiva con la heterocigosidad: al suprimirles el consumo de agua, los individuos más heterócigos perdieron menos peso que los menos heterócigos. No se encontró relación en cuanto a la utilización del alimento. Finalmente, se encontró una asociación significativa entre los cambios en el número de loci heterócigos y las fluctuaciones de densidad poblacional, en la que en periodos de baja densidad se observó un aumento de los niveles de heterocigosidad y su disminución en los periodos de mayor densidad.

Se sugiere que el exceso de homocigotos, aunado a la diferenciación y subdivisión genética observada entre poblaciones, puede ser reflejo de la estructura social de

esta especie y de las marcadas fluctuaciones de su densidad poblacional. Los resultados negativos sobre la utilización del alimento pueden estar asociados a la alta eficiencia alimenticia que presentaron los individuos. La estructura genética de *Liomys pictus*, su relación significativa con componentes de adecuación y con patrones demográficos están directamente relacionados con las características estacionales de su hábitat y con la habilidad de los individuos de mantener poblaciones en estos ambientes físicamente severos e impredecibles como son las selvas tropicales de Chamela, Jalisco, México.

ABSTRACT

The genetic structure of the heteromyid rodent, *Liomys pictus*, from the tropical forests of Chamela, Jalisco, Mexico, were studied in order to evaluate four particular questions. To obtain detailed information about the genetic variability of the species in this area. Considering the hypothesis of a positive relationship between heterozygosity levels and environmental heterogeneity, and between heterozygosity and fitness-correlated characters, to examine if genetic differences could be observed associated to the seasonality and heterogeneity of two contrasting habitats, the deciduous and semideciduous forests. Also, if a positive relationship between individual protein heterozygosity levels and certain components of fitness, such as initial body weight and the efficient utilization of food and conservation of water existed. Finally, based on the hypothesis that changes in genetic variability can be effects of demographic changes, to evaluate if the population density fluctuations were associated to changes in genetic variability measures.

Thirty presumptive gene loci were examined with starch-gel electrophoresis. Genetic results showed that the populations of *L. pictus* from Chamela, Jalisco, have genetic variability levels (P = 73.3 a 94.7; H = 0.089 a 0.198) markedly higher than previously reported for the species; they also presented a significant homozygotes excess, which indicates strong inbreeding. No differences were found between populations associated to the contrasting seasonality of the two habitats. In relation to the components of fitness, a positive and significant correlation was found between the number of heterozygous loci and body weight of individuals. The efficient conservation of water also showed a positive correlation with heterozygosity: when individuals were deprived from drinking water, the more heterozygous individuals lost less weight than the less heterozygous ones. No relationship was observed regarding the utilization of food. Finally, a positive association was found between changes in heterozygosity levels and population density fluctuations, in which the mean number of heterozygous loci declined during the increasing period of the density cycle and increased during the declining phase.

It is suggested that the observed homozygotes excess, together with the genetic differentiation and subdivision found among populations, can be associated with the species social structure and the marked fluctuations in population numbers. The negative results about food utilization can be

related to the observed high feeding efficiency of individuals. The genetic structure of *Liomys pictus*, its relationship with fitness components and with the population demographic fluctuatios, are directly related with the seasonal characteristics of its habitat and with the ability of individuals to maintain populations in the physically severe and unpredictable forests of Chamela, Jalisco, Mexico.

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INTRODUCCION GENERAL

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Estimación de la variación genética

La aplicación de técnicas de electroforesis para el estudio de la estructura genética en poblaciones naturales, a través del uso de aloenzimas, ha permitido conocer los niveles de variación genética tanto en plantas como animales (Selander 1976; Nevo 1978; Hamrick 1983; Lewontin 1985).

En poblaciones naturales, muchas de estas enzimas son polimórficas. Además, se pueden observar diferencias entre genotipos en cuanto al funcionamiento de las enzimas; tales diferencias se pueden detectar también a nivel individual y/o poblacional (Mitton y Grant 1984). Así, se han podido describir diferencias genéticas entre individuos dentro de una población y entre poblaciones de una misma especie (Selander 1976; Allendorf 1983; Leberg, 1996).

La estructura genética de las poblaciones naturales puede variar por diferentes causas: en función de fuerzas evolutivas como deriva, flujo génico, mutación, selección natural (Ayala 1976; Slatkin 1981; Allendorf 1983; Slatkin y Barton 1989) y por factores tales como tamaño de la población y diferenciación geográfica, entre otros (Ayala 1976; Soulé 1976; Nevo 1978). También, cierta proporción de la variación genética se mantiene como resultado de la heterogeneidad ambiental; por ejemplo, se ha encontrado una correlación positiva entre la diversidad ambiental y los polimorfismos genéticos en poblaciones naturales (Powell 1971; McDonald y Ayala 1974; Smith et al. 1975; Riddle et

al. 1983), aunque existen excepciones a este patrón (Ayala y Valentine 1974; Ayala et al. 1975).

Para describir la variación genética de una población se consideran comúnmente las frecuencias alélicas de los diferentes loci, la proporción de loci polimórficos (*P*; un locus se considera polimórfico cuando el alelo más común tiene una frecuencia menor a 0.95), la heterocigosidad observada (*H*; el porcentaje de genotipos observados en los que el individuo promedio es heterócigo) y el número de loci heterócigos por individuo (Nei 1973, 1987; Selander 1976; Frankel y Soulé 1981; Hedrick 1983; Mitton 1993). En general, *H* es considerado un mejor indicador de la variación genética ya que depende menos del tamaño de muestra y puede definirse de manera menos ambigua (Nevo 1978; Brown y Weir 1983; Eguiarte 1990). El número de loci heterócigos se ha utilizado ampliamente en estudios que relacionan la variación genética con adecuación, como se explicará en detalle más adelante.

Heterosis

En estudios con especies domesticadas se han documentado ampliamente los efectos nocivos de la pérdida de variación genética como resultado de endogamia, lo mismo que las ventajas que presentan los individuos heterócigos (Mitton 1989; Wolff y Haeck 1990). Al llevar a cabo cruzas entre poblaciones o líneas diferenciadas de estas especies, se ha demostrado que existe un incremento general del `vigor´ (fertilidad, sobrevivencia, crecimiento), el cual está asociado al aumento de los niveles de heterocigosidad de la progenie; a este fenómeno se le conoce como heterosis

(Lerner 1954; Frankel 1983; Allendorf y Leary 1986; Mitton 1989).

Evaluar el fenómeno de heterosis en poblaciones naturales no ha sido tan directo como en especies domesticadas. Debido a la gran dificultad para estimar diferencias en adecuación entre genotipos (Lewontin 1974), el estudio de la heterosis se ha enfocado a evaluar la relación entre niveles de heterocigosidad y características que pueden afectar la adecuación.

Se ha establecido que ciertos caracteres morfológicos, fisiológicos, conductuales y demográficos están frecuentemente relacionados con la variación genética (Smith et al. 1975; Dear et al. 1992). Así, características tales como tasa de crecimiento, tamaño corporal, eficiencia metabólica, fecundidad, resistencia a enfermedades, que afectan directa o indirectamente la sobrevivencia de los organismos, son consideradas como componentes de adecuación. El enfoque general para estudiar la heterosis ha sido evaluar la variación en los niveles de heterocigosidad entre individuos dentro de una población, y si estas diferencias están asociadas a componentes de adecuación (Allendorf y Leary 1986; Mitton 1993).

Heterocigosidad y componentes de adecuación

a) Heterocigosidad y masa corporal

La correlación positiva entre la variación genética, medida como heterocigosidad individual, y diversos componentes de adecuación ha sido extensamente documentada; esto ha generado el consenso de que cualquier disminución en la variación genética estará acompañada por un decremento en

la adecuación de los individuos (Frankel y Soulé 1981; Allendorf y Leary 1986; Nei 1987; Mitton 1989, 1993; Bush y Smouse 1992). Sin embargo, no puede considerarse una generalidad pues existen también ejemplos donde no se ha encontrado esta relación (Selander y Kaufman 1973; Bonnell y Selander 1974; McAndrew et al. 1982; Houle 1989; Booth et al. 1990; Whitlock 1993).

Se ha relacionado positivamente la heterocigosidad en plantas con características como tasa de crecimiento, fecundidad, fisiología, productividad en plantas cultivadas, o una combinación de éstos (Mitton y Grant 1984; Mitton 1989; Wolff y Haeck 1990; Oostermeijer et al. 1995; para una amplia revisión ver Bush y Smouse 1992).

En animales, las características más frecuentemente relacionadas con heterocigosidad son el tamaño corporal, tasa de crecimiento, sobrevivencia, conducta, caracteres morfológicos, reproducción y metabolismo (Pierce y Mitton 1982; Allendorf y Leary 1986; Patarnello y Battaglia 1992; Mitton 1993; Scapini et al. 1995; tabla 1).

En mamíferos en particular, el número de estudios es menor comparado con plantas e invertebrados, sin embargo, varios de éstos estudios han podido establecer la asociación entre un amplio espectro de características consideradas componentes de adecuación y la variabilidad genética (tabla 1). Así, se ha encontrado una relación positiva entre la heterocigosidad y la masa corporal, lo que a su vez se ha asociado a ventajas en otras características relacionadas con la adecuación, tales como crecimiento, fecundidad,

tamaño de las crías, conducta y reproducción (Wooten y Smith 1984; Allendorf y Leary 1986; Mitton 1993).

Por ejemplo, en el venado cola blanca, *Odocoileus virginianus*, las hembras adultas que presentaban altos niveles de heterocigosidad enzimática eran más pesadas que los individuos homócigos, sus crías también eran significativamente más pesadas, y con mayor frecuencia las hembras tenían camadas de dos crías; el nivel de variación genética se asoció con la optimización de la energía para procesos de crecimiento y reproducción (Cothran et al. 1983; Mitton y Grant 1984). Asímismo, se encontró que la masa corporal estuvo significativamente correlacionada con el número de loci heterócigos en el roedor *Peromyscus polionotus*. Esta asociación fue determinante en la ventaja que presentaban los individuos heterócigos respecto a los homócigos en otras características directamente relacionadas con sobrevivencia, tales como habilidad competitiva, dominancia, reproducción y conducta (Garten 1976, 1977; Kaufman y Kaufman 1987).

b) Heterocigosidad y metabolismo

Si la variación genética influye directamente en factores correlacionados con la adecuación, la asociación entre estos factores y la heterocigosidad debería reflejarse en características del metabolismo (Mitton y Grant 1984). Se ha observado que la variabilidad genética puede tener efectos directos en la variación de caracteres metabólicos y fisiológicos, lo que sugiere el patrón general de que la

eficiencia metabólica aumenta con la heterocigosidad (Mitton 1989, 1993).

Por ejemplo, la relación entre heterocigosidad y parámetros fisiológicos indicativos de crecimiento ha sido estudiada con detalle en invertebrados marinos. Se ha encontrado que los individuos más heterócigos presentan un metabolismo más eficiente, con valores menores de metabolismo basal, y que son capaces de destinar proporcionalmente mayor energía hacia funciones de crecimiento, en las almejas *Crassostrea virginica* (Koehn y Shumway 1982) y *Mulina lateralis* (Garton et al 1984) y en el gasterópodo *Thais hemostomata* (Garton 1984), entre otros.

En cuanto a los mamíferos, se ha observado que variables relacionadas de manera indirecta con el metabolismo, tales como masa corporal y crecimiento, también se correlacionan positivamente con la heterocigosidad. Particularmente, en el roedor *Peromyscus polionotus* se evaluó directamente el metabolismo y se observó que la habilidad de asimilar eficientemente el alimento estuvo relacionada con los niveles de heterocigosidad (Teska et al. 1990). En otro estudio se encontró una relación directa entre la variación de ciertos genes que codifican para hemoglobina (relacionada directamente con metabolismo) y la distribución altitudinal de este roedor; en los extremos de la distribución se observó el máximo metabolismo (Snyder 1981; Chappell y Snyder 1984).

c) Heterocigosidad y heterogeneidad ambiental

Se ha sugerido que el grado de variación genética en las poblaciones debería estar correlacionado con el grado de heterogeneidad del ambiente (Powell 1971; McDonald y Ayala 1974). Por ello, la asociación entre heterocigosidad y componentes de adecuación podría ser más fuerte en ambientes estacionales, ya que las ventajas que presentan los individuos heterócigos aumenta con la heterogeneidad ambiental (Koehn et al. 1980; Mitton y Grant 1984). Por ejemplo, poblaciones de *Drosophila willistoni* y *D. pseudoobscura* que se mantuvieron experimentalmente en ambientes espacial y temporalmente heterogéneos, presentaron mayor variación genética que las poblaciones de ambientes estables (Powell 1971; McDonald y Ayala 1974).

Considerando los patrones observados sobre heterosis y su relación con aspectos fisiológicos y ambientales, se ha sugerido también que la asociación entre heterocigosidad y componentes de adecuación puede ser más evidente si se evalúa en condiciones de estrés (Mitton y Grant 1984). En estudios con la almeja Americana, *Crassostrea americana* (Rodhouse y Gaffney 1984) y el roedor *Peromyscus polionotus* (Teska et al. 1990) realizados en condiciones experimentales estresantes de temperatura y alimentación, los individuos más heterócigos mantuvieron mejor el peso corporal que los menos heterócigos (Mitton 1993). En estos casos, cambios en ciertos componentes del metabolismo como es la asimilación del alimento, resultaron en cambios considerables en la energía disponible para el crecimiento y la reproducción. Esto, a su vez, pudo influir en la adecuación de los individuos ya que se afectan características de historia de

vida (Teska et al. 1990). Estos estudios apoyan la hipótesis de que la heterocigosidad amplía el intervalo de tolerancia y función fisiológicas, confiriendo una relativa mayor flexibilidad y latitud de los procesos bioquímicos (Samollow and Soulé 1983).

d) Heterocigosidad y demografía

La variabilidad genética también se ha relacionado con patrones demográficos. Los mamíferos frecuentemente presentan cambios genéticos ya sea temporales, espaciales y/o relacionados con la estructura de edad (Smith et al. 1975; Flowerdew 1987); por ello, se ha sugerido que cambios concomitantes en la conducta, genética y densidad en mamíferos pueden estar asociados con cambios en el nivel de heterocigosidad de las poblaciones (Gaines y Krebs 1971; Smith et al. 1975; Zimmerman 1988; Scribner et al. 1991). Muchas de estas observaciones han sido interpretadas como evidencia que apoya la hipótesis de Charlesworth y Giesel (1972), la cual menciona que en poblaciones que presentan sobrelapamiento de generaciones, los cambios en la variación genética pueden ser el resultado de cambios en la densidad.

La información más completa sobre esta asociación entre variación genética y adecuación, particularmente en mamíferos, se ha adquirido a través de estudios que consideran varios aspectos a la vez: los ciclos de densidad poblacional estacionales y no estacionales, los cambios en la variabilidad genética de los individuos y la relación de estos cambios genéticos con parámetros demográficos y con componentes de adecuación.

En estos estudios se han relacionado los cambios en las frecuencias alélicas y en los niveles de heterocigosidad con cambios en los números poblaciones, en roedores microtinos (Gaines y Krebs 1971; Gaines et al. 1978), en el roedor *Peromyscus polionotus* (Smith et al. 1975), el conejo cola de algodón *Sylvilagus floridanus* (Scribner et al. 1983), el venado cola blanca *Odocoileus virginianus* (Chesser et al. 1982; Scribner et al. 1985) y el venado bura *O. hemionus* (Scribner et al. 1991). En la mayoría de estos estudios se utilizaron componentes de adecuación para explicar la correlación entre la variabilidad genética y la densidad: se observó que los individuos más heterócigos presentaban una ventaja significativa en cuanto a características como sobrevivencia, reproducción, masa corporal y tasa de crecimiento, en relación a los menos heterócigos (Gaines y Krebs 1971; Smith et al. 1975; Gaines et al. 1978).

Variación genética, adaptación y conservación

Los estudios genéticos son parte importante de un área crítica de la conservación por varias razones: la pérdida de la diversidad genética reduce las opciones evolutivas futuras (Fisher 1930); niveles reducidos de heterocigosidad individual pueden ocasionar disminución en la adecuación; y, la diversidad genética global de las especies representa toda la información existente de todos los procesos biológicos. Por ello, la pérdida de diversidad genética puede tener efectos negativos en la adecuación y dificultar el cambio adaptativo en las poblaciones (en el corto y mediano plazos) y disminuir las posibilidades de especiación (en el largo plazo), lo que aumenta las posibilidades de

extinción de poblaciones y especies (Meffe y Carroll 1994; Myers 1997).

La viabilidad de las especies que sobreviven problemas demográficos y ambientales puede depender de la diversidad genética que poseen. Así, el estudio de la variabilidad genética provee un entendimiento de los procesos evolutivos tanto actuales como históricos que han generado los patrones de biodiversidad que observamos; la preservación de estos patrones deben ser componentes importantes de los planes de conservación (Smith et al. 1993; Smith y Wayne 1996).

Se pone así de manifiesto la importancia de la variabilidad genética y su relación con aspectos de adecuación y adaptación, para la conservación de especies. Una propuesta integrada de conservación requiere del uso de información ecológica, demográfica, morfológica y genética para permitir la preservación de una cantidad significativa de diversidad evolutiva (Smith y Wayne 1996).

ROEDORES HETEROMIDOS

La familia Heteromyidae agrupa a roedores exclusivamente del nuevo mundo. Incluye a las ratas y ratones canguro y a los ratones espinosos de los desiertos, pastizales y matorrales del oeste de Norteamérica, y de las selvas tropicales secas y siempre verdes de Norteamérica y Centroamérica y del norte de Sudamérica (Genoways y Brown 1993).

Los heterómidos son conocidos por sus bajas tasas de metabolismo basal y de uso de energía (French 1993). A lo largo de su radiación adaptativa, en la que colonizaron ambientes estacionales desérticos y semidesérticos,

adquirieron características morfológicas, conductuales y fisiológicas especializadas, tales como una dieta granívora, abazones para transportar semillas que almacenan en sus madrigueras, y la habilidad de sobrevivir por largos periodos con una dieta de semillas secas y sin disponibilidad de agua (Fleming 1977; Genoways y Brown 1993; Randall 1993).

La mayoría de estos organismos asimilan cerca del 90% del alimento que consumen, con lo que minimizan la cantidad de material no digerido y la pérdida del agua asociada (French 1976, 1993; Withers 1982). Estas características reflejan adaptaciones para el uso moderado de la energía (alimento) y el agua, que están disponibles de forma estacional en los ambientes que ocupan (McNab 1979; MacMillan 1983, French 1993). Dichas adaptaciones pueden afectar diferentes características relacionadas con procesos metabólicos y de productividad secundaria y, por lo tanto, afectar la adecuación general de los individuos.

Solo ciertas especies de heterómidos (principalmente de los géneros *Dipodomys*, *Chaetodipus* y *Microdipodops*) han sido estudiadas respecto a su estructura genética. La mayoría de estos estudios se han enfocado a medir niveles de variación genética considerando un número relativamente bajo de loci. Esta información, a su vez, se ha utilizado para estimar relaciones entre taxa y para explicar patrones de variabilidad y distribución geográfica (Hafner et al. 1979; Beck et al. 1981; Patton et al. 1981; Elliot et al. 1989; Patton y Rogers 1993) y, de manera menos intensa, para investigar aspectos de demografía (Johnson y Selander 1971)

y niveles de endogamia en poblaciones locales (Hamilton et al. 1987; para un resumen completo, ver Genoways y Brown 1993).

Liomys pictus

El ratón espinoso, *Liomys pictus*, pertenece a la familia Heteromyidae. Es una especie endémica del oeste de México (Hall 1981; Ceballos y Miranda 1986; Williams et al. 1993), abundante en las selvas tropicales secas a lo largo de la costa del Pacífico. Ha sido ampliamente estudiada en la selva tropical caducifolia y subcaducifolia de Chamela, Jalisco, México (Genoways 1973; Collet et al. 1975; Ceballos 1989; Rogers 1990; Mendoza 1997); estos estudios han demostrado que los patrones de distribución y abundancia de la especie están directamente relacionados con la marcada estacionalidad característica de estas selvas.

A pesar de que *L. pictus* comparte su hábitat con otras especies de roedores, es la especie dominante en la selva caducifolia, sobre todo durante la época seca, en la que su fuente principal de energía y agua proviene de las semillas que consume (Ceballos 1989; French 1993; Mendoza 1997). Por sus características morfológicas, fisiológicas y conductuales, esta especie es capaz de mantener poblaciones durante todo el año y enfrentar la marcada estacionalidad del hábitat (McNab 1979; MacMillan 1983; Ceballos 1991). De tal manera que, debido a las largas sequías y periodos de escasez de alimento que caracterizan el ambiente, la eficiente asimilación del alimento y la capacidad de conservar el agua son factores importantes para la sobrevivencia de los individuos (Fleming 1977; Ceballos

1989; French 1993), características que a su vez pueden ser determinantes de la adecuación (Genoways y Brown 1993).

OBJETIVOS

El objetivo general del presente trabajo es llevar a cabo un estudio completo sobre la estructura genética del roedor heterómido, *Liomys pictus*, para evaluar si existen diferencias genéticas entre poblaciones de dos ambientes estacionales contrastantes. A su vez, evaluar conjuntamente la relación entre la variación genética y aspectos fisiológicos y demográficos de la especie y su efecto sobre ciertos componentes de adecuación.

De manera específica, los objetivos particulares son:

1. Describir la estructura genética de las poblaciones de *Liomys pictus* en las selvas tropicales estacionales de Chamela, Jalisco, México.
2. Para evaluar la hipótesis sobre la correlación positiva entre variación genética y el grado de heterogeneidad del ambiente, examinar si existen diferencias genéticas en *L. pictus* relacionadas a la marcada estacionalidad y a las características ambientales contrastantes de las selvas caducifolia y subcaducifolia de Chamela, Jalisco, México.
3. Evaluar la hipótesis sobre la relación positiva entre los niveles de heterocigosidad individual y ciertos factores considerados como componentes de adecuación:

a) de manera indirecta examinando la relación entre heterocigosidad y la masa corporal de los individuos de *L. pictus*.

b) de manera directa examinando, bajo condiciones de estrés, la relación entre heterocigosidad individual y las características fisiológicas de la eficiencia en la utilización del alimento y la conservación de agua.

4. Evaluar la hipótesis que establece que cambios en la estructura genética de las poblaciones pueden estar directamente relacionados con cambios en la densidad poblacional. Esto, a través del estudio de los cambios en los niveles de heterocigosidad individual y los cambios espaciales y temporales de la densidad de *Liomys pictus* en Chamela, Jalisco, México.

ESTRUCTURA DE LA TESIS

El presente trabajo está estructurado en seis capítulos. El primero y el quinto comprenden, respectivamente, una introducción general de los temas examinados en el trabajo de tesis y una discusión general de los resultados obtenidos; ambos están escritos en español. El sexto comprende la literatura citada en estos dos capítulos.

En el capítulo 2 se presenta la estructura genética de *Liomys pictus* y se examinan las diferencias en la variación genética entre las poblaciones de las selvas caducifolia y subcaducifolia en Chamela, Jalisco, México

El capítulo 3 se refiere al estudio de la relación entre heterocigosidad y la utilización eficiente del alimento y la conservación de agua en individuos de *L. pictus*. Esto, a través de experimentos de laboratorio y bajo diferentes condiciones de estrés alimenticio y de disponibilidad de agua.

Finalmente, en el capítulo 4 se presenta el estudio de la relación entre variación genética y demografía, a través del estudio de los cambios en la densidad poblacional de *L. pictus*, a lo largo de 14 meses, en las selvas tropicales de Chamela, Jalisco, México.

Estos tres capítulos están escritos en formato de artículo y en inglés.

SITIOS DE ESTUDIO

Los dos primeros estudios (Capítulos 2 y 3) del presente trabajo se llevaron a cabo en la Reserva de la Biósfera Chamela-Cuixmala y el último (Capítulo 4), en la Estación de Biología "Chamela".

El 42% de los ecosistemas tropicales del mundo son selvas decíduas y, en el neotrópico, se distribuyen desde México hasta el norte de Argentina, ocupando el 22% del área con selvas en Sudamérica y casi el 50% en Centroamérica (Murphy y Lugo, 1986). En México, cubren alrededor del 20% de la superficie del país (Rzedowski 1978). Estas selvas se caracterizan por presentar una marcada estacionalidad climática que conlleva cambios fenológicos asociados a la disponibilidad de agua, y que se traduce en diferencias en la heterogeneidad y en la disponibilidad de recursos tales como agua y alimento (MacArthur 1972; Brown y Gibson 1983; Ceballos y García 1995). El periodo de lluvias está concentrado en pocos meses del año mientras que el periodo de secas dura de tres a ocho meses, en el cual la humedad del suelo y el agua disponible disminuyen rápidamente y

cerca del 95% de las especies del dosel pierden las hojas (Rzedowski 1978, Martínez-Yrízar y Sarukhán 1990).

La Reserva de la Biósfera Chamela-Cuixmala se localiza en la porción sur del estado de Jalisco, en la costa del Pacífico mexicano (19°25'N y 105°00'W; figura 1). La vegetación predominante es selva tropical decídua o caducifolia (selva baja de aquí en adelante) y semidecídua o subcaducifolia (selva media; Rzedowski 1978; Ceballos 1989; Ceballos y García 1995). La temperatura promedio en la zona es de 24.9 °C y la precipitación media anual de 748 mm (Bullock 1986). La estación de lluvias va de julio a octubre, meses en los que se concentra aproximadamente el 80% de la precipitación total, mientras que el resto del año se caracteriza por una severa estación seca en la que la mayoría de las plantas pierden sus hojas (Bullock 1986; García-Oliva et al. 1991).

La Estación de Biología "Chamela", de la Universidad Nacional Autónoma de México, se localiza también en el sur del estado de Jalisco (19°29'N y 105°01'W), relativamente cerca de Chamela-Cuixmala (figura 1), por lo que las características climáticas y el tipo de vegetación son los mismos (Bullock 1986; García-Oliva et al. 1991).

Tabla 1. Resumen de los estudios más relevantes sobre la evaluación de la relación positiva entre niveles de heterocigosidad y componentes de adecuación en animales.

Especie	relación positiva con	Autores
Invertebrados		
Drosophila sp.	heterogeneidad ambiental metabolismo, fecundidad	McDonald & Ayala 1974; Stearns et al. 1995; Houle 1989
Anfípodos (*Gammarus* sp)	metabolismo	Patarnello & Battaglia 1992
Ostión americano (*Crassostrea virginica*)	crecimiento, metabolismo	Singh 1982; Zouros et al. 1980: Koehn & Shumway 1982
Almeja negra (*Mulina lateralis*)	crecimiento, tamaño	Garton et al. 1984
Mejillón azul (*Mytilus edulis*)	sobrevivencia, fecundidad osmoregulación	Diehl et al. 1986; Rodhouse et al. 1986
Saltamontes (*Talitrus saltator*)	conducta (orientación)	Scapini et al. 1995
Mariposa (*Colias philodice eriphyle*)	sobrevivencia, metabolismo éxito reproductivo	Watt 1979; Watt et al. 1983; Watt et al. 1986
Peces		
Bacalao (*Gadus morhua*)	sobrevivencia	Mork & Sundness 1985
Trucha arcoiris (*Salmo gairdneri*)	metabolismo, morfología	Danzmann, Ferguson & Allendorf 1987, 1988; Leary et al. 1984
Pez teleosto (*Fundulus heteroclitus*)	metabolismo, desarrollo	DiMichele & Powers 1982
Reptiles y Anfibios		
Rana manchada (*Pseudacris clarkii*)	factores de historia de vida	Whitehurst & Pierce 1991
Sapo occidental (*Bufo boreas*)	sobrevivencia, fisiología	Samollow & Soulé 1983
Salamandra tigre (*Ambystoma tigrinum*)	crecimiento, metabolismo	Pierce & Mitton 1982; Mitton et al. 1986
Aves		
Paloma (*Columba livia*)	resistencia a enfermedades	Frelinger 1972
Gorrión (*Passer domesticus*)	morfología (asimetría)	Fleischer et al. 1983

Tabla 1. Continuación...

Mamíferos		
Venado cola-blanca (*Odocoileus virginianus*)	crecimiento hembras y peso fetos, fecundidad	Cothran et al. 1983; Mitton & Grant 1984
Venado bura (*O. hemionus*)	densidad poblacional	Scribner et al. 1991
Ratón canguro (*Peromyscus polionotus*)	masa corporal, conducta, metabolismo, demografía	Garten 1976, 1977; Kaufman & Kaufman 1987; Teska et al. 1990; Smith et al. 1975; Chappell & Snyder 1984
Roedor microtino (*Microtus ochrogaster*)	ciclos poblacionales	Gaines et al. 1978
Conejo cola de algodón (*Sylvilagus floridanus*)	densidad poblacional	Scribner et al. 1983

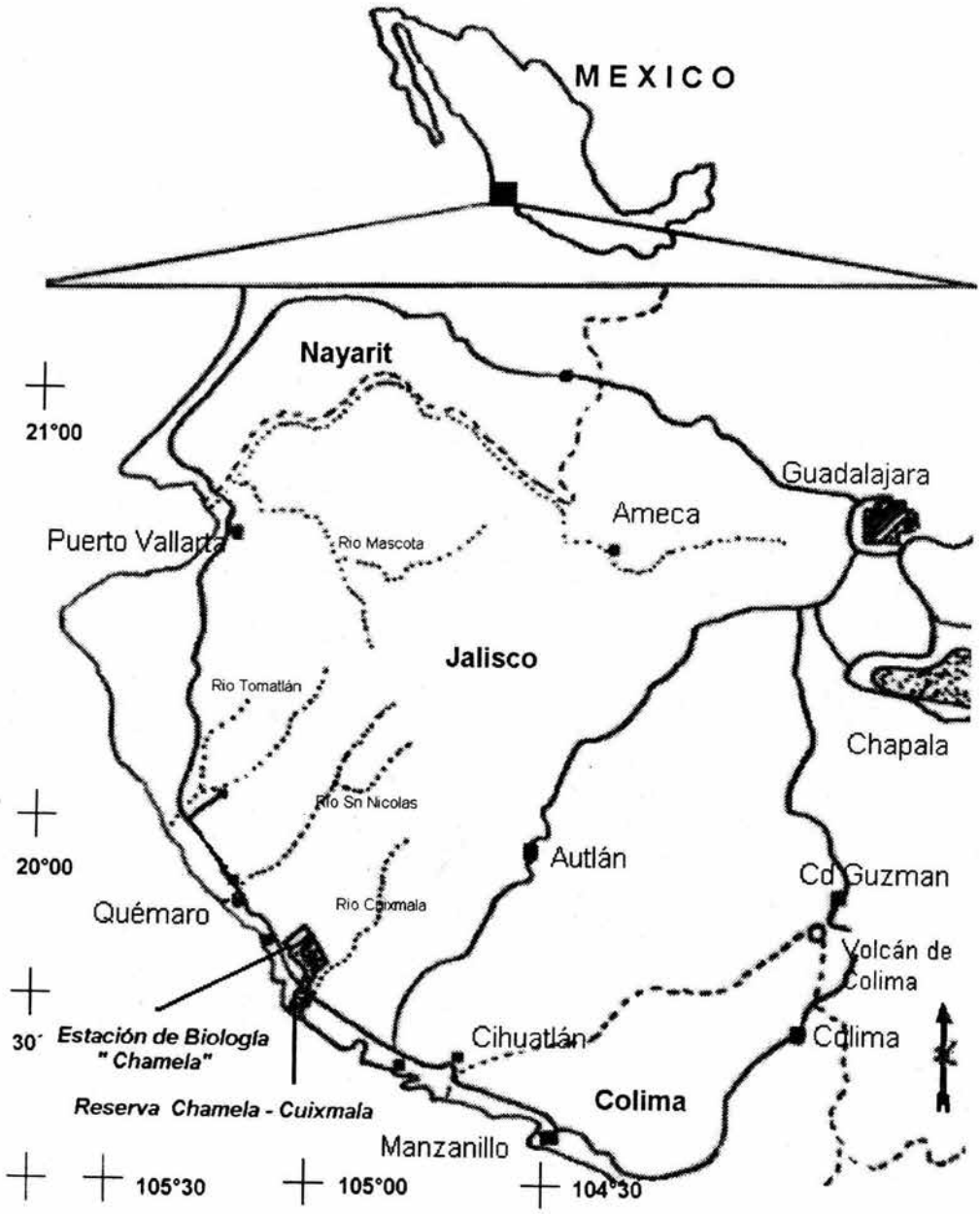

Figura 1.- Sitios de estudio. Modificado de Lott 1993.

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GENETIC VARIATION, ENVIRONMENTAL HETEROGENEITY, AND HETEROZYGOSITY OF THE RODENT *LIOMYS PICTUS*, IN DRY DECIDUOUS AND SEMIDECIDUOUS FORESTS IN WESTERN MEXICO.

GENETIC VARIATION, ENVIRONMENTAL HETEROGENEITY, AND HETEROZYGOSITY OF THE RODENT *LIOMYS PICTUS*, IN DRY DECIDUOUS AND SEMIDECIDUOUS FORESTS IN WESTERN MEXICO.

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Genetic structure of individuals of *Liomys pictus* from Chamela, Jalisco, Mexico, was analyzed. Also, the genetic variability differences between populations from two habitats of contrasting seasonality, the dry deciduous and semideciduous forests, and the relationship between individual heterozygosity and weight were investigated. Thirty presumptive gene loci were analyzed using starch-gel electrophoresis. The mean number of alleles per locus (A = 2.1), percentage of polymorphic loci (P = 73.3), and the observed heterozygosity (H = 0.089), were higher than values previously reported for this species. These results confirm that the extensive genetic variation reported for other heteromyid genera is also characteristic of *Liomys pictus* in Chamela. Populations showed significant homozygote excess which could be related to the moderately aggressive social system of *L. pictus*. Finally, individual weight, observed genotypic frequencies, and observed heterozygosity values, were not statistically different between populations of the two habitats. Weight was also not significantly correlated with heterozygosity values. This results indicate that the

hypothesis that selection favors heterozygous genotypes may not, in fact, hold generally.

Key words: heteromyid rodents, *Liomys pictus*, protein electrophoresis, heterozygosity

The influence of habitat heterogeneity (i.e., climatic seasonality and habitat complexity) as an ecological and evolutionary force has been recognized for a long time (Andrewartha and Birch 1954), and it plays a key role in processes at population, community, and ecosystem levels (Lomnicki 1980, 1987). Also, habitat heterogeneity can affect, among other things, genetic polymorphisms (Hendrick et al. 1976). Accordingly, populations are composed of individuals living in mosaics of macro- and microhabitats that influence individuals fitness and largely determine population dynamics (Lomnicki 1987).

High levels of genetic variability are usually present in natural populations (Allendorf and Leary, 1986; Mitton and Pierce, 1980; Powell, 1971; Selander, 1976). Some of this variability is maintained, to some extent, by environmental heterogeneity; some studies have shown a positive correlation between environmental diversity and genetic polymorphism (McDonald and Ayala, 1974; Powell, 1971; Riddle at al., 1983, Smith, et al., 1975), although this relationship is not always present (Ayala and Valentine, 1974; Ayala, et al., 1975).

It has been amply observed that, in general, components of fitness such as growth rate, body size, physiological

efficiency, and fecundity increase with genetic variability (measured as individual heterozygosity; Mitton, 1993 and references therein). These associations may be enhanced in fluctuating environments, likely because the advantages that the more heterozygous individuals exhibit tend to increase with environmental heterogeneity (Koehn et al. 1980; Mitton and Grant, 1984). For example, genetic variation was higher in populations of *Drosophila willistoni* and *D. pseudoobscura* maintained in heterogeneous environments than in populations in more constant environments (Powell, 1971; McDonald and Ayala, 1974).

Particularly, a positive and significant relationship between heterozygosity and either body size or weight has been found in a broad range of organisms (Allendorf and Leary; 1986, Frankel and Soulé, 1981; Mitton and Grant, 1984). However, there are few examples of this relationship in mammals. In white-tailed deer, *Odocoileus virginianus*, adult females with high levels of enzyme heterozygosity weigh more than homozygous individuals. These heavier females also had heavier fetuses and were more fertile (Cothran et al., 1983). In rodents, Garten (1976) found that mean body weight was significantly correlated to the number of heterozygous loci in the oldfield mouse, *Peromyscus polionotus*. This association was determinant of the advantages observed in the heterozygous individuals in other characteristics directly related with survival, such as competitive ability, reproduction, and behavior (Garten 1976, 1977; Mitton y Grant 1984; Kaufman y Kaufman 1987).

In Western Mexico, tropical dry forests along the Pacific coast are particularly heterogeneous and fluctuating environments. The deciduous and semideciduous forests of Chamela, Jalisco, Mexico show a strong climatic seasonality determined by the amount and pattern of temporal distribution of rainfall, which has direct effects on phenology and food availability. These forests reflect a gradient of increasing spatial structural complexity and decreasing temporal seasonality owing to the greater availability of water in the semideciduous forest (Ceballos 1989; Bullock, 1986; García-Oliva et al., 1991; Ceballos and García, 1995).

The spiny pocket mice *Liomys pictus*, an endemic species of western and southern Mexico (Ceballos and Miranda, 1986; Hall, 1981; Williams, et al., 1993), is abundant in these tropical forests and has been extensively studied in Chamela, Jalisco, Mexico (Ceballos, 1989, 1991; Collet, et al., 1975; Genoways, 1973; Rogers, 1990). These studies have shown patterns of distribution and abundance directly related to the environmental seasonality: *L. pictus* is the most abundant species in the deciduous forest where it is present throughout the dry season; density is higher at the end of the rainy season and beginning of the dry season; and reproduction and population fluctuations are strongly influenced by seasonality in food availability (Ceballos 1989, 1991; Collet et al., 1975; Mendoza, 1997; Morales and Engstrom, 1989). Because of its morphological, behavioral, and physiological characteristics, this species is able to maintain populations in the dry forest and cope with the

high environmental heterogeneity (Ceballos, 1989, 1991, 1995; French, 1993; MacMillan, 1983; McNab, 1979; Randall, 1993; Wolda, 1987).

The populations of *Liomys pictus* in Chamela, Jalisco, Mexico, provide an excellent opportunity to review the hypothesis which establishes that the degree of genetic variation in a population should be correlated with the degree of heterogeneity of its environment (McDonald and Ayala, 1974). Because of the significance of body weight in the performance of individuals in characteristics related to survival, together with our objective of evaluating the relationship between heterozygosity and heterogeneity in individuals of *Liomys pictus*, we examined the possible associations between the component of fitness -body weight- and heterozygosity at the population level, while providing detailed information about the species genetic structure, heterozygosity levels, and inbreeding.

MATERIALS AND METHODS

Field Work

Rodents were trapped at the Chamela-Cuixmala Biosphere Reserve, which is located in the southern portion of the State of Jalisco, on Mexico's west coast, at 19°25'N and 105°00'W. The vegetation is predominantly tropical deciduous forest (hereafter dry forest) and semideciduous forest (arroyo forest; Ceballos, 1989; Ceballos and García, 1995; Rzedowski, 1978). The climate is characterized by its dry-wet seasonality, with an average monthly temperature of 24.9 °C and a mean precipitation of 748 mm/year, 80% of which occurs between July and October (Bullock, 1986; García-Oliva

et al., 1991). The rest of the year is characterized by a marked dry season, when most plants shed their leaves.

Individuals of *L. pictus* were collected at dry and arroyo forests, on April and September, 1994, for a total of 52 individuals per forest. Trapping areas are approximately 5 km apart. Mice were trapped using Sherman live-traps, baited with a mixture of rolled oats, peanut butter and vanilla extract, sexed, and weighed to the nearest 0.1 g.

Genetic Variability

Blood and tissue samples of all individuals were used to assay 34 enzymes with horizontal starch-gel electrophoresis, obtaining good resolution for 19 enzymes encoding 30 presumptive loci. Stains and buffers were used as described by Pasteur et al. (1988), Selander et al. (1971), and Teska et al. (1990). Buffer systems and enzymes studied are summarized in Appendix I.

Genetic variability within populations was calculated and expressed as the mean number of alleles per locus (*A*), the percentage of polymorphic loci per population (*P*, using the 95% criterion; Nei, 1973, 1987), and the proportion of loci heterozygous per individual at each locality (*H*; Hedrick, 1983). These estimates were first calculated for each population and then for the species. A *G* test was used to evaluate differences in observed heterozygosity values between dry and arroyo forests (Sokal and Rohlf, 1981; Wayne, 1990).

Genotypic frequencies for variable loci were tested for deviation from those expected under Hardy-Weinberg equilibrium with a chi-square test, using Levene (1949)

method for small samples and Yates correction for continuity (Sokal and Rohlf, 1981). Also, allele frequency distribution between populations was analyzed with a *G* test.

To examine heterozygote proportions within and between dry and arroyo populations, Wright´s *F*-statistics (Hedrick, 1983; Wright, 1965) were calculated for all polymorphic loci. These indices are F_{IS} (within populations), F_{ST} (between populations), and F_{IT} (population as a whole). To evaluate if these indices were different from zero, a X^2 test was performed, following Hedrick (1983) and Workman and Niswander (1970) and, because with multiple comparisons the chance of an error increases, we used the Bonferroni´s approximation (α/m; Fry, 1993) to calculate a suitable significance level.

Heterozygosity and Weight

In order to avoid sex biased results, we tested if differences existed between males and females regarding number of heterozygous loci with a *G* test for contingency tables (Wayne, 1990). Each individual was assigned a heterozygosity score of 0, 1, 2, 3 ,4, 5, and ≥6 number of heterozygous loci. Next, a two-way analysis of variance was used to examine differences in weight between both dry and arroyo forests and among the heterozygosity score. A log transformation was applied to each body weight (Zar, 1984). Finally, in order to evaluate the association between heterozygosity and weight, a Spearman´s rank correlation test, which does not depend on the assumption of normality, was applied to individual weight values and heterozygosity score (Wayne, 1990).

For a more detailed test about the relationship between heterozygosity and weight, we used the approach of Zouros et al. (1980): first, the population sample was divided into five mean weight classes (<33.9, 34-38.9, 39-43.9, 44-48.9, and ≥49 g); second, the deviation in the number of heterozygotes from that expected from Hardy-Weinberg equilibrium (*D*, which is Wright´s genotypic fixation index with changed sign) and the mean heterozygosity values, within each weight class, were calculated; third, a Spearman´s rank correlation test was used to asses the relationship between mean weight class and *D* averaged across loci, and between mean weight class and mean observed heterozygosity values.

RESULTS

In the dry forest population 29 males and 23 females were collected, and 25 and 27, respectively, in the arroyo forest population. Average weight of males was 42.3 ± 5.6 and 41.2 ± 6.3 g, and of females 38.0 ± 4.8 and 38.5 ± 4.3 g, for dry and arroyo forests, respectively.

Dry and Arroyo Populations

In the electrophoretic analyses, 23 of 30 loci examined were polymorphic (Table 1). Mean number of alleles per locus and percentage of polymorphic loci were slightly higher for the dry forest, although mean heterozygosity per population was slightly higher in the arroyo forest (Table 2a). In consequence, species estimates were very similar to population estimates (Table 2b) and the observed heterozygosity values (*H*) were not significantly different between the two forests ($P > 0.05$; Table 2a).

Departure from Hardy-Weinberg expectation for the observed genotypic frequencies were significant for 20 of the polymorphic loci (Table 1; $P < 0.001$), with the exception of ME1, MPI2, and GP1, for both forests. These results agree with the observed F_{IS} and F_{IT} indices, where ME1, MPI2, and GP1 have small values (F_{IS} = -0.057, 0.060, and -0.074; F_{IT} = -0.057, 0.060, and -0.069, respectively), which are not different from zero ($P > 0.05$), whereas the remaining 20 loci showed significant positive values (mean F_{IS} = 0.724 and F_{IT} = 0.730; $P < 0.001$), indicating a homozygotes excess (Table 3).

Allele frequency distribution differed significantly between dry and arroyo forests for five loci (ACO1, G6PD1, G6PD2, LDH2, and PEPA2; Table 1), and genetic differentiation between populations for heterozygote proportions (F_{ST}) was significant for ACO1, G6PD1, G6PD2, LDH1, LDH2, PEPA2, and GP4 (30% of polymorphic loci), although mean F_{ST} = 0.023 was not significantly different from zero after Bonferroni´s correction (Table 3).

Because of the lack of significant differences in heterozygosity values between dry and arroyo populations, and in order to explore the movement of individuals between sites from a genetic point of view, we estimated the number of migrants per generation (*Nm*) through an indirect method proposed by Crow and Aoki (1984), which is the product of the effective population size and the migration rate. *Nm* results indicated that, in average, 2.6 individuals move between the two populations per generation.

Heterozygosity and Weight

Individuals were heterozygous at as many as 8 loci and the number of heterozygous loci did not differ statistically for males and females (*G* test; $P > 0.05$). The analysis of variance performed to examine differences of weight measures, indicated that individual weight was not significantly different between dry and arroyo forests (Table 4). It was also not different among heterozygosity score (i.e., among individuals with different number of heterozygous loci; Table 4).

A Spearman´s rank correlation test for the association between individual weight and heterozygosity, considering both dry and arroyo forests as a single population, was not significant ($r_s = 0.056$; $P > 0.50$). Results of this test for each dry and arroyo populations separately also showed no correlation. The association test between weight and heterozygosity was done considering both forests together as one population because of this latter result, and also because of the consistent lack of significant differences between populations with respect to the previous genetic variation and weight measures (Tables 2a, 2b, and 3).

As a final analysis of the association between genetic variability and weight, the value of *D* (deficiency of heterozygosity) was plotted against mean class weight for the 104 individuals (Fig. 1). A general trend of decreasing D with increasing weight class is observed (individuals weigh more as they have more heterozygous loci), with a positive but non-significant correlation ($r_s = 0.667$, $P = 0.223$). The results considering the observed heterozygosity

value instead of *D* were also not significant (r_s = 0.718, *P* = 0.133).

DISCUSSION

Dry and Arroyo Populations

Population numbers, species composition, and demography patterns that characterize rodent populations in Chamela are directly correlated to the fluctuating environment and seasonal patterns present (Ceballos 1989, 1991; Mendoza, 1997). Despite the fact that this characteristics would support the genetic variability-heterogeneity hypothesis, dry and arroyo populations in our study showed no significant differences for several of the variables measured, i.e., number and weight of individuals, loci for which genotypic frequencies deviated from those expected under Hardy-Weinberg equilibrium, and observed heterozygosity values.

This results could be partially explained in terms of the spatial and temporal shifts in genetic variability expected in fluctuating populations with overlapping generations, in which genetic variability changes can be responses to fluctuations in population density; this changes could conceal possible genetic differences in these populations that were sampled in a single point in time, for which more time series sampling could reveal (Charlesworth and Giesel, 1972; Smith et al., 1975).

Nevertheless, this does not necessarily indicate that no differences at all exist between forests, which more detailed researches could confirm and could also asses which factors are directly related: measuring temporal changes in

genetic variability, through repeated sampling of a population, may provide insights into associations between genetic variability measures and demographic and environmental factors such as cyclic population fluctuations (Frankel and Soulé 1981; Tamarin and Krebs 1969; Wolda 1987). Also, performing controlled laboratory experiments with which performance of individuals in the contrasting environments could be more finely measured (McDonald and Ayala, 1974; Powell, 1971; Smith, et al., 1975).

Genetic Structure of Liomys pictus

Taking into account the several caveats inherent to heterozygosity estimates from electromorphic analyses (e.g., inter- and intra-locus sampling variance and errors), the problems of different sample sizes, and numbers of and specific loci examined in different studies (Mitton, 1993; Mitton and Pierce, 1980; Nei and Roychourdhuri, 1974), we will refer to some differences found in our study with respect to previous ones.

The available information regarding genetic variability of *Liomys pictus* comes from Rogers' work (1986, 1990). He examined three populations (one from Sonora, one from Chiapas, and one from Jalisco), which summed a total of 12 individuals. Of the 30 loci he studied, two loci in the Sonoran population, and one locus in the other two populations were polymorphic (P = 0.060 and 0.030, respectively). Twelve of the proteins we examined are presented in Rogers' study (1990), out of which we found nine to be polymorphic.

Although differences in the kind of proteins scored and number of individuals studied must be considered carefully, our results indeed contrast with Rogers' findings (1986, 1990) and with those described by Patton and Rogers (1993) about biochemical genetics of heteromyids: the *H* reported for the genus *Liomys* and specifically for the species *L. pictus* (0.018, range 0.022-0.033), both are markedly lower than the values in our study. Patton and Rogers (1993) also reported that, while the average rodent species is heterozygous at between 4 and 5 percent of its allozyme loci (Nevo, 1978; Selander and Kaufman, 1973), the genus *Liomys* has about one-fourth this level ($H = 0.016$).

If we take 12 individuals at random from our study population in Chamela, the *H* index maintains its high value (0.099). This may indicate that Rogers' results (1986, 1990) for *L. pictus* could be biased since his estimates come from single populations with rather small sample sizes. The genetic analysis of a larger number of populations and individuals, comprising a wider geographical range, could enlighten this information. It might also be considered that in the populations of Sonora and Chiapas particular biological and/or historical factors, such as different environmental and demographic characteristics, could be determining low heterozygosity values (Smith et al., 1975).

Among heteromyids, *Chaetodipus* and *Microdipodops* have been considered the most genetically variable genera (Patton and Rogers, 1993). It is now evident that the reported extensive variation in heterozygosity in many species of *Chaetodipus* and *Microdipodops* also characterizes *L. pictus*

which, in Chamela, presents high heterozygosity values. This supports the highlighted necessity of more complete genetic surveys in order to have more reliable information for the species and the heteromyid family.

Heterozygosity and Weight

Male-female proportions and mean weight of individuals found in the present study are similar to those reported for the species for the last 8 years (Ceballos, 1989, Mendoza, 1997). Individual weight was not statistically different among the heterozygosity score, i.e., individuals did not weigh different depending in their number of heterozygous loci (Table 4); weight was also not correlated with heterozygosity score. These results contrast to those reported for the rodent *Peromyscus polionotus* (Garten, 1976, 1977), in which the hypothesis that increased individual heterozygosity influences morphological and physiological attributes in oldfield mice was partially supported by the positive correlation between body weight and heterozygosity, and by the influence of body weight on behavioral performance found in Garten´s work (1976, 1977).

Similarly, although the association of mean class weight with the deficiency of heterozygosity, *D*, and with the actual heterozygosity values, has proven to be a reliable approach in several studies (Frankel and Soulé, 1981; Schaal and Levin, 1976; Zouros et al., 1980), this association is not significant in our results, despite the tendency for heavier individuals to have higher *D* values (have less heterozygotes deficiency).

It is difficult to venture any hypothesis for this lack of correlation but it must be mentioned that, as Allendorf and Leary (1986) pointed out, comparing levels of heterozygosity between size (weight) classes within a natural population, and estimating this relationship at a single point in time, may be a less direct and effective method than investigating temporal changes in heterozygosity within a cohort or population. Also, body weight is not independent of environmental factors (McNab, 1979), thus it is possible that correlation results may vary if changes in weight of individuals that result from seasonal resources availability are considered, for which more time series data are needed.

Population Structure and Genetic Variability

Our results indicate that the populations of L. *pictus* studied are characterized by a higher number of homozygotes than expected by chance alone (F_{IS} and F_{IT} values; Table 3), which indicates strong inbreeding (Hartl, 1980).

Studies of *Mus* and *Peromyscus* rodents (Selander, 1970*a*, 1970*b*) have demonstrated some consequences of population structure in genetic variation: the effect of the tribal, territorial social system of *Mus* results in the clustering of similar genotypes at several loci, the subdivision of adjacent populations, and inbreeding; in *Peromyscus*, with a monogamous mating system and young not remaining in parental grounds, there is considerably less inbreeding.

In this respect, *Liomys* species show little intraspecific social tolerance and aggressive conduct in laboratory encounters (Eisenberg, 1963; Fleming, 1974;

Jones, 1993), with some evidence of social groupings among adults where both sexes share dens during nonbreeding seasons (Jones, 1993); also, reproductively active females live alone and maintain distinct home ranges (Wagner, 1961), and aggression among litter mates and their mothers has been observed in laboratory (Eisenberg, 1963). In Chamela, Mendoza (1997) reports dens where male and female individuals are found together.

Thus, *Liomys* social system may be considered in between the highly territorial system of *Mus* and the more flexible of *Peromyscus*. These characteristics will, in consequence, result in some inbreeding as that found in our *Liomys* populations, with some measurable degree of subdivision reflected in the significant differences in allele frequencies among populations (e.g., F_{ST} values indicate significant differentiation between populations in 30% of the polymorphic loci; Table 3). Similar *F*-statistics results were reported for the heteromyid rodent, *Dipodomys elator* (mean F_{IS} = 0.769 and F_{ST} = 0.102; Hamilton, et al., 1987). Species of *Dipodomys* are generally characterized by the same solitary spacing pattern, less aggression, and more social flexibility as that reported for *Liomys* (Jones, 1993).

Nevertheless, *Liomys* populations in Chamela are not as effectively isolated as those of *Mus* (Selander, 1970a). Although F_{IS} values indicate inbreeding, differentiation between populations is small and, in most of the other genetic variability measures studied, there were not statistical differences. This could be accounted for by the movement of individuals among populations; Ceballos (1989,

1991) reported that approximately 10 animals per year move between capture areas, whereas our results indicate that, from a genetic stand point, 2.6 animals per generation move between the populations studied. This suggestion is in agreement with Harrison and Hastings (1996) proposed type of patchy population -a 'metapopulation' that is not truly subdivided on the demographic time scale- in which a combination of moderate population differentiation and appreciable rates of turnover are expected.

Our results show that *Liomys pictus* has a greater genetic variation than previously reported, for which we suggest that the information on the degree of genetic variability and differentiation at the population and species level, among and within heteromyid rodents, will become more accurate as more specific studies are available. Studies that consider a larger number of individuals, populations, species, and enzymes are necessary. Also, because negative results are probably under-reported (Booth et al., 1990; Whitlock, 1993), the lack of genetic differentiation associated to environmental heterogeneity, as well as the lack of relationship between heterozygosity and fitness components found in our study, indicate that the hypothesis may not, in fact, hold generally. It is evident that further studies are needed to determine how frequently fitness differentials conform to the predictions that selection favors heterozygous genotypes, which will allow elucidation of patterns and processes of the association and the generality of the phenomenon.

ACKNOWLEDGMENTS

This study resulted from research conducted in partial fulfillment of requirements for the Ph.D. degree in the Instituto de Ecología, Universidad Nacional Autónoma de México by EV. We thank the staff of the Chamela-Cuixmala Biosphere Reserve for providing lodging, and laboratory and field work facilities. A. Gómez Poyou and his wife, Marietta Tuena, who kindly taught EV the mice bleeding technique. León Cázares and Olivia Reynoso for technical assistance with the homogenization methods and laboratory facilities, and C. Chávez and A. Flores for statistical help. L. Eguiarte and J. Golubov made helpful comments on the manuscript. Partial funding was provided by Idea Wild (thanks to Wally van Sickle support) and by the Fundación Ecológica de Cuixmala, A.C. First author´s scholarship was provided by the National Council of Science and Technology (CONACYT; registration number 86298).

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APPENDIX I

Protein loci and electrophoretic conditions for *Liomys pictus*.

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

(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.

Table 1.-- Allelic frequencies for 30 loci (abbreviations defined in Appendix I) and *G* test for differences in allele frequency distributions, in populations of *Liomys pictus* from dry and arroyo forests in Chamela, Jalisco, Mexico.

locus	allele	dry	arroyo	*G*	locus	allele	dry	arroyo	*G*
ACO1	1	0.362	0.673	9.75**	LAP1	1	0.688	0.750	0.483
	2	0.638	0.327			2	0.313	0.250	
ACP1	1	1.000	1.000		LDH1	1	0.729	0.519	4.95
AK1	1	0.981	1.000	0.863		2	0.250	0.462	
	2	0.019	0.000			3	0.021	0.019	
AAT1	1	0.683	0.567	1.418	LDH2	1	0.347	0.596	6.35*
	2	0.317	0.433			2	0.653	0.404	
ES1	1	0.224	0.250	0.091	MDH1	1	1.000	1.000	
	2	0.776	0.750		MNR1	1	0.538	0.470	3.757
ES2	1	0.857	0.856	0.032		2	0.462	0.470	
	2	0.143	0.144			3	0.000	0.060	
ES3	1	0.365	0.340	0.095	MNR2	1	0.462	0.385	1.437
	2	0.510	0.520			2	0.529	0.577	
	3	0.125	0.140			3	0.010	0.038	
GLD1	1	0.404	0.452	2.251	ME1	1	0.950	0.942	0.029
	2	0.577	0.529			2	0.050	0.058	
	3	0.019	0.019		MPI1	1	0.061	0.019	1.215
GP1	1	0.490	0.558	0.467		2	0.939	0.981	
	2	0.510	0.442		MPI2	1	0.929	0.923	0.097

Table 1.-- Continued...

GP2	1	1.000	1.000			2	0.071	0.077	
GP3	1	1.000	1.000		PEPA1	1	0.538	0.587	0.289
GP4	1	0.347	0.353	5.20		2	0.442	0.413	
	2	0.459	0.588			3	0.019	0.000	
	3	0.194	0.059		PEPA2	1	0.288	0.644	16.8***
G3PDH1	1	0.561	0.686	0.249		2	0.567	0.356	
	2	0.418	0.314			3	0.144	0.000	
	3	0.020	0.000		PEPB1	1	1.000	0.990	0.309
GPI1	1	0.357	0.337	0.012		2	0.000	0.010	
	2	0.643	0.663		PER1	1	0.635	0.596	0.163
G6PD1	1	0.667	0.471	6.98**		2	0.365	0.404	
	2	0.333	0.529		6PGD1	1	1.000	1.000	
G6PD2	1	0.438	0.240	4.38*					
	2	0.563	0.760						

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Table 2.-- Genetic variation in 30 loci for individuals of *Liomys pictus* (standard errors shown in parentheses) in Chamela, Jalisco, Mexico; a) dry (DF) and arroyo (AF) populations, b) total. Abbrevations are explained in text.

	ind/locus[a]	*A*	*P*	*Ho* [b]	*He* (H-W) [c]
a) populations					
DF	50.0	2.1	76.7	0.085	0.328
	(0.3)	(0.1)		(0.021)	(0.040)
AF	51.7	2.0	73.3	0.094	0.320
	(0.1)	(0.1)		(0.022)	(0.040)
b) total					
	101.6	2.1	73.3	0.089	0.331
	(0.3)	(0.1)		(0.021)	(0.041)

[a] mean number of individuals per locus

[b] observed heterozygosity

[c] expected heterozygosity, unbiased estimate (see Nei, 1978)

Table 3--. Summary of F-statistics at polymorphic loci for *Liomys pictus* in Chamela, Jalisco, Mexico.

locus	F_{IS}	F_{IT}	F_{ST}
AAT1	0.917***	0.918***	0.014
ACO1	0.650***	0.684***	0.097***
ES1	0.449***	0.449***	0.001
ES2	0.472***	0.472***	0
ES3	0.456***	0.456***	0
GLD1	0.766***	0.770***	0.014
GP1	-0.074	-0.069	0.005
GP4	0.982***	0.983***	0.015**
G3PDH1	0.792***	0.793***	0.002
GPI1	0.956***	0.956***	0
G6PD1	0.828***	0.835***	0.039**
G6PD2	0.933***	0.936***	0.043**
LAP1	1.000***	1.000***	0.005
LDH1	1.000***	1.000***	0.046***
LDH2	1.000***	1.000***	0.062***
ME1	-0.057	-0.057	0
MNR1	0.756***	0.757***	0.004
MNR2	0.887***	0.888***	0.004
MPI1	0.213*	0.222*	0.011
MPI2	0.060	0.060	0
PEPA1	0.596***	0.596***	0.002
PEPA2	0.814***	0.830***	0.085***
PER1	0.674***	0.675***	0.002
Mean[a]	0.724***	0.730***	0.023

[a] Bonferroni's correction applied (Fry, 1993)

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Table 4.-- Two-way analysis of variance of body weight in *Liomys pictus* for dry and arroyo forests in Chamela, Jalisco, Mexico.

Source of variation	*d.f.*	*SS*	*MS*	*F*	*P*
forest	1	0.0015	0.0015	0.0832	0.773
heterozygosity score[a]	6	0.1023	0.0170	0.9222	0.483
forest x heterozygosity score	6	0.1651	0.0275	1.4894	0.191
residual	90	1.6637	0.0185		
total	103	1.9056	0.0185		

[a] 0, 1, 2, 3, 4, 5, and > 6 number of heterozygous loci

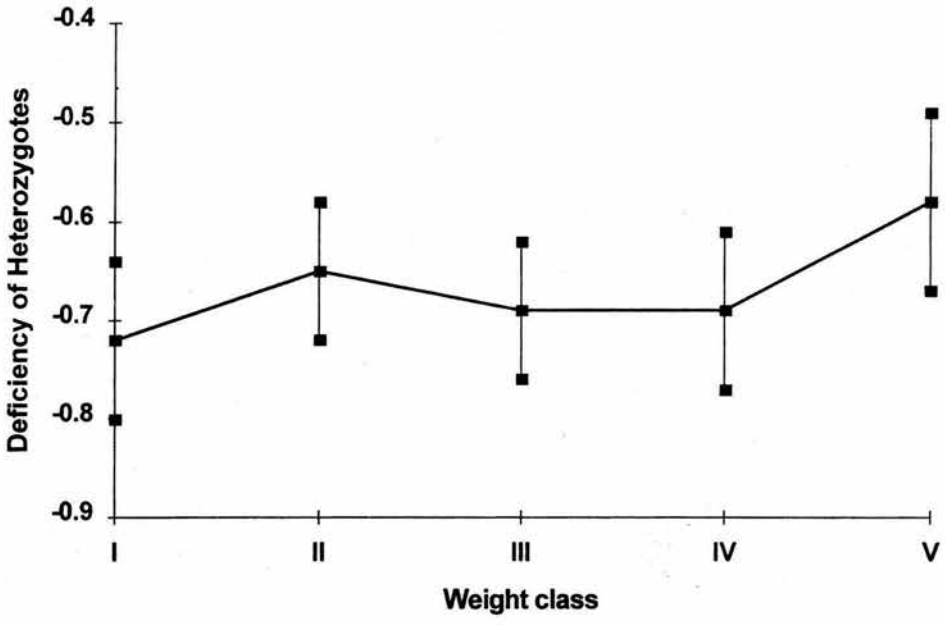

Figure 1. Mean *D* values (Zouros et al. 1980) over polymorphic loci plotted against weight class, in *Liomys pictus* from Chamela, Jalisco, Mexico. Weight classes: I (0-33.9), II (34-38.9), III (39-43.9), IV (44-48.9), and V (49g-).

3

HETEROZYGOSITY PATTERNS AND ITS RELATION WITH FITNESS COMPONENTS IN EXPERIMENTAL POPULATIONS OF *LIOMYS PICTUS* FROM TROPICAL FORESTS IN WESTERN MEXICO.

HETEROZYGOSITY PATTERNS AND ITS RELATION WITH FITNESS COMPONENTS IN EXPERIMENTAL POPULATIONS OF *LIOMYS PICTUS* FROM TROPICAL FORESTS IN WESTERN MEXICO.

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Abstract

We investigated the relationship between individual heterozygosity and the utilisation 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 heterozygosity levels, and mean body weight was used as a direct measure of the individuals´ performance under food and water stressful conditions. *L. pictus* individuals subjected to a sequentially decreasing food treatment showed high feeding efficiency: their ratio of food absorbed/food consumed was almost one. The association between food utilisation and heterozygosity was not statistically significant, despite the trend observed that the more heterozygous individuals maintained their weight better during the food treatment. Water utilisation was positively associated with heterozygosity levels: when deprived from water, the more heterozygous individuals lost less weight than the less heterozygous ones. The ability of the more heterozygous individuals for better water and

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energy conservation may contribute to their adaptation to the extreme seasonality of the Chamela forests.

Key words: Heterozygosity; fitness components; *Liomys pictus*; allozymes.

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 (Koehn and Shumway, 1982; Pierce and Mitton, 1982; Cothran et al., 1983; Teska et al., 1990; Mitton, 1993), although there are important exceptions (McAndrew, et al., 1982; Houle, 1989; Booth, et al., 1990; Whitlock, 1993).

Variables related to metabolic processes such as body size, body weight, growth, energy storage, oxygen consumption, and reproduction have been found to be strong correlates of fitness in vertebrates (Mitton and Grant, 1984; Allendorf and Leary, 1986; Mitton et al., 1986; 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 and Kaufman, 1987).

It has been hypothesised 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 and Grant, 1984). Also, that heterozygosity broadens the range of physiological tolerance and function relative to homozygosity (Samollow and Soulé, 1983). Accordingly, in experimental conditions more heterozygous individuals maintained weight better than the less heterozygous, when exposed to stressful conditions regarding temperatures in the American oyster, *Crassostrea virginica* (Rodhouse and Gaffney, 1984). Oldfield mice, *Peromyscus polionotus*, that were more heterozygous utilised food and maintained body weight under varying degrees of dietary stress better than their less genetically variable 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 specialised behavioural, morphological, and physiological characteristics in their adaptive radiation to colonise 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;

Genoways and Brown, 1993; Randall, 1993). Also, these organisms often assimilate over 90% of the food ingested, minimising the amount of undigested material and associated water that is passed through the body (French 1976, 1993; Withers, 1982).

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), adaptations which may affect characters influenced by metabolic processes and secondary productivity, and thus, overall fitness.

The spiny pocket mice *Liomys pictus*, an endemic heteromyid species of western and southern Mexico (Ceballos and Miranda, 1986; Hall, 1981; Williams, et al., 1993), is present in the tropical dry deciduous and semideciduous forests of Chamela, Jalisco, Mexico (Ceballos, 1989; Genoways, 1973; Rogers, 1990). Although *L. pictus* shares the habitat with several other rodent species, it is the dominant species in the deciduous forest, specially 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, characterised by periods of food scarcity and long droughts, food utilisation and water conservation capacities are of primary importance for individual survival (Fleming, 1977; Ceballos, 1989), which, in turn, may be important determinants of fitness.

Hence, the main objective of our study was to examine the hypothesis of greater advantage of the heterozygotes

during stress than during optimal environmental conditions. For this, we evaluated the relationship between individual isozyme heterozygosity levels and the utilisation of food and conservation of water, under varying degrees of stress, in experimental populations of *Liomys pictus* from Chamela, Jalisco, Mexico.

Materials 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 West coast (19°25'N and 105°00'W). The site is characterised 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 presents a severe dry season, when most plants shed their leaves (Bullock, 1986; García-Oliva et al., 1991). The vegetation is predominantly tropical deciduous forest (hereafter dry forest) and semideciduous forest (arroyo forest; Rzedowski, 1978; Ceballos, 1989).

A total of 52 individuals of *L. pictus* were trapped with Sherman live-traps on each the dry and arroyo forests, on April and September, 1994. Trapping areas were approximately 5 km apart. Mice were 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 in 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 two-week acclimation period, each mouse was sequentially fed with diets of three quantities: high, medium, and low, which corresponded to 100, 50, and 25% of the reference value, respectively. Each diet was fed to the rodents for a six-day treatment period, and water was given *ad libitum* Teska et al., 1990). We measured the individuals´ initial body weight at the start of each period, and its weight change and amount of food eaten and feces produced, midway and at the end of each six-day period. The change in the animals' weight was considered a measure of their performance under stress. Feces produced and seeds not consumed of every individual 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 and food consumed.

Water treatment

The animals in the water experiment had no food restriction, but had no water available. Body weight changes were measured every two 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

weight increment was measured every two 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 enzymes with horizontal starch-gel electrophoresis, obtaining good resolution for 19 enzymes 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 enzymes studied are: 1) Tris maleate, pH 7.4, 100 mA, 15 h: glucose-6-phosphate dehydrogenase, 1.1.1.49 (G6PDH1, G6PDH2), 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, GP2, GP3, GP4), 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); 4) Tris-Citrate, pH 8.0, 120 V, 7 h: acid phosphatase, 3.1.3.2 (ACP), aspartate aminotransferase, 2.6.1.1 (AAT), glutamate dehydrogenase, 1.4.1.2 (GLD), glycerophosphate-3-dehydrogenase, 1.1.1.8 (G3PDH), peroxidase, 1.11.1.7 (PER); 5) Lithium, pH 8.0, 100 V, 7 h: esterase, 3.1.1.1 (ES3), menadione reductase, 1.6.99.2 (MNR1, MNR2); 6) Tris-Citrate,

pH 6.3, 120 V, 5 h: aconitase, 4.2.1.3 (ACO), adelinate kinase, 2.7.4.3 (AK).

Of the 30 loci examined, 23 were polymorphic with a mean number of alleles per locus of 2.0 and 2.1, and a mean 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 et al., in prep.). 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 and more. Because heterozygosity levels 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 and more). Because the statistical analyses did not differ between both groupings and in order to have even groups for comparisons, our results are given considering only two categories.

Statistical Analyses

First, differences between dry and arroyo populations in relation to individuals´ initial body weight, for each food and water treatments, were tested by means of a *t*-test (Zar, 1984). Next, in order to avoid sex biased results, we

tested for differences between males and females regarding the number of heterozygous loci (heterozygosity category) with a *G* test (Wayne, 1990).

Finally, to evaluate if the individuals' ability to maintain body weight was related to their heterozygosity, we analysed the data from the food and water treatments with a covariance analysis, considering a design with repeated measures. 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 six-day period, was used as a covariate, and the heterozygosity category as a classification variable. Also, post-hoc comparisons were performed with a Tukey test with unequal replication (Zar, 1984; Tabachnick and 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; also, the same covariate and classification variable were used.

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 g ± 7.4 and 40.9 g ± 5.6, respectively; Fig. 1). Body weight decreased during the dietary experiment for all mice, reaching values of 38.8 g ±

5.1 and 37.0 g ± 5.3, in dry and arroyo populations, respectively (Fig. 1).

Mice were heterozygous at as many as 8 loci and the number of heterozygous loci did not differ statistically between males and females (G test; $P > 0.05$). Thus, covariance analyses were performed with both female and male individuals together. Considering the body weights recorded for each individual within each dietary experiment (each six-day period), least square means were computed for the two heterozygosity categories (Figs. 2a and b).

In both the dry and arroyo forest populations, mice within the high 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 weight, low and high heterozygosity categories respectively; thus, the observable pattern is that the more heterozygous individuals lost less weight (Fig. 2a, b).

Results from the covariance analysis for the dietary treatment showed that variation in body weight was not statistically different between dry and arroyo forests (Tab. 1). In this analysis, food quantity was a highly significant source of variation; nevertheless, contrary to what might be expected from the patterns observed, heterozygosity category and the interaction for population and heterozygosity category were not significant (Tab. 1). Although, if we consider 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 high quantity diet. This suggests that individuals in the two heterozygosity categories 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 than the more homozygous (Figs. 2a and b).

Percentage of feeding efficiency was markedly high for dry and arroyo populations (Tab. 2). Covariance analyses for feeding efficiency were similar to the food treatment results in both populations: dietary quantity (treatment) was a highly significant variable ($P < 0.001$), while heterozygosity category and their interaction were not.

Water Treatment

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

As weight change is partitioned among the two heterozygosity categories, some patterns can be appreciated (Figs. 3 and 4): individuals from the dry forest within the low and high categories lost closely the same percentage of their initial body weight. For the recovery period, the tendency is a greater weight recovery rate in more heterozygous individuals; this is, mice within the high

heterozygosity category recovered a greater percentage (99%) of their lost weight than those in the low category (87%; Figs. 3a and 4a). In the arroyo population, weight lost is also similar in the two heterozygosity categories; however, individuals in the high category recovered less weight (86%) than those in the low category (95%; Figs. 3b and 4b).

The covariance analysis showed significant differences between dry and arroyo populations for individuals' weight lost during the 12-day with no water available (Tab. 4). Individuals from the arroyo population lost, on average, less weight than those from the dry population (Fig. 4); the former individuals within the high heterozygosity category also showed the least weight loss for both populations (Figs. 3 and 4). Likewise, the interaction for population and heterozygosity category was significant for weight lost (Tab. 4), further indicating that individuals with different heterozygosity levels, in each population, performed significantly different. Finally, results for the recovery period were not statistically significant for differences between populations nor for the different variable interactions (Tab. 4).

Discussion

Heterozygosity and food utilisation

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, 1980; French, 1993).

Under such environmental conditions, food as a limiting factor has been documented for many heteromyid species, including *Liomys pictus* (Ceballos, 1989; Brown and Harney, 1993; Mendoza, 1997), and also for not heteromyid species living in seasonal environments (*Peromyscus polionotus*; Smith, 1971). Likewise, feeding efficiency has been found to be positively correlated with heterozygosity in *P. polionotus* (Teska et al., 1990), in which more heterozygous mice utilise food and maintain body weight better (assimilate food more efficiently) than more homozygous individuals, when experimentally stressed by limited availability of food.

In the present study, the association between food utilisation and heterozygosity levels 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. Nevertheless, and taking into account that post-hoc comparisons consider statistically less degrees of freedom, these comparisons indicated 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 that the traits under consideration might not be affected by the loci studied (Mitton and Pierce 1980; Booth et al., 1990), we think these considerations do not explain the present results because 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). Also, in many studies that report a positive relationship, virtually all loci analysed, regardless of function, appear to contribute to the trend (McAndrew et al., 1982, and references therein); finally, as Johnson (1978) emphasised, 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 utilising of energy), such as food utilisation.

In a study with *Tribolium castaneum* (Riddle et al., 1983), the authors found dietary effects on some, but not all, of the fitness components examined. Probably, if we had examined different fitness correlates such as survival, fecundity, or developmental time, we might have observed a more direct association. Also, the negative results could be related to an inadequate experimental protocol of dietary stress, which did not induce a physiological response dependant of the level of heterozygosity in individuals.

It must also be considered that several studies have reported a positive association at some loci but not at

others (Koehn et al., 1988; Pemberton, et al., 1988), so analyses based on multilocus heterozygosity such as ours may miss some single-locus effects. Nevertheless, it has also been suggested that overall heterozygosity may be more important than specific alleles or multiple alleles in affecting individuals fitness (Smith et al., 1975).

Although feeding efficiency was not statistically associated with heterozygosity, it is important to mention that *L. pictus* showed rather high values of efficiency: their average feeding efficiency was from 95 to 97% for all three dietary quantities. This is, they absorbed almost one hundred percent of the food they consumed. Efficient utilisation of food has been detected to be a determinant factor during unfavourable times when food declines in quality and abundance (Teska et al., 1990), and could had masked the effects of the dietary stress.

Heterozygosity and water metabolisation

Water conservation (metabolization) was an important source of variation, as shown by the results of weight lost, in which differences between populations as well as the interaction of population and heterozygosity category were statistically significant. These results are consistent with the trend that weight loss in the two populations were affected differently by the heterozygosity levels, in which individuals with a low number of heterozygous loci lost more weight than those with more heterozygous loci.

The fact that recovered weight results were not statistically significant might indicate that, although individuals with 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 as an association with their heterozygosity levels. This could also be related with the different trends seen for the dry and arroyo populations; in the former, individuals in the high category recovered more weight than those in the low category, while in the latter the individuals that recovered less weight were those in the high category.

The significant differences found between dry and arroyo populations 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), so certain amount of food and water (free water in the food and metabolic water) are available all the year round, in contrast with the dry forest where food and water are scarce during drought months. Thus, 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.

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). Other example is *L. salvini* from Nicaragua, which can live for at least 24 days in the absence of water and lose 17% of its weight (Hudson and Rummel, 1966). In the present study, *L. pictus* lasted 12 days and lost nearly 3% of its initial weight per day (31-34% in total). As other heteromyid species, it is able to survive on a dry diet because it has enhanced physiological and behaviouràl abilities to reduce losses when water stressed (Hinds and MacMillen, 1985; French, 1993) and thus, cope with a severe reduction in water ingestion as expected from the fact that, in the wild, it experiences a seven-month dry season (Bullock, 1986; García-Oliva, et al., 1991).

It has been suggested that the rigors of unpredictable environmental conditions that vary in time, space and severity, are precisely the sort of inconstancy against which heterozygotes, by virtue of their predicted greater physiological flexibility, would be superiorly buffered (Samollow and Soulé, 1993). The magnitude of energy and water turnover in heteromyids and the degree in which they rely on the water produced during oxidative metabolism are related to the harshness of the environment (French, 1993); these adaptations should have correspondence with energy availability (metabolism and secondary productivity) which, in turn, are important in determining fitness (Mitton and Grant, 1984). Our results support the prediction that, under stressful conditions, *Liomys pictus* individuals that are genetically more variable conserve (metabolise) water better

than their less variable counterparts. This characteristic should contribute to the ability of the better adapted individuals to maintain abundant populations in the physically severe, unpredictably semiarid dry and arroyo forests of Chamela, Jalisco, Mexico.

There is much to be understood about the relationship between genetic variability and population structure in natural populations of this species. In the light of the present results, the relationship between heterozygosity patterns and fitness components in *Liomys pictus* from Chamela is not appreciated when mice are decreasingly deprived of food, probably because of their high feeding efficiency; nevertheless, this association is clearly seen when they are water stressed, as the more heterozygous individuals maintain weight better than the less heterozygous ones. Hence, *L. pictus* individuals with higher heterozygosity levels, and corresponding capabilities for better water and energy conservation, may have greater physiological flexibility for dealing with the seasonal environmental conditions of its habitat.

Acknowledgements

We thank the staff of the Chamela-Cuixmala Biosphere Reserve and the Fundación Ecológica de Cuixmala, A.C. for providing lodging, and laboratory and field work facilities. C. Chávez and A. Flores for statistical help. L. Eguiarte made helpful comments on the manuscript. First author´s scholarship was provided by the National Council of Science and Technology (CONACYT; registration number 86298), and this study resulted in partial fulfilment of requirements

for her Ph.D. degree in the Instituto de Ecologia, Universidad Nacional Autónoma de México.

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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 six-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 Materials and methods)

Table 2. Feeding efficiency percentages in each high, medium, and low food quantity diets 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.

Population/food quantity	Heterozygosity category	
	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

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

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	0.984
Pop*Hcat*Time	5	0.3	0.5	0.762	4.6	2.4	0.049

[a] Time refers to weight measured every two-day during the 12-day treatment for weight lost, and the 10-day recovery period (repeated measures)

[b] and [c] Abbreviations as in Table 1

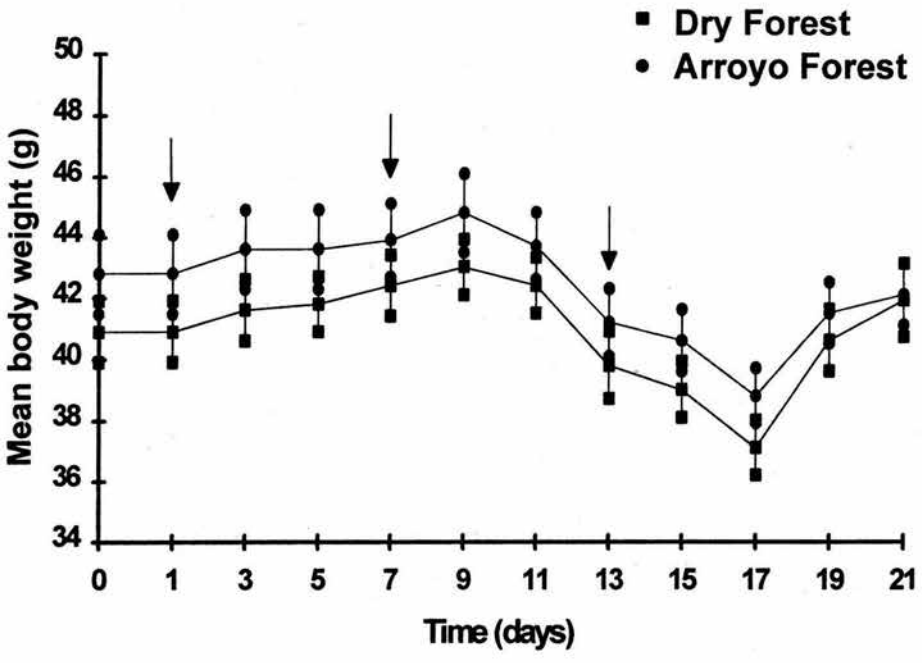

Figure 1. Mean body weight change during the decreasing food treatment for the experimental populations of *Liomys pictus* from Chamela, Jalisco, Mexico. Commencement of high, medium and low food quantity periods are indicated by arrows. The bars above and below each value represent one standard error.

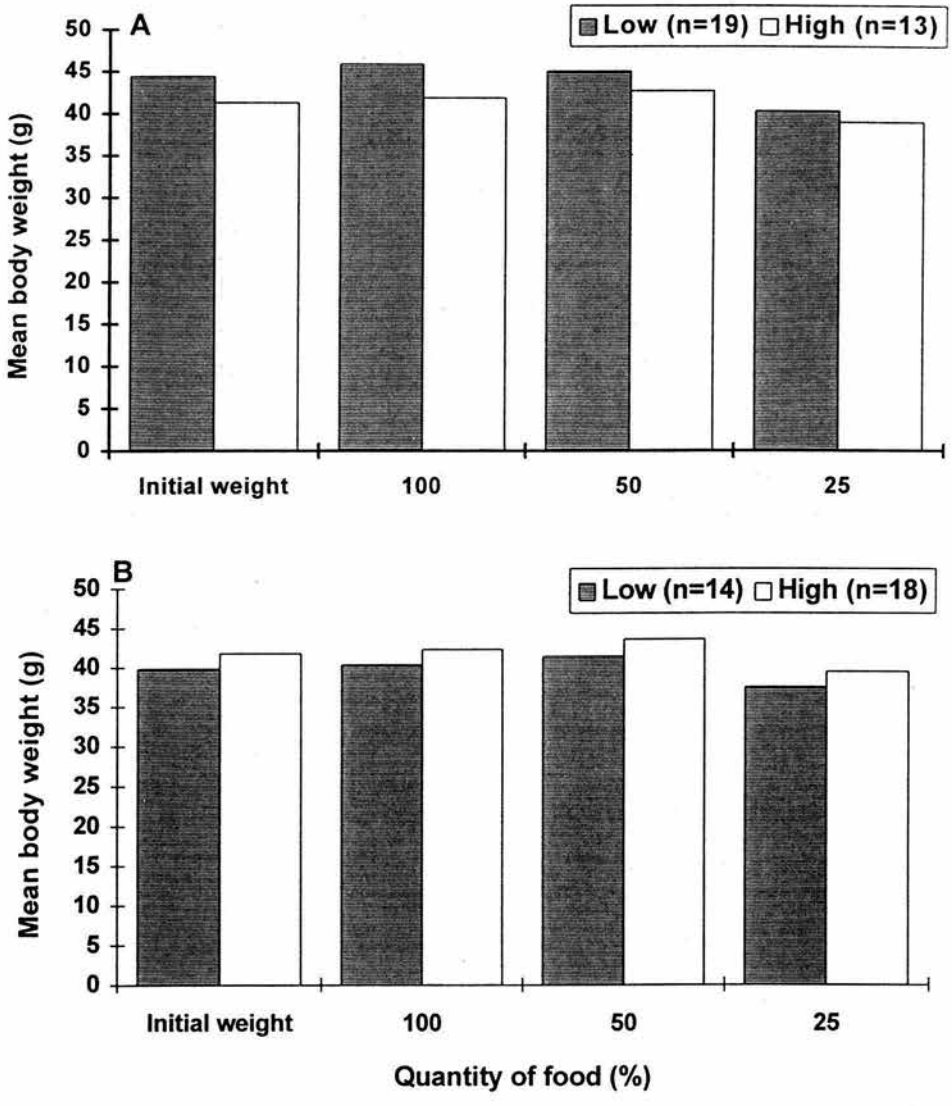

Figure 2. Least square means for initial body weight and weignt change in each high, medium, and low food quantity periods, for *Liomys pictus* in (A) dry forest and (B) arroyo forest experimental populations from Chamela, Jalisco, Mexico. Low (0 to 2 heterozygous loci) and high (3 or more) heterozygosity 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 0.7-1.5g).

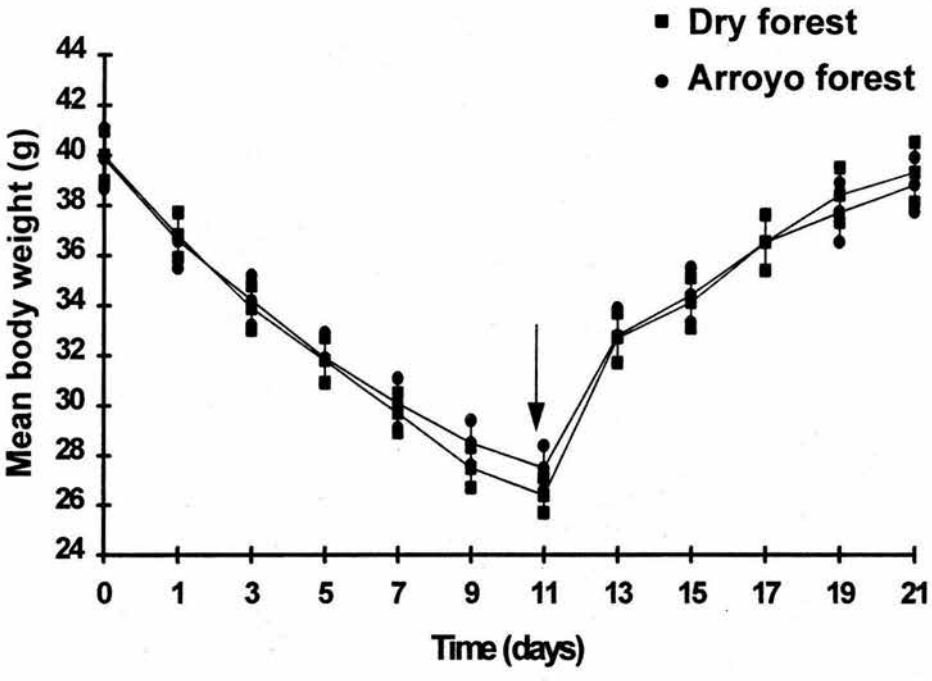

Figure 3. Mean body weight change during the water deprivation treatment for the experimental populations of *Liomys pictus* from Chamela, Jalisco, Mexico. The arrow indicates the recovery period starting point. The bars above and below each value represent one standard error.

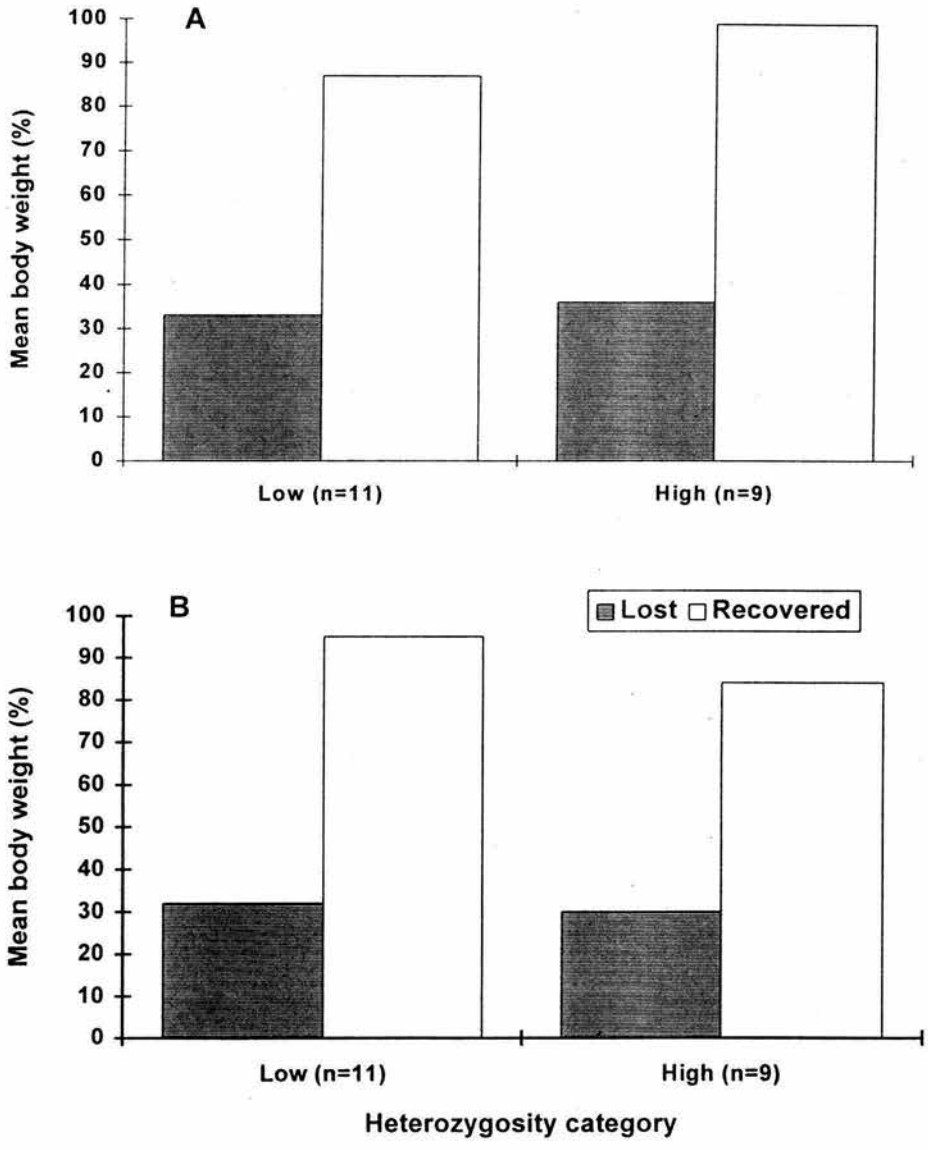

Figure 4. Percentage of weight lost and weight recovered during the water deprivation treatment, for individuals of *Liomys pictus* in (A) dry forest and (B) arroyo forest experimental populations from Chamela, Jalisco, Mexico. Heterozygosity categories refer to: low (0 to 2 heterozygous loci) and high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

4

LINKING HETEROZYGOSITY, DEMOGRAPHY, AND FITNESS COMPONENTS: EVIDENCE FROM SEASONAL TROPICAL FOREST POPULATIONS OF THE RODENT *LIOMYS PICTUS*

LINKING HETEROZYGOSITY, DEMOGRAPHY, AND FITNESS COMPONENTS: EVIDENCE FROM SEASONAL TROPICAL POPULATIONS OF THE RODENT *LIOMYS PICTUS*

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Abstract.-- We studied the relationship between heterozygosity and spatial and temporal changes in population density, and between heterozygosity and body weight, in four populations of the spiny pocket mice, *Liomys pictus*, from tropical dry forests in Chamela, Jalisco, Mexico. *L. pictus* individuals experience profound population fluctuations mainly due to the strong environmental seasonality of their habitat. Eighteen presumptive gene loci were assayed using starch-gel electrophoresis to estimate heterozygosity levels, and mean body weight was analyzed as a fitness-correlated character. Observed mean heterozygosity values were markedly high (H = range from 0.188 to 0.198), whereas populations showed a significant deficiency of heterozygotes (D = from -0.377 to -0.312). Changes in number of individuals and number of heterozygous loci were found to be associated with different phases of the yearly population cycle of *L. pictus*: during the increasing phase, persistence of individuals was higher and mean heterozygosity values declined probably due to inbreeding. During the declining period when food and water were scarce, heterozygosity increased and adult individuals, which showed overall less

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deficiency of heterozygotes, were those significantly more abundant. Also, mean number of heterozygous loci and body weight showed a positive and significant correlation. These results agreed with the hypothesis that changes in genetic variability may be effects of demographic changes, and that, consequently, traits associated with survival could show correlations with genic heterozygosity.

Key words.-- Heterozygosity, population density, Heteromyid rodents, *Liomys pictus*, allozymes.

Genetic attributes of natural populations may diverge as a result of factors such as differential selection, demographic variation, or dispersal, among others (Soulé 1976; Lacy 1987; Scribner et al. 1991). To assess which factors are particularly related with demography, repeated sampling of a population may provide insights into associations between genetic variability measures and cyclic population fluctuations (Tamarin and Krebs 1969; Frankel and Soulé 1981; Wolda 1987), dispersal (Krebs and Myers 1974; Smith et al. 1975; Scribner et al. 1983), reproductive performance (Smith et al. 1975), and other demographic variables, considering the environmental factors associated (Charlesworth and Giesel 1972; Wooten and Smith 1984).

Behavioral, morphological, and physiological traits might show correlations with genic heterozygosity whenever these characters directly or indirectly affect an individual´s probability of survival (Smith et al. 1975; Dear et al. 1992; Mitton 1993). Particularly, in studies

with small mammals, a positive and significant relationship has been found between heterozygosity and such features like 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). For an ample review see Frankel and Soulé (1981), Allendorf and Leary (1986), and Mitton (1993).

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

Studies that have considered seasonal and non-seasonal fluctuations in population density in mammals, their changes in genetic variability, and the relationship between these genetic changes with demographic parameters and with components of fitness, have provided further insights into these particular associations. Significant changes in allelic frequencies, genotypic proportions, and heterozygosity, have been related to changes in population numbers in microtine rodents (Gaines and Krebs 1971; Gaines et al. 1978), in the oldfield mice *Peromyscus polionotus* (Smith et al. 1975), eastern cottontail rabbit (Scribner et

al. 1983), white-tailed deer (Chesser et al. 1982; Scribner et al. 1985), and mule deer (Scribner et al. 1991). These studies showed a positive and significant correlation between genetic variability and density; moreover, fitness-correlated characters were used to explain these associations, in which the more heterozygous individuals showed a significant advantage regarding survival, reproduction, body weight, and growth rates (Gaines and Krebs 1971; Smith et al. 1975; Gaines et al. 1978).

Local populations of the spiny pocket mice, *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 largely food limited, thus density fluctuations and persistence of individuals are directly associated with temporal variation in productivity (Ceballos 1989; Brown and Harney 1993; French 1993; Mendoza 1997). Population density typically increases during the favorable periods of high food supply following the rainy season and then decline during the eight-month dry season.

The populations of *Liomys pictus* in Chamela, Jalisco, Mexico, provide an excellent opportunity to review the associations between demographic parameters and genetic variability. Hence, our objective was to evaluate, through a 14-month study of four populations of *L. pictus*, the hypothesis that changes of individual heterozygosity levels

could be a direct response to fluctuations in population numbers. The concomitant hypothesis that traits associated with survival should show correlations with genetic variability was also tested by examining the relationship between mean body weight and heterozygosity.

MATERIALS AND METHODS

The study was conducted in the Chamela Biological Station (National Autonomous University of Mexico), located on the Pacific coast of Mexico, in the southern portion of the State of Jalisco (19°29'N and 105°01'W). The dominant vegetation types are tropical deciduous forest (hereafter dry forest) and semideciduous forest (arroyo forest; Rzedowski 1978; Lott et al. 1987; Ceballos and García 1995). The climate is characterized by its dry-wet seasonality, with an average monthly temperature of 24.9 °C and a mean precipitation of 748 mm/year, 80% of which is concentrated between July and 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 and DRY2) and two in the arroyo forest (WET1, WET2), all of which were approximately 5 km apart. Sixty-four Sherman live-traps, baited with a mixture of rolled oats, peanut butter and vanilla extract, were set in each plot, 8 m apart in a 8 x 8 grid arrangement. Traps were checked on a bimonthly schedule, three consecutive nights during the new moon, for 14 months from November 1994 to January 1996. Upon first capture, mice were sexed, marked by toe-clipping, and individual 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 weight to the nearest 0.1 g of each individual were recorded in each capture.

Electrophoretic techniques

Horizontal starch-gel electrophoresis was carried out following the methods, stains, and buffers as described by Selander et al. (1971), Pasteur et al. (1988), and Teska et al. (1990). We assayed 26 enzymes and obtained good resolution for 12, encoding 19 presumptive loci. Buffer systems employed and enzymes studied are: 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).

Genetic variability within populations was calculated and expressed as the mean number of alleles per locus ($\bar{A}$), the percentage of loci polymorphic per population (P, using the 95% criterion; Nei, 1973, 1987), and the proportion of loci heterozygous per individual at each locality (H; Hedrick, 1983). The average fixation index (F; Hedrick 1983) was also calculated for each grid.

Statistical analyses

The number of heterozygous loci was the genetic variability (heterozygosity) measure used for all analyses and comparisons. Firstly, differences in number of heterozygous loci among grids and between sexes were analyzed with a Two-way Anova (Zar 1984; Tabachnick and Fidell 1989). To further explore genetic structure differences among individuals, mice were grouped in two age classes according to their specific body weight and which represented the extremes: juveniles ≤35g and adults ≥45g (Ceballos, 1989), which is an indirect method to asses age. 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).

In order to evaluate the patterns of weight of individuals at capture, differences in initial body weight among the four grids, between males and females, and among the number of heterozygous loci per individual, were examined with an analysis of variance (Sokal and Rohlf 1981). Also, in order to ascertain if an association between heterozygosity and body weight existed, a Pearson correlation coefficient test was applied to individual weight values and number of heterozygous loci (Sokal and Rohlf 1981).

Population densities were calculated by the direct enumeration method, which estimates the minimum number of individuals known to be alive and gives a reliable estimate of population size if the probability of capture for an average individual is above 50%, avoiding unrealistic

assumptions implicit in capture-recapture methods (Krebs 1966; Gaines et al. 1978). Differences in average population densities within forests were examined with a *t*-test (Zar 1984). Temporal (bimonthly) and spatial (within and between dry and arroyo forests) changes in population densities were compared by an analysis of variance (Sokal and Rohlf 1981).

To test if the demographic and genetic variables were related, the relationship between changes in mean number of heterozygous loci and density fluctuations during the 14-month period was investigated by calculating correlation coefficients between these two variables. In order to have another measure of how genetic structure varies along the fluctuating density periods, we used a heterozygotes deficiency index. We compared the number of observed (*Ho*) and expected heterozygotes (*He*) using the relationship $D = (Ho - He)/He$ (Selander 1970; Zouros et al. 1980), in which a positive or negative value of D indicates an excess or deficiency of heterozygotes, respectively; the average D value over the study was correlated with density (Gaines et al. 1978).

Another feature directly related to the population dynamics of *L. pictus* is persistence (Ceballos 1989; Mendoza 1997). Thus, we also calculated a persistence measure defined as the percentage of individuals from a single cohort that persist in the sampling site; excluded from this estimation are individuals captured only once or in the last trapping month (Ostfeld et al. 1985; Ceballos 1989). To estimate a percentage of persistence

for each grid, we divided the number of individuals that persisted 1, 2, 3, up to 6 months by the total number of individuals trapped in each grid, and examined percentage differences among grids and among trapping months with an Anova on Ranks test (Zar 1984). Finally, we estimated correlation coefficients to evaluate the relationship between persistence (considering number of trapping periods that each individual persisted in each grid) and their number of heterozygous loci.

RESULTS

A total of 179 individuals of *Liomys pictus* were trapped during the eight bimonthly 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

Genetic structure analyses showed few differences among grids and individuals. Out of the 19 loci studied, all but one (ME) were polymorphic in all grids, one (MDH) in DRY1 and WET1 grids, and one (LDH2) in WET2 (table 2). The DRY2 grid showed a higher percentage of polymorphic loci than the other three grids, and the highest observed heterozygosity value was found in the WET2 grid (table 3). No statistical differences were found in observed heterozygosity values among grids (Anova on Ranks, $P > 0.05$; Wayne 1990). Average fixation (F) values were all positive, indicating a deficiency of heterozygotes within each grid (table 3).

Mice were heterozygous at as many as 10 loci and the number of heterozygous loci did not differ statistically between males and females (F = 0.337, df 1; P = 0.562), nor among grids (F = 0.319, df 3; P = 0.811). However, when mice were grouped in age classes, genetic differences between juvenile and adult individuals were statistically significant (F = 4.107, df 1; P = 0.045), in which adults showed consistently higher mean number of heterozygous loci, irrespective of grid.

Heterozygosity and weight

Individual initial body weight did not differ among grids but it was significantly different between sexes (males wre heavier than females) and among individuals with different number of heterozygous loci (in average, those with more heterozygous loci weighed more; see below). The interaction for grid and number of heterozygous loci was significant, which may indicate that, although individual weight alone is not different among dry and arroyo forests, it differs among grids when considering weights of mice with different number of heterozygous loci (table 4).

Because of the lack of differences between trapping grids within forests in relation to number of heterozygous loci, grids were considered together as one set of data. With this, individual initial body weight and number of heterozygous loci showed a positive and significant correlation (r = 0.223, $P < 0.01$; fig. 1), further indicating that individuals weigh more as they have more heterozygous loci. This result agreed with the analysis of

age classes in which adult individuals, defined indirectly based on body weight, have more heterozygous loci.

Population density

Average population densities in grids DRY1 and DRY2 (20 and 20 individuals/ha, respectively), as well as in grids WET1 and WET2 (18 and 14 inds/ha), were not statistically different; neither were mean densities different when considering both grids together for each forest (20 and 16 inds/ha, dry and arroyo populations respectively). The average percentage of recapture of mice known to be alive during the study varied between 76 and 89% in the four grids, well above the 50% required for using the direct enumeration method for calculating density. Temporal changes in density during the eight trapping periods showed similar patterns in the four grids (fig. 2): an initial peak density in January 1995 followed by a decline in all grids by the end of the dry season (May-June), which continued throughout the rainy season (July-September), with a recovery period towards the middle of the next dry season (January 1996).

Anova results for differences in density fluctuations among grids were not significant ($P > 0.05$). Therefore, the four grids were considered together and results showed significant differences among trapping periods ($F = 8.230$, df 7; $P < 0.001$): the peak density observed in January 1995 was significantly different in relation to all other bimonthly trapping periods; also, months with the lowest density (May-July-September 1995) were different with respect to the increasing (November 1994 and November 1995-January 1996) and peak periods (fig. 2).

Changes in the mean number of heterozygous loci during the populations cycles were also evaluated with an Anova analysis, and results were similar to those for density fluctuations (fig. 3): in relation to trapping periods, statistical differences were observed for the low density months in relation to the recovery months (November 1995-January 1996), but not to the peak density phase (January 1995).

The analysis of the association between number of heterozygous loci and density for each dry and arroyo populations over the study showed a positive, non-significant trend (r = 0.344, P = 0.192; r = 0.294, P = 0.269, dry and arroyo forest populations respectively). Thus, considering the four grids together, we grouped the increasing, peak, and decreasing density periods separately and calculated how average density and mean number of heterozygous loci changed among them. Results showed a consistent pattern: the lowest mean number of heterozygous loci was observed in the increasing period and the highest during the decreasing 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, inds/ha, respectively (fig. 4a). The mean number of heterozygous loci was significantly different between the increasing and decreasing periods (t test; $P < 0.01$).

Moreover, both dry and arroyo populations showed a marked deficiency of heterozygotes (mean D = -0.377 and -0.312, respectively) and, for both forests considered together, the average D value was negatively correlated with

density (r = -0.399, P = 0.024). This indicates that, as population density increases, there is a greater deficiency of heterozygotes compared to the expected number based on Hardy-Weinberg equilibrium. We also evaluated the adult-juvenile changes in the deficiency of heterozygotes and found significant smaller values (less deficiency) in adults (average D = -0.338) than in juveniles (-0.514; Mann-Whitney test, P = 0.027).

Persistence

Most individuals persisted few months, whereas only a small percentage persisted more than 5 months (Anova; $P < 0.05$; fig. 5), while no differences among grids were found (Anova; $P > 0.05$). The correlation between the individuals´ persistence and their number of heterozygous loci was also not statistically significant. For consistency with the density analyses, we also grouped the increasing, peak, and decreasing density periods for the four grids together, and calculated the number of heterozygous loci of the individuals that persisted in each phase of the cycle. Results are also similar to those of density: the lowest mean number of heterozygous loci was observed in the increasing period and the highest during the decreasing one (3.5 and 4.4, respectively), while the peak period showed an intermediate value (3.9; fig. 4b). Mean number of individuals that persisted were 17.2, 11.7 and 14.3, increasing, decreasing and peak phases respectively (fig. 4b).

DISCUSSION

Genetic variability

Many species that have large, sexually reproducing, cross-fertilizing populations, carry large amounts of genetic variability (Allendorf and Leary 1986; Carson 1990). Utilization of electrophoretic analyses in comparative studies within and between species has been extremely useful in the study of genetic diversity in natural populations (e.g., Selander 1976; Nevo 1978; Mitton 1993; Leberg 1996).

In the present study we explored several questions through the study of four populations of *Liomys pictus*, in Chamela, Jalisco, Mexico. Firstly, how is the genetic structure of this species? Mean observed heterozygosity values in these populations were markedly high (range 0.188-0.198) comparatively to previous studies on this species (Rogers 1986, 1990; Patton and Rogers 1993), and also to a recent study of two *L. pictus* populations from an ecologically similar habitat (i.e., also in dry and arroyo forests, some 20 km apart from the present study sites). In the latter, in which 30 loci from tissue and blood samples of 104 individuals were analyzed, a mean observed heterozygosity value of 0.089 was observed (Vázquez et al. in prep. *a*). For a better comparison, we reanalyzed the data in that study considering the same 19 blood enzymes used in the present work, and mean heterozygosity maintained a similar value (H = 0.097).

Thus, taking into account the caveats inherent to heterozygosity estimates from electromorphic analyses (e.g., inter- and intra-locus sampling variance and errors; Nei and Roychourdhuri 1974; Lewontin 1985), we found different heterozygosity values in ecologically similar populations,

with different proportions of young and adult individuals, studied one year apart. Nevertheless, expected heterozygosity values were similar in both cases (0.331 and 0.333, total mean values, previous and present studies respectively).

Heterozygosity can be changed in a natural population in various ways: the number of polymorphic loci, number of alleles, and allele frequencies determine heterozygosity values (Ayala 1976; Nevo 1978); however, all these parameters were very similar in the populations from both studies. Temporal, spatial, or biological subdivision of the populations also have an effect on heterozygosity (Smith et al. 1975; Soulé 1976; Harrison and Hastings 1996); also, age structure and gene frequencies are intimately related, thus a change in one may lead to a change in the other (Endler 1992).

The marked fluctuations in population numbers in these *L. pictus* populations may result in a high rate of population turnover and young-adult age structure fluctuations, as well as in the cumulative recruitment of offspring that differ in genotypic composition from their parents. All the above may enhance the potential for short-term changes in genetic composition (Harrison and Hastings 1996). Likewise, dispersion and social structure may be important factors that result in genetic differences even over short distances and time intervals (Scribner et al. 1991; Harrison and Hastings 1996). Indeed, social structure and dispersal have been shown to be determinants of the

genetic composition in populations of *Liomys pictus* from Chamela, Jalisco, Mexico (Vázquez et al. in prep. a).

Heterozygosity and weight

Is the relationship between the fitness-correlated character (weight at first capture) positively associated with heterozygosity levels? Our results support the predictions of the hypothesis: we found a positive and significant correlation indicating that individuals weigh more as they have more heterozygous loci.

Interestingly, another difference between the previous study of *L. pictus* mentioned above (Vázquez et al. in prep. a) and the present one is that, in the former, the correlation between heterozygosity and initial body weight was consistently nonsignificant. The lack of consistency in these results may best be accounted for by the way we evaluated the relationship in both studies. This is, as Allendorf and Leary (1986) pointed out, comparing levels of heterozygosity and individuals´ body weight within a natural population and estimating this relationship at a single point in time, although it has been used succesfully (Mitton and Grant 1984), can be a less direct and effective method than investigating temporal changes in heterozygosity within a cohort or population.

Accordingly, in the present study the information about body weight and genetic variability of individuals was gathered during a 14-month period, in contrast with the previous study in which only two sampling events were carried out. This allowed the sampling of more individuals in the adult weight-range (female = 38.2 and 40.2 g; male =

41.8 and 48.9 g mean body weight, previous and present studies respectively).

Is heterozygosity associated with age? It has been reported that heterozygosity increases from younger to older ages (Allendorf and Leary 1986; Mitton 1993). Our results agree with the above because we found that adult individuals have a higher number of heterozygous loci, i.e., higher genetic variation, than juveniles; we also found less deficiency of heterozygotes in adults than in juveniles. Hence, it was observed that the more heterozygous individuals weigh more, a pattern, in turn, related to the fact that adults have a higher number of heterozygous loci and overall less deficiency of heterozygotes, all of which is also related to density parameters as it can be appreciated in our results.

In the oldfield mice *Peromyscus polionotus*, body weight was positively correlated with heterozygosity and was important in determining the response of other characteristics such as social dominance, competitive ability, reproduction, and exploratory behavior (Garten 1976, 1977; Kaufman and Kaufman, 1987). Thus, we suggest that the superiority of the genetically more variable individuals may convey advantages to *L. pictus*, which were not directly measured in the present study. This could be tested for in future studies.

Heterozygosity and population density

How are heterozygosity levels associated to demographic parameters in *L. pictus*? Our results support the hypothesis of Charlesworth and Giesel (1972) in that genetic

equilibrium is apparently dependent upon demographic characteristics, and also with Scribner et al. (1983) who stated that fluctuations in population age structure due to characteristics which may be nonspecific with respect to genotype (e.g., changes in mortality or fecundity), can result in significant changes in genetic variability.

We observed fluctuating density patterns and temporal changes in heterozygosity to be significantly related, in both dry and arroyo populations. This is, the decreasing density months (May-July-September 1995) are significantly different with respect to the increasing periods (November 1995-January 1996), concerning changes in population numbers as well as number of heterozygous loci.

Furthermore, our results indicate that the mean number of heterozygous loci declined during the increasing period of the density cycle and increased during the declining phase. Also, as population density increases, a greater deficiency of heterozygotes is observed. These significant changes in heterozygosity agree with studies of population cycles and genetic changes in several species of small mammals, which have shown that during the early parts of the increasing phase, when densities are low, mice do not disperse and observed heterozygosity declines due to inbreeding (*Peromyscus polionotus*, Briese and Smith 1974); in the peak phase, dispersal occurs and the population becomes more outbred and, during the declining phase, heterozygosity increases probably due to selection pressures against the relatively homozygous animals and superior fitness of heterozygous individuals (*Peromyscus polionotus*,

Smith et al. 1975; *Microtus pennsylvanicus*, Krebs et al. 1973; *Sylvilagus floridanus*, Scribner et al. 1983).

In addition, the results regarding persistence agree with the above in the sense that, during the increasing phase when it has been suggested that individuals do not disperse, we found the highest number of individuals that persisted in the study area, as well as lower heterozygosity values. During the declining phase, which encompassed the dry season months and food supply was scarce, less individuals persisted and heterozygosity values increased.

In the light of our results, the lack of significant correlations between heterozygosity and both density and persistence might indicate that, in order to have a more reliable view of the relationship between demographic and genetic parameters, studies must not consider correlation tests as the only sources of exploration. This is supported by the density, persistence, and genetic variability patterns found in the present study, and their particular and significative changes observed among the different phases of the population cycles.

Liomys pictus in Chamela, Jalisco experiences drastic fluctuations in population numbers mainly due to the strong environmental seasonality of its habitat, characterized by severe droughts and long periods of food scarcity (Ceballos 1989, 1991; Mendoza 1997); this population structure and declining fluctuations suggest events of inbreeding. Likewise, our previous (Vázquez et al. in prep. *a*) and present results indicate that the populations of *L. pictus* studied are characterized by a significant deficiency of

heterozygotes, which indicates strong inbreeding (Hartl, 1980). Also, although the populations studied are moderately spatially structured (i.e., they show low population differentiation; average F_{ST} = 0.023, Vázquez et al. in prep. *a*), and it has been stated that inbreeding is enhanced by spatial structuring, it can occur in its absence and increase proportions of homozygotes within groups or populations (Scribner et al. 1991). The fact that in the present results adult individuals have a significant higher number of heterozygous loci and a smaller deficiency of heterozygotes, also supports the pattern that the heterozygosity increase during the declining phase is probably due to the superior fitness of the more heterozygous individuals (Smith 1971; Krebs et al. 1973; Briese and Smith 1974; Scribner et al. 1983).

Smith et al. (1975) suggested that changes in heterozygosity could be a mechanism linking demography and genetics in small mammal populations. Evidence for this comes from studies of heterosis and the correlation between heterozygosity and characteristics of individuals and populations. In such cases, behavioral, morphological, and physiological traits associated with survival have shown correlations with genic heterozygosity. The studies we have been conducting represent the first evidence of the above that have been observed in a tropical species from a seasonal environment.

First, changes in number of heterozygous loci accompany fluctuations (increasing and decreasing phases) in population numbers, in which the most genetically variable

individuals are present in the declining periods. It is important to notice that these results represent a one year survey, thus, it will be worth to follow these populations for several years and to explore if these results hold constant. Second, the apparent superior fitness of heterozygous individuals is supported by the significant correlations found between heterozygosity and morphological and physiological traits: in the present study, body weight was positively associated with heterozygosity; similarly, water metabolization was also correlated with heterozygosity in a previous study, in which we observed that the more heterozygous *L. pictus* individuals had a better ability for water and energy conservation (Vázquez et al. in prep. *b*). Our results are consistent with the hypothesis that changes in genetic variability measures can be related to demographic changes (Charlesworth and Giesel 1972) and that genetic composition of fluctuating populations is continually changing (Gaines et al. 1978).

ACKNOWLEDGMENTS

We thank the staff of the Chamela Biology Reserve for providing lodging, and laboratory and field work facilities. We are particularly grateful to A. Mendoza for her invaluable assistance and company in the field. L. Eguiarte, K. Oyama, L. Medrano, J.C. Morales and R. Medellín made helpful comments on the manuscript. This study resulted from research conducted in partial fulfillment of requirements for the Ph.D. degree in the Instituto de Ecología, Universidad Nacional Autónoma de México by EV, for whom

scholarship was provided by the National Council of Science and Technology (CONACYT; registration number 86298).

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Table 1.-- Total number of female and male individuals of *Liomys pictus* trapped in two dry forest (DRY1 and DRY2) and two arroyo forest grids (WET1 and WET2), during eight bimonthly trapping periods in Chamela, Jalisco, Mexico. Mean weight and mean number of heterozygous loci are indicated for each sex (standard error in parenthesis).

	number of individuals		mean body weight			mean number of heterozygous loci	
grid	f[a]	m[b]	f	m		f	m
DRY1	26	18	39.0	47.9	***	3.5	3.4
			(6.9)	(6.9)		(0.3)	(0.5)
DRY2	27	25	42.9	47.4		3.4	3.8
			(6.8)	(10.0)		(0.4)	(0.5)
WET1	26	20	39.3	49.5	***	4.0	3.0
			(6.8)	(11.7)		(0.3)	(0.4)
WET2	18	19	39.2	51.5	***	3.8	3.9
			(6.1)	(8.2)		(0.4)	(0.4)

[a] females and [b] males

*** *t*-test, $P < 0.001$

Table 2.-- Allelic frequencies for 19 loci (abbreviations defined in Appendix I) in populations of *Liomys pictus* from dry and arroyo forests in Chamela, Jalisco, Mexico. Sample sizes are in parenthesis.

		grid			
		DRY1	DRY2	WET1	WET2
locus	allele	(44)	(52)	(46)	(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

Table 2.-- Continued...

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

Table 3.-- Genetic variation in 19 loci for individuals of *Liomys pictus* from Chamela, Jalisco, Mexico (standard errors in parenthesis). Sites: dry (DRY1 and DRY2) and arroyo (WET1 and WET2) grids. Abbreviations are explained in text.

	indv/locus[a]	*A*	*P*	*Ho*	*He* (H-W)[b]	*F*[c]
sites						
DRY1	43.2	2.1	89.5	0.183	0.338	0.429
	(0.3)	(0.1)		(0.032)	(0.038)	(0.074)
DRY2	51.5	2.1	94.7	0.192	0.328	0.389
	(0.2)	(0.1)		(0.025)	(0.037)	(0.054)
total	94.6	2.1	94.7	0.188	0.339	0.429
	(0.4)	(0.1)		(0.026)	(0.036)	(0.051)
WET1	45.7	2.1	89.5	0.191	0.314	0.370
	(0.1)	(0.1)		(0.029)	(0.039)	(0.056)
WET2	36.4	2.1	89.5	0.207	0.332	0.329
	(0.1)	(0.1)		(0.031)	(0.041)	(0.068)
total	82.1	2.1	94.7	0.198	0.327	0.350
	(0.3)	(0.1)		(0.029)	(0.039)	(0.043)

[a] mean number of individuals per locus

[b] unbiased estimate (see Nei, 1978)

[c] fixation index

Table 4.-- Analysis of variance of initial body weight in populations of *Liomys pictus*, in Chamela, Jalisco, Mexico.

Source of variation	*d.f.*	*SS*	*MS*	*F*	*P*
grid[a]	3	156.67	52.2	0.92	0.434
sex[b]	2	3395.3	3395.3	59.74	0.000
# of loci[c]	10	1484.6	148.5	2.6194	0.007
grid-sex	3	511.4	170.5	3.0	0.034
grid-# loci	20	2036.5	101.8	1.79	0.029
sex-# loci	9	400.58	44.5	0.78	0.632
grid-sex-# loci	18	1181.3	65.6	1.15	0.311
residual	114	6479.0	56.8		
total	178	15645.5	87.9		

[a] grid refers to dry and arroyo forest trapping grids

[b] male and female individuals

[c] number of heterozygous loci per individual

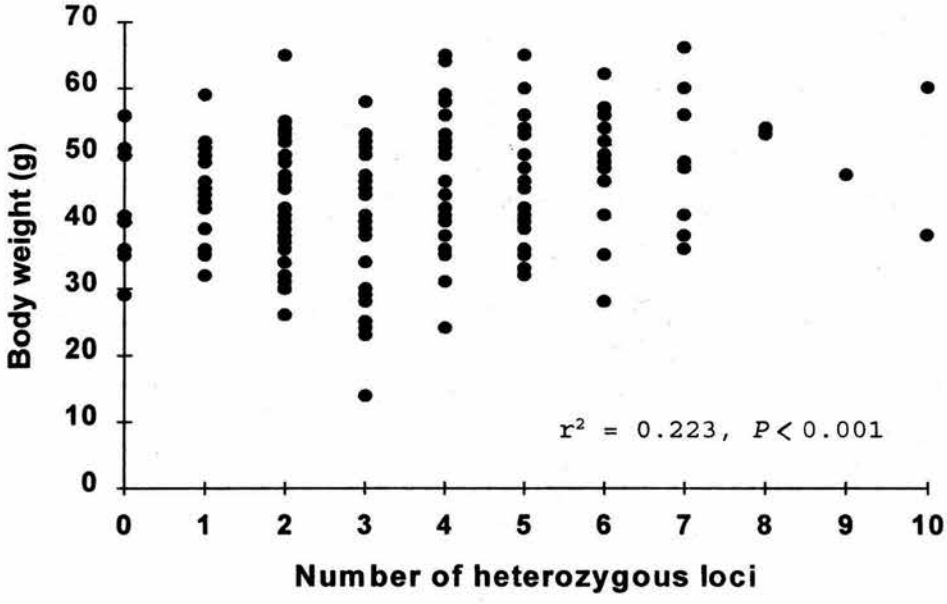

Figure 1. Correlation between individual number of heterozygous loci and initial body weight in individuals of *Liomys pictus* from Chamela, Jalisco, Mexico (n = 179).

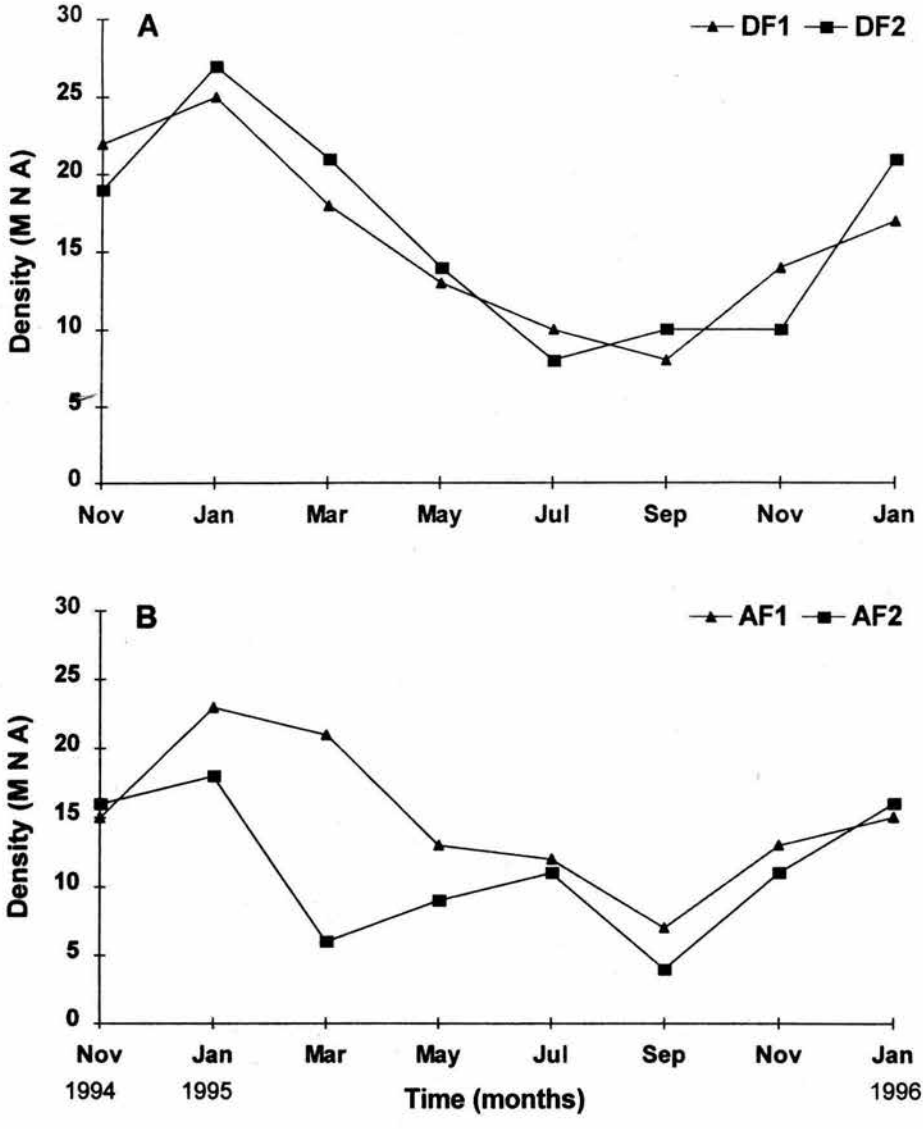

Figure 2. Changes in population density (MNA: minimum number of individuals known to be alive) of *Liomys pictus* in (A) dry and (B) arroyo forest grids from Chamela, Jalisco, Mexico, from November 1994 to January 1996.

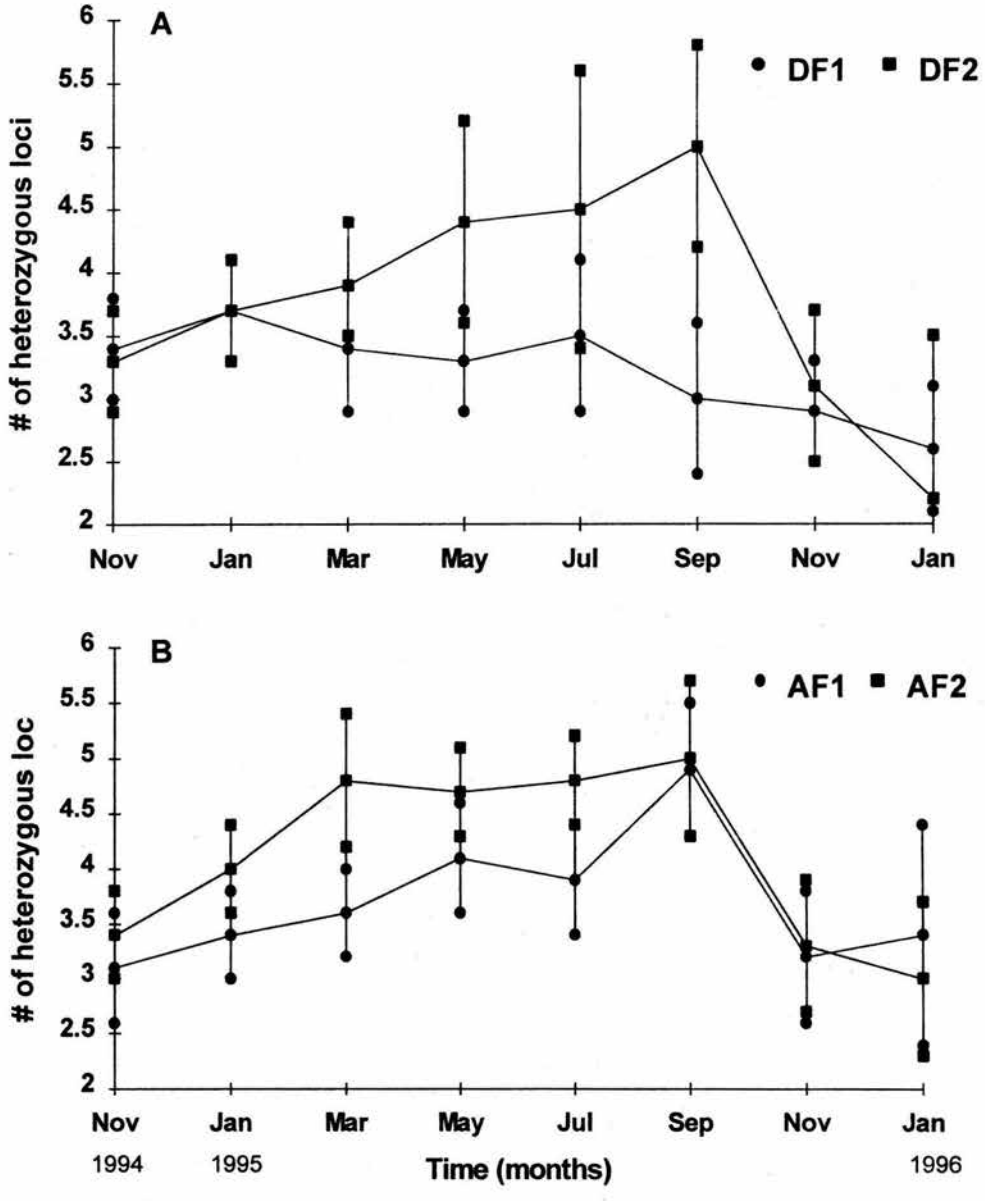

Figure 3. Changes in mean number of heterozygous loci of individuals of *Liomys pictus* in (A) dry and (B) arròyo forest grids, from Chamela, Jalisco, Mexico, from November 1994 to January 1996. The bars above and below each value represent one standard error.

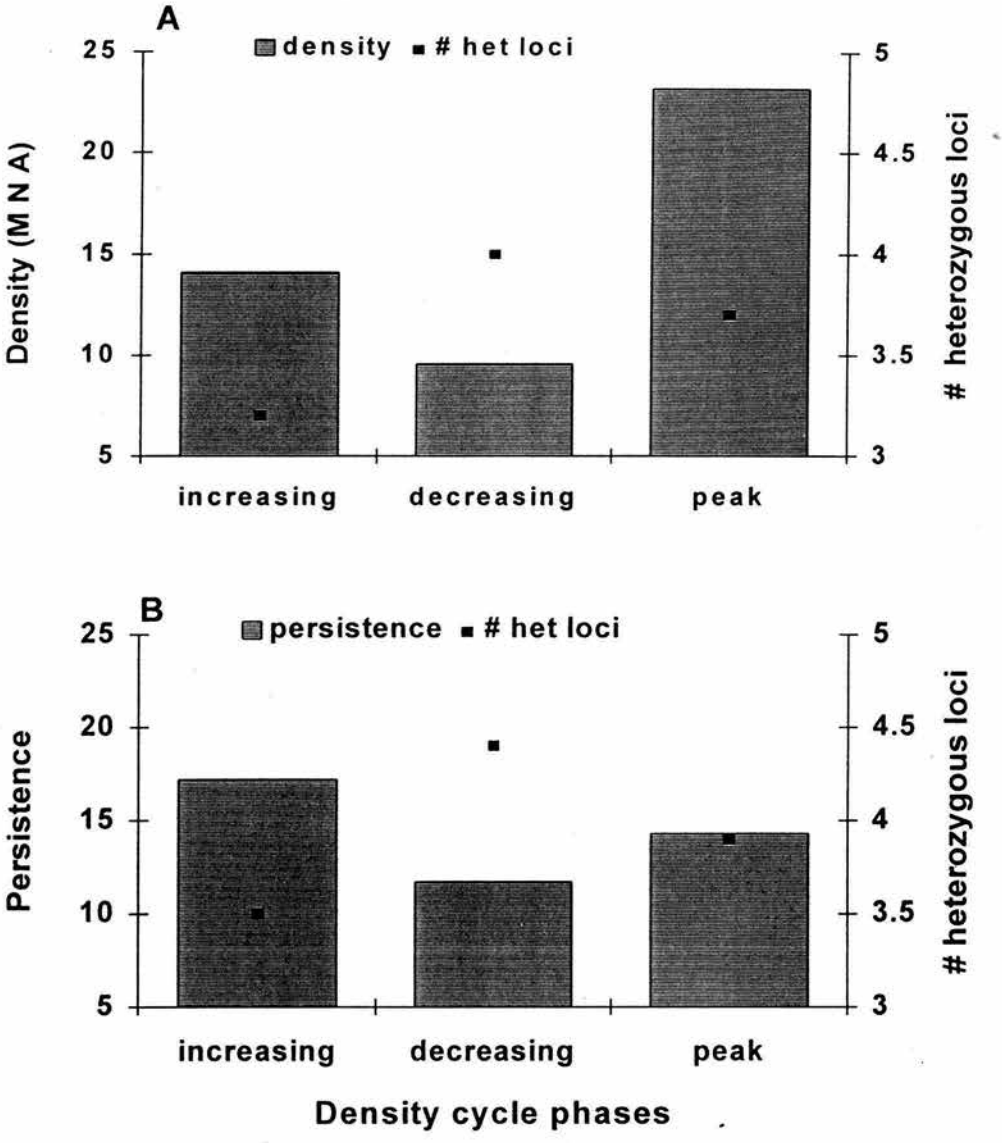

Figure 4. (A) Population density (MNA: minimum number of individuals known to be alive) and (B) number of individuals that persisted in the study grids, during the increasing, decreasing, and peak phases of the fluctuating population cycles of *Liomys pictus* from Chamela, Jalisco, Mexico.

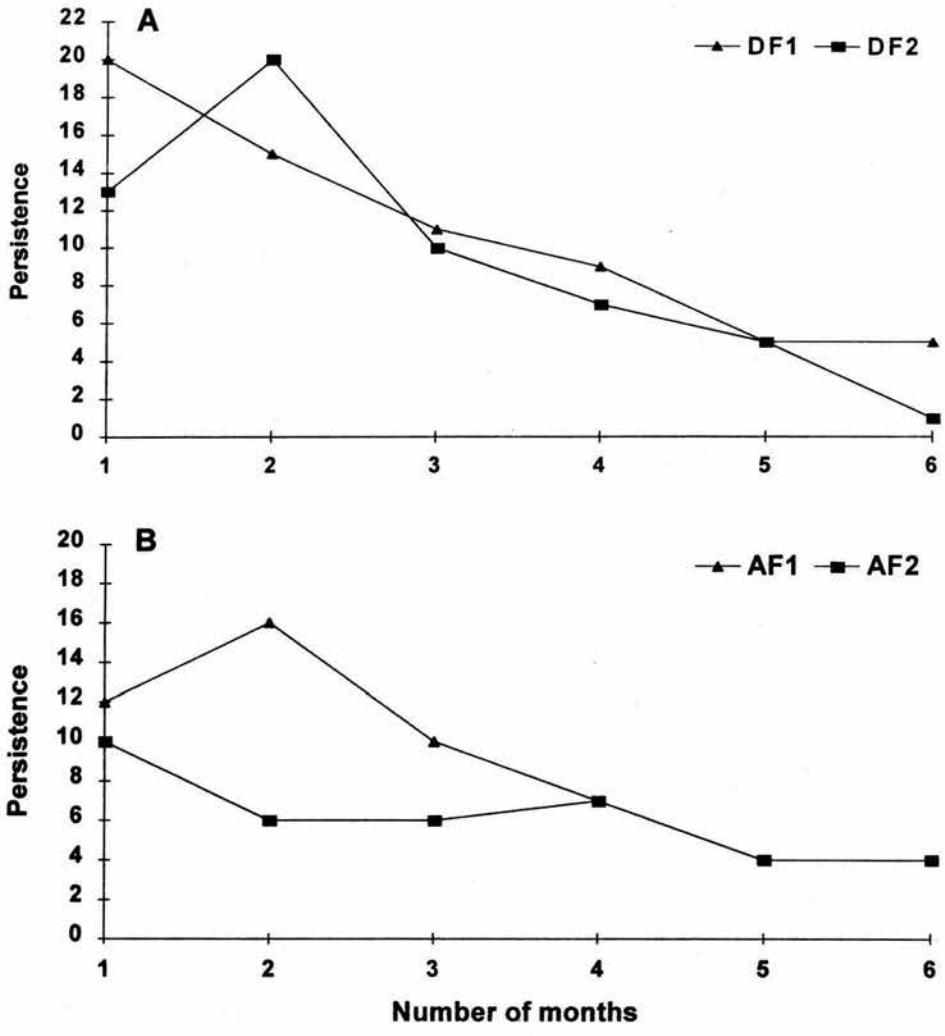

Figure 5. Number of individuals of *Liomys pictus* in (A) dry and (B) arroyo forest grids from Chamela, Jalisco, Mexico, that persisted in the study grids one, two, up to six months, from November 1994 to January 1996.

5

DISCUSION GENERAL

DISCUSION GENERAL

Variación genética de *Liomys pictus*

En las poblaciones naturales de plantas y animales existen altos niveles de variación genética (Selander 1976; Nei 1978; Mitton y Pierce 1980), por lo menos en lo que se refiere a los genes estructurales que codifican enzimas (Johnson 1976; Lewontin 1985). Muchas especies que tienen poblaciones grandes, reproducción sexual y fertilización cruzada muestran proporcionalmente una gran variabilidad genética (Allendorf y Leary 1986; Carson 1990).

Las poblaciones de *Liomys pictus* de Chamela, Jalisco, México, presentan valores altos de variación genética (H = 0.089-0.198, en este estudio), comparado tanto respecto al valor promedio de heterocigosidad reportado para los roedores en general (0.045; Selander y Kaufman 1973; Nevo 1978), como para el género *Liomys* en particular (0.016; Patton y Rogers 1993).

Existen problemas inherentes en la estimación de niveles de heterocigosidad a partir de análisis electroforéticos y en la comparación de éstos en diferentes poblaciones: la varianza y error del muestreo inter e intralocus, el hecho de tener tamaños de muestra distintos y variación en el número y tipo de loci analizados en diferentes estudios (Nei y Roychourdhuri 1974; Mitton y Pierce, 1980; Mitton, 1993). Tomando en cuenta lo anterior, es importante mencionar las diferencias que se encontraron en el presente trabajo respecto a estudios previos sobre esta especie.

La única información disponible sobre la variabilidad genética de *Liomys pictus* (Rogers 1986, 1990; tabla 1) reporta valores de heterocigosidad entre 0.022 y 0.033, marcadamente menores que los encontrados en el presente estudio (intervalo de 0.089 a 0.198; capítulos 2 y 4). Rogers (1986, 1990) estudió tres poblaciones geográficamente diferentes (de Sonora, Chiapas y Jalisco); así, los niveles de heterocigosidad que reporta para la especie podrían estar sesgados debido a que sus estimaciones se basan en una sola población de cada sito y con tamaños de muestra muy pequeños (12 individuos).

Es posible también que factores biológicos e históricos particulares en las poblaciones de Sonora y Chiapas, tales como características ambientales y demográficas diferentes, pudieran estar determinando bajos niveles de heterocigosidad (Smith et al. 1975). Evidentemente, el análsis genético de un número mayor de poblaciones e individuos, que considerara todo el rango geográfico de la especie, podría mejorar la información que se tiene sobre la especie.

Dentro de la familia Heteromyidae, *Chaetodipus* y *Microdipodops* son considerados los géneros más variables genéticamente (Patton y Rogers 1993; tabla 1). Sin embargo, a la luz de nuestros resultados, es evidente que la extensa variación encontrada en diferentes especies de estos géneros también caracteriza a las poblaciones de *L. pictus* en Chamela, Jalisco, donde presentan altos niveles de heterocigosidad.

Las diferencias observadas en cuanto a los valores de heterocigosidad entre las poblaciones de los estudios de

Rogers y el nuestro, así como entre las poblaciones de Chamela-Cuixmala y las de Chamela (capítulos 2 y 4), pueden tener diversas causas, entre las que se pueden mencionar: el número de loci polimórficos, el número de alelos y las frecuencias alélicas presentes en las poblaciones naturales determinan diferentes valores de heterocigosidad (Ayala 1976; Nevo 1978).

Por otro lado, la subdivisión temporal, espacial y/o biológica de las poblaciones y la estructura de edades, íntimamente relacionada con las frecuencias alélicas, también tienen efecto sobre la heterocigosidad (Smith et al. 1975; Soulé 1976; Endler 1992). De tal forma que factores como la alta tasa de intercambio poblacional (i.e., marcadas fluctuaciones de la estructura de edades juveniles-adultos), el reclutamiento acumulativo de progenie, la dispersión y la estructura social que caracterizan a las poblaciones de *L. pictus* en Chamela (Ceballos 1989; Mendoza 1997), pueden ser factores determinantes que se reflejan en diferencias en la estructura y diversidad genética de los individuos, tanto en distancias como en intervalos de tiempo relativamente cortos (Scribner et al. 1991). Efectivamente, la estructura social y la dispersión son factores determinantes de la composición genética de *Liomys pictus* en Chamela, como se discutirá a continuación.

Estructura social

Las poblaciones de *Liomys pictus* estudiadas se caracterizan por presentar un número de homocigotos mayor que el esperado por azar (valores promedio de F_{IS} = 0.724 y F_{IT} = 0.730; capítulo 2), lo cual es indicativo de una marcada endogamia

(Hartl 1980). *Liomys pictus* en Chamela presenta marcadas fluctuaciones en densidad poblacional debido, principalmente, a la estacionalidad ambiental caracterizada por severas sequías y largos periodos de escasez de alimento y agua (Ceballos 1989, 1991; Mendoza 1997); esta estructura poblacional fluctuante sugiere eventos de endogamia.

La estructura social de *Liomys* se describe como de baja tolerancia social intraespecífica y con cierta conducta agresiva en encuentros de laboratorio (Eisenberg 1963; Fleming 1974; Jones 1993), aunque con variados grados de agrupamiento social entre los adultos, donde ambos sexos comparten madrigueras durante la estación no reproductiva (Jones 1993); las hembras reproductivas viven solas y mantienen ámbitos hogareños distintos (Wagner 1961) y, en laboratorio, se ha observado que hay agresión entre miembros de la camada y sus madres (Eisenberg 1963). En Chamela, Mendoza (1997) ha reportado madrigueras donde individuos machos y hembras se encuentran juntos.

Diferentes estudios han demostrado la relación directa entre la estructura social y la variación genética en pequeños mamíferos, como en los roedores *Mus* y *Peromyscus* (Selander 1970*a*, 1970*b*). Las características territoriales de los individuos de *L. pictus*, junto a una marcada fluctuación de sus poblaciones, indicarían alta endogamia como se aprecia en este estudio por el exceso de homocigotos observado. Sin embargo, también presentan cierto grado de subdivisión poblacional la cual se refleja en las diferencias en las frecuencias alélicas que existen entre poblaciones (valores de F_{ST}). El roedor *Dipodomys elator*

presentó valores similares a los observados en *Liomys* (F_{ST} = 0.102; Hamilton et al. 1987) y esta especie, junto con otras del género *Dipodomys*, presentan una organización social parecida a la reportada en *Liomys*.

El movimiento de los individuos es otro factor que puede estar relacionado con la subdivisión poblacional observada en *Liomys*: mientras que Ceballos (1989, 1991) reporta que se mueven un promedio de 10 animales por año entre sitios de captura en las poblaciones de *Liomys* en Chamela, nuestros resultados indican que, desde el punto de vista genético, 2.6 individuos por generación se mueven entre las poblaciones (capítulo 2). Este movimiento de individuos entre poblaciones puede ser un factor que disminuya la endogamia, que de otra forma podría reducir la variabilidad genética en las poblaciones (Ayala 1976; Allendorf 1983); esto concuerda con la estructura poblacional en parches propuesta por Harrison y Hastings (1996), en la que se espera una combinación de niveles medios de diferenciación entre poblaciones y cierta tasa de recombinación de individuos.

Componentes de adecuación

Los ambientes estacionales en que habitan los heterómidos se caracterizan por presentar altas temperaturas en verano, precipitación impredecible y productividad primaria efímera, lo que sugiere adaptaciones extremas de los individuos para la conservación del agua y la energía (McNab 1979; French 1993). Bajo estas condiciones ambientales extremas, se ha documentado que el alimento es un factor limitante para muchos heterómidos, incluyendo a *Liomys pictus* (Ceballos

1989; Brown y Harney 1993; Mendoza 1997), y también en roedores no heterómidos que habitan ambientes similares (*Peromyscus polionotus*; Smith 1971).

De igual forma, se ha reportado que la eficiencia alimenticia está positivamente correlacionada con la heterocigosidad en *P. polionotus* (Teska et al. 1990), en donde los individuos más heterócigos utilizan el alimento y mantienen la masa corporal mejor (asimilan el alimento más eficientemente) que los más homócigos. En esta misma especie se encontró una correlación positiva entre masa corporal y heterocigosidad, relación que, además, influyó directamente en la conducta de los individuos (Garten 1976, 1977), lo cual apoya la hipótesis de que la heterocigosidad está directamente asociada con ciertos atributos morfológicos y fisiológicos ue este roedor.

A este respecto, en el primer estudio (capítulo 2) no se observó relación entre la masa corporal inicial (i.e., al momento de captura) y la heterocigosidad, mientras que en el tercero (capítulo 4), se encontró una correlación positiva y significativa, en donde los individuos más heterócigos tienen mayor masa corporal. La falta de consistencia en los resultados puede estar relacionada con la forma en que se evaluó la relación en ambos estudios. Esto es, el comparar niveles de heterocigosidad y peso individual dentro de una población, y estimar la relación entre estos factores en un solo momento (muestreo) en el tiempo, es un método de estudio que ha sido empleado exitosamente (Cothran et al. 1983; Mitton y Grant 1984). Sin embargo, en el presente estudio pudo ser un método menos efectivo y directo que el

investigar los cambios temporales de la heterocigosidad dentro de la cohorte o población (Allendorf y Leary 1986).

Así, la relación positiva se observó cuando se evaluaron las poblaciones a lo largo de 14 meses; esta forma resultó más adecuada ya que se consiguió el muestreo de individuos dentro de un mayor intervalo de masas corporales; a su vez, como la edad se estimó indirectamente considerando precisamente la masa corporal, se tuvo un mayor número de individuos muestreados dentro del intervalo de peso de los adultos.

Se ha reportado que la heterocigosidad aumenta positivamente en relación a las clases de edad (Mitton 1993 y referencias). Nuestros resultados indican que los individuos más heterócigos presentan mayor masa corporal; esto confirma el patrón observado de que los individuos adultos, definidos de manera indirecta a partir de los valores de masa corporal, tienen un mayor número de loci heterócigos y menor deficiencia de heterócigos que los juveniles. Por lo tanto, es posible que el muestreo temporal de individuos dentro de un intervalo de peso (masa corporal) más amplio, que presentan diferencias genéticas significativas entre juveniles y adultos, permitiera detectar la relación entre heterocigosidad y el componente de adecuación medido (Allendorf y Leary 1986). Es posible, también, que la superioridad observada en los individuos más heterócigos esté relacionada con ventajas en otras características, tales como dominancia, habilidad competitiva, reproducción o conducta, como sucede en otros roedores (Garten 1976, 1977; Kaufman y Kaufman, 1987) y que

no fueron directamente evaluadas en el presente trabajo. Sin embargo, esto es sólo una especulación que pudiera ponerse a prueba en futuros estudios.

La relación entre la utilización del alimento y heterocigosidad en las poblaciones experimentales de *L. pictus* tampoco fue significativa, a pesar de la tendencia observada de que los individuos más heterócigos presentaron mayor masa corporal y/o mantuvieron mejor el peso cuando el estrés alimenticio fue más severo (capítulo 3). Es probable que se hubiera observado una asociación más directa si se hubieran evaluado diferentes factores correlacionados con la adecuación como son sobrevivencia, fecundidad o desarrollo (Riddle et al. 1983). También, debe considerarse que diferentes estudios han reportado una asociación positiva para algunos loci pero no para otros (Koehn et al. 1988; Pemberton et al. 1988), por lo que en análisis que consideran la heterocigosidad multiloci, como el nuestro, se pueden pasar por alto ciertos efectos de loci individuales. Sin embargo, se ha sugerido también que la heterocigosis total puede ser más importante, cuando se evalúa su efecto sobre la adecuación individual, que considerar alelos específicos (Smith et al. 1975).

A pesar de que no se encontró una asociación significativa entre la eficiencia alimenticia y la heterocigosidad, es importante mencionar que *L. pictus* mostró valores de eficiencia alimenticia marcadamente altos: en promedio tuvieron una eficiencia del 95 al 97%, esto es, los individuos absorbieron cerca del cien por ciento del alimento que consumieron. Se ha demostrado que la

utilización eficiente del alimento es un factor determinante bajo condiciones de escasez (Teska et al. 1990), como sucede durante la época seca en las selvas de Chamela, cuando el alimento disminuye en cantidad y en calidad (Ceballos 1989). Se sugiere que este factor pudo haber enmascarado los efectos del tratamiento alimenticio.

Por el contrario, la conservación (metabolización) del agua resultó ser un factor de variación importante entre selvas y entre individuos (capítulo 3). La pérdida de masa corporal, como resultado del estrés hídrico, se vio afectada de manera diferente en relación a los niveles de heterocigosidad: los individuos con menor número de loci heterócigos perdieron más peso que aquellos con mayor número de loci heterócigos. Se observó también que los individuos de *L. pictus* en Chamela son capaces de tolerar una severa reducción de masa corporal cuando se les priva de agua. Como otros heterómidos, son capaces de sobrevivir a base de una dieta seca (semillas) por que tienen la habilidad de reducir la pérdida de agua, gracias a ciertas características fisiológicas y conductuales (Hinds y MacMillen 1985; French 1993) y así, contender con una severa reducción en la ingestión de agua durante los meses de sequía en las selvas de Chamela.

Se observaron diferencias entre la selva baja y la selva media respecto a la recuperación de masa corporal al final del experimento en que se restringió a los individuos de ingerir agua. El patrón observado fue que los individuos de la selva baja, que fueron los que perdieron, en promedio, mayor peso durante el experimento, también recuperaron un

mayor porcentaje del peso perdido comparados con los de la selva media.

Aquí cabe mencionar que consistentemente no se encontraron diferencias entre la selva baja y la selva media respecto a algunas de las variables medidas, i.e., loci en los cuales las frecuencias genotípicas no estaban en equilibrio Hardy-Weinberg, valores de heterocigosidad observada y número de loci heterócigos (capítulos 2 y 4), por lo que se sugiere que la estructura genética y la variabilidad, tal como fueron estimadas en el presente trabajo, no reflejan las posibles diferencias entre las poblaciones de los dos tipos de hábitat. Sin embargo, las diferencias encontradas entre selvas en relación al desempeño de los individuos bajo estrés hídrico apoyan la idea de que estudios más detallados, como experimentos controlados de laboratorio, entre otros, podrían confirmar diferencias entre hábitats (Powell 1971; McDonald y Ayala 1974; Smith et al. 1975).

Las diferencias observadas podrían estar relacionadas a las características ambientales particulares de cada sitio. Esto es, la selva baja es un ambiente relativamente más mésico en el que no todas las plantas pierden las hojas en la época seca, por lo que cierta cantidad de alimento y agua están disponibles todo el año; en contraste, en la selva baja hay escasez de recursos durante los meses de sequía (Bullock 1986; Ceballos 1989; García-Oliva et al. 1991). De esta forma, los individuos en la selva baja comúnmente enfrentan un estrés de falta de alimento y agua más severo que los de la selva media.

La magnitud del intercambio de energía y agua en los heterómidos, y el grado en el que dependen del agua producida durante el metabolismo oxidativo, están estrechamente relacionadas con la severidad del ambiente (French 1993). Las adaptaciones de estos roedores deben estar asociadas, entonces, con la energía disponible del metabolismo y la productividad secundaria que, a su vez, son importantes determinantes de la adecuación de los individuos (Mitton y Grant 1984). Nuestros resultados apoyan la predicción de que, bajo condiciones estresantes, los individuos de *Liomys pictus* que son genéticamente más variables, conservan (metabolizan) mejor el agua que aquellos menos variables. Esta característica debe contribuir a la habilidad de esta especie de mantener poblaciones en ambientes semiáridos, físicamente severos e impredecibles como las selvas tropicales de Chamela, Jalisco, México.

Densidad poblacional

Los resultados del estudio poblacional indican patrones consistentes en la densidad y persistencia de los individuos, en relación con los cambios temporales de la heterocigosidad. Los meses en que disminuyó la densidad poblacional fueron significativamente diferentes respecto a los periodos en que se incrementó, tanto en relación a los números poblacionales como al número de individuos que persisten y al número de loci heterócigos (capítulo 4). Además, el número promedio de loci heterócigos disminuyó durante la fase de incremento poblacional del ciclo de densidad, y aumentó durante la fase de decremento. Al

aumentar la densidad poblacional, también se observó una mayor deficiencia de heterócigos (*D*).

Estos cambios significativos en los niveles de heterocigosidad concuerdan con estudios sobre ciclos poblacionales y cambios genéticos en diferentes especies de pequeños mamíferos, en los que se ha encontrado que durante la primera parte de la fase ascendente del ciclo, cuando la densidad es baja, los animales no se dispersan y la heterocigosidad observada disminuye debido a procesos de endogamia; en la fase más alta del ciclo los individuos se dispersan y, durante la fase descendente, la heterocigosidad aumenta debido probablemente a presiones de selección en contra de los animales relativamente homócigos y a la mayor adecuación de los heterócigos (*Peromyscus polionotus*, Smith 1971; Briese y Smith 1974; *Microtus pennsylvanicus*, Krebs et al. 1973; *Sylvilagus floridanus*, Scribner et al. 1983).

En las poblaciones de *L. pictus* se observó el mayor número de individuos que persistieron en el área de estudio durante la fase ascendente (en la que se sugiere que los individuos no se dispersan). Durante la fase descendente, que comprende los meses secos en que hubo escasez de alimento y agua, persistieron un menor número de individuos.

Por lo tanto, los resultados de densidad y persistencia apoyan la hipótesis de Charlesworth y Giesel (1972) que señala que el equilibrio genético puede estar directamente relacionado con características demográficas; concuerdan también con Scribner et al. (1983), quienes indican que las fluctuaciones de la estructura de edades debidas a características que pueden no ser específicas del genotipo

(e.g., cambios en mortalidad o fecundidad), pueden resultar en cambios significativos de la variabilidad genética. El hecho de que los individuos adultos presentan un número significativamente mayor de loci heterócigos y menor deficiencia de heterócigos, también apoya el patrón de que los heterocigotos aumentan durante la fase descendente debido a la mayor adecuación de los individuos heterócigos (Smith 1971; Krebs et al. 1973; Briese y Smith 1974; Scribner et al. 1983).

Se ha sugerido que un mecanismo que vincula la demografía y la genética en pequeños mamíferos son los cambios en la heterocigosidad de los individuos y cuya evidencia proviene de estudios sobre heterosis; por ello, las características morfológicas, fisiológicas y conductuales asociadas con la sobrevivencia deberían mostrar correlación con la heterocigosidad (Smith et al. 1975). Los estudios aquí descritos representan la primer evidencia que apoya lo anterior que se haya observado en una especie tropical de un ambiente estacional.

Primeramente, los cambios en el número de loci heterócigos están directamente relacionados con las diferentes fases del ciclo de densidad de las poblaciones. Debido a que estos resultados representan el comportamiento de las poblaciones a lo largo de poco mas de un año, sería interesante obtener resultados de varios años y verificar si estos patrones poblacionales y genéticos se mantienen constantes. También, la hipótesis acerca de una mayor adecuación de los individuos heterócigos (Allendorf y Leary 1986; Mitton 1993) es apoyada por las correlaciones

significativas observadas entre heterocigosidad y ciertos caracteres morfológicos y fisiológicos. Estos caracteres están asociados directamente con las características ambientales marcadamente estacionales de las selvas de Chamela y pueden ser considerados importantes componentes de la adecuación de los individuos. Finalmente, se observó que los cambios en las estimaciones de la variabilidad genética son resultado de cambios demográficos (Charlesworth y Giesel 1972) y de que la composición genética de estas poblaciones fluctuantes está cambiando continuamente (Gaines et al. 1978).

Conclusiones

De los resultados encontrados en el presente trabajo, se puede concluir que:

a) las poblaciones de *Liomys pictus* en Chamela, Jalisco, México presentan niveles mayores de variación genética que los reportados anteriormente para la especie.

b) estas poblaciones están caracterizadas por un número mayor de homocigotos que lo esperado por azar (valores de F_{IS} y F_{IT}), lo cual indica una fuerte endogamia; se sugiere que esto puede estar relacionado con la estructura social de la especie.

c) la relación entre los patrones de heterocigosidad y los componentes de adecuación no es apreciable cuando experimentalmente se disminuye la cantidad de alimento disponible para los individuos, lo que puede estar directamente relacionado con la alta eficiencia alimenticia que presentan.

d) pero sí se observa en que los individuos más heterócigos presentaron mayor masa corporal que los menos heterócigos; a su vez, los adultos presentaron mayor variabilidad genética que los juveniles y menor deficiencia de heterócigos, patrones que, además, se relacionaron directamente con factores demográficos.

e) bajo condiciones de estrés hídrico, los individuos más heterócigos mantuvieron mejor la masa corporal (perdieron menos peso). Por lo que se sugiere que los individuos más variables genéticamente, con la capacidad asociada de mejor conservación del agua y de la energía, pueden tener mayor flexibilidad fisiológica para enfrentar las condiciones estacionales extremas de su hábitat.

f) los resultados apoyan las hipótesis que indican que los cambios en la variabilidad genética en las poblaciones pueden ser resultado de cambios demográficos y, consecuentemente, que ciertas características asociadas con sobrevivencia (componentes de adecuación) pueden mostrar correlaciones con la heterocigosidad.

Recomendaciones

A la luz de los resultados del presente trabajo, se sugiere lo siguiente:

1. La información sobre la estructura genética de *Liomys pictus* sería más completa si se estudiara un número mayor de individuos, pero más importante, un mayor número de poblaciones que abarque el total de su rango geográfico.
2. Aspectos sobre demografía y fisiología como los analizados en el presente estudio se mejorarían grandemente

si se tuvieran datos más finos de dispersión, paternidad, edad, y que abarcaran un lapso de tiempo mayor. Particularmente,

- para el estudio sobre alimentación se sugiere que podría medirse la eficiencia de la respuesta fisiológica de los diferentes niveles de alimento, (e.g., medir la tasa metabólica con una bomba calorimétrica). También, evaluar el efecto conjunto de variación en la disponibilidad de agua y de alimento, como sucede naturalmente en el campo.

- para el estudio demográfico, obtener información de la variación genética y los diferentes parámetros demográficos para varios años. Esto permitiría evaluar la asociación heterocigosidad-demografía a lo largo del tiempo y con relación a características ambientales que cambian año con año.

3. Estudiar con detalle la estructura social de *Liomys pictus* en Chamela, ayudaría a corroborar la idea de que la endogamia y la subdivisión poblacional observadas en este estudio pueden estar relacionadas con la estructura social semiterritorial y con las marcadas fluctuaciones estacionales que presentan las poblaciones.

4. Es evidente que la información sobre el grado de variabilidad genética y diferenciación al nivel de población y de especie, entre y dentro de los roedores heterómidos, será más exacta conforme se tenga más información disponible de estudios detallados.

Tabla 1. Valores promedio de heterocigosidad para diferentes géneros de roedores (número de especies entre paréntesis). Se indican el número de individuos (y su intervalo), de poblaciones y de loci promedio.

Género (# spp)	Num indvs	Num Pobls	Num Loci	*H* (intervalo)
Chaetodipus[a] (13 spp)	74 (2-289)	7	26	0.047 (0-0.096)
Dipodomys[b] (13 spp)	75 (2-405)	4	19	0.023 (0-0.065)
Microdipodops[c] (2 spp)	20	1	22	0.041 (0-0.064)
Liomys[d] (5 spp)	6 (1-12)	2	30	0.016 (0-0.018)
Heteromys[e] (7 spp)	19 (1-15)	4	30	0.013 (0-0.033)
Peromyscus[f] (1 sp)	12	8	18	0.054 (0.03-0.091)
Orizomys[g]	7 (1-34)	2	13	0.036 (0-0.065)

[a,b,c,d,e] Patton y Rogers (1993; tablas 1, 2, 3 y 4); [f] Garten et al. (1976); [g] Schmidt y Engstrom (1994).

6

LITERATURA CITADA

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AGRADECIMIENTOS

Con la advertencia de que cualquier omisión es totalmente ajena a mis mejores intenciones de agradecer a todos quienes de una u otra forma contribuyeron a la realización de esta tesis, voy como sigue.

Sin la compañía, el apoyo y el amor de Jorge, hacer un doctorado no hubiera sido nunca igual de posible, satisfactorio y placentero. Con todo mi amor, gracias.

Quiero agradecer profundamente al tutor de esta tesis, no solo por el apoyo y asesoria al trabajo que, a pesar de largas filas frente a su puerta, siempre fue pronta y valiosa. También, por haberme acojido en su laboratorio e involucrado en su vida académica y laboral; por su amistad, camaderia y consejos, que fueron parte sustancial del disfrute de llevar a cabo esta tesis con Gerardo Ceballos. Muchas, muchas gracias.

Otro pilar indispensable de este trabajo de tesis y a quien agradezco de corazón la asesoría en todas las cuestiones genéticas, su apoyo incondicional, amistad y sinceridad, y quien contribuyó a que el doctorado me pareciera una empresa posible, Daniel Piñero, todo mi agradecimiento.

Luis Eguiarte se recetó todos los pedazos y todas las versiones de esta tesis y nunca protestó! Gracias a eso el trabajo final resultó mucho mejor analizado, escrito y terminado. Muchas gracias Luis.

Los miembros del Comité Tutorial, Gerardo Ceballos, Daniel Piñero y Héctor Arita, obviamente también fueron escuchando y corrigiendo todas las piezas del rompecabezas desde antes de que éste fuera siquiera un proyecto de tesis con todas las de la ley. Siempre fue un comité muy solidario y apapachador, lo cual fue muy importante para mi.

Tampoco sería la tesis el trabajo final que es sin los acertadísimos comentarios y sugerencias de los sinodales del jurado, que se enfrentaron a todo el escrito de un sopetón. Muchas gracias a Ken Oyama, Rodrigo Medellín, Luis Medrano y Juan Carlos Morales. Gerardo Ceballos, Daniel Piñero y Luis Eguiarte formaron también parte del jurado.

El trabajo de tesis nunca hubiera sido posible sin el apoyo de instuticiones y centros de investigación. El Instituto (Centro, durante casi toda mi estancia como estudiante) de Ecología de la UNAM, que me permitió el uso de instalaciones y equipo y que fue mi casa durante cinco años y medio.

La Reserva de la Biósfera Chamela-Cuixmala, donde realicé gran parte del trabajo de campo y donde siempre se me brindó amablemente hospedaje y apoyo logístico para las tareas de trabajo de campo y de laboratorio. Esta tesis no hubiera sido posible ni hubiera sido tan divertida sin la gran ayuda que me dieron tanto el personal directivo y administrativo, como trabajadores y peones de la Reserva. Mi inmenso agradecimiento a todos ellos.

El resto del trabajo de campo lo llevé a cabo en la Estación de Biología "Chamela", del Instituto de Biología de la UNAM. También aquí, el uso de instalaciones y recursos fue fundamental para llevar a cabo el trabajo de campo y laboratorio. La convivencia y ayuda de todo el personal, los académicos y los compañeros con los que coincidí hicieron de mis estancias un verdadero disfrute.

El apoyo financiero para realizar la tesis fue no solamente indispensable, como muy gratificante. El Consejo Nacional de Ciencia y Tecnología (CONACYT; números de registro 80562 y 86298) me otorgó las becas de maestría y doctorado durante cinco años y medio. Sobra decir que sin este apoyo jamás hubiera hecho el doctorado.

La Fundación Ecológica de Cuixmala A.C. me otorgó financiamiento para adquirir gran parte de los reactivos empleados en el trabajo de laboratorio y para la estancia en la Reserva de Chamela-Cuixmala.

Idea Wild, a través del apoyo de su director Wally van Sickle, financió parte del trabajo de campo. Gerardo Ceballos siempre urgó exitosamente entre sus proyectos para "acompletar" los recursos monetarios que hicieran falta. Y, Daniel Piñero me permitió hacer uso de todo el material, reactivos y sustancias en su laboratorio, lo que ayudó grandemente al financiamiento del trabajo.

Creo que la parte más importante de estudiar un doctorado y hacer un trabajo como éste, es la oportunidad de hacer amigos y convivir con tanta gente. La lista de la gente que

quiero y aprecio tanto es, afortunadamente, muy larga y no tiene ningún orden predeterminado.

Con Pilar, Liz, América, Roxana, Angeles, Cristina, Meli y Marce, compartí muchos ratos, comidas, cafés y experiencias, pero más importante, la amistad y el cariño que hicieron de estos años una experiencia maravillosa, y que me permitieron hacer amigas de toda la vida. Las quiero mucho!

Mis compañeros de generación David, Reyna, Julio, Daniel, Alvaro, Ofelia, con quienes me divertí y compartí muchos ratos buenos. En el laboratorio de manejo y conservación de vertebrados (Angeles, Pilar, Cuauh, D. Valenzuela, mi primo D. Vázquez, Alvaro, Chucho Pacheco y Chucho Ramírez, G. Suzán, G. Carreón, Gisselle, Lupita, Iván, César, todos me brindaron su amistad y se los agradezco cariñosamente. Además, Lupita y Gisselle siempre me ayudaron en las broncas administrativas y Cuauh merece una mención especial por ser mi salvador (y el de todos!) en las broncas estadísticas de todos los días. Aunque no trabajamos directamente juntos, con Fernanda, Karina, Astrid y Jorge Uribe pasé ratos increíbles; amigos atesorables.

En el laboratorio de Genética, donde hice mis primeros amigos en el centro, va mi cariño y mi eterna amistad con Liz, América (y Armando), Lalo, Nidia, Fabián y Gaby. También, para Vali, Gaby Jiménez, Alice Altesor, Luis García, Consuelo y Glenn. Dentro del Centro (Instituto) de Ecología, quiero agradecer de manera particular la ayuda incondicional de tanta gente que aligeró cargas administrativas, académicas, etc. Elena, Gloria, Alicia, Caro, Chelito, Paty, Adriana, Virgilio y Ernesto. Jorge Soberón, Exequiel Ezcurra y Hugh Drummond no solo fueron excelentes coordinadores académicos de posgrado, sino buenos amigos. Mil gracias a todos!

En Chamela y Cuixmala, el trabajo de campo no hubiera sido tan agradable y reconfortante si no lo hubiera compartido con Angelitos, de quien además aprendí todo lo que se sobre ratones y quien me ayudó a mantener la condición física!, y con David, Andrés, Marciano y Alvaro, con quienes además me divertí a mares. Gracias por todo.

También, al Dr. A. Gómez Poyou y su esposa, Marietta Tuena, que me enseñaron la técnica de sangrado que utilicé con los ratones y que, para suerte de éstos, no les hizo ningún daño; el Dr. León Cázares y Olivia Reynoso me

permitieron utilizar las instalaciones de su laboratorio y me enseñaron los métodos de homogenización de tejidos. En las talachas estadísticas, Arturo Flores también me echó una mano.

Mi familia, Jorge, Quety, Luis, Adriana, Polo, Alicia, Stephanie y Paola y Teté, Mayté, Pancho, Chiquis, Daniela y Marifer. Con mi amor y mi agradecimiento, los quiero siempre!