

Body mass dynamics and growth patterns of leaf-eared mice *Phyllotis darwini* in a semi-arid region of the Neotropics

Mauricio LIMA*, Francisco BOZINOVIC and Fabian M. JAKSIC

Lima M., Bozinovic F. and Jaksic F. M. 1997. Body mass dynamics and growth patterns of leaf-eared mice *Phyllotis darwini* in a semi-arid region of the Neotropics. Acta Theriologica 42: 15–24.

We report on body mass dynamics, field growth rates and age-specific growth curves for the leaf-eared mouse *Phyllotis darwini* (Waterhouse, 1837). Mark-recapture methods provided data for a population of *P. darwini* in a semi-arid region of Chile from 1987 to 1996. There were significant effects of sex, season, and slope exposure on body mass. In addition, we found significant effects of sex, mass class, and season on field growth rates. Individuals had highest growth rates during spring and summer and lowest during fall, males grew faster than females, and juveniles grew faster than adults. Growth rates of males were positively correlated with precipitation levels. This result suggests that higher somatic growth rates during periods of unusual high precipitation may account for population outbreaks observed in this species in semi-arid regions of Chile. Age-specific growth curves of body mass for both sexes showed a strong sexual dimorphism. This sexual dimorphism in body mass may be related to a polygynous mating system and strong male-male sexual competition during breeding periods.

Departamento de Ecología, Facultad de Ciencias Biológicas, P. Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Key words: cricetid rodent, body mass, growth rates, seasonality, sexual dimorphism, Chile

Introduction

Growth, survival, and reproduction are the main components of the life cycle. The interaction between life cycle and spatio-temporal variability of the environment determines the dynamics and structure of natural populations (Zeng and Brown 1987, Caswell 1989). In particular, individual growth rates may reflect changes in the environment, by being correlated with life history traits such as survival and reproduction (Roff 1992). Therefore, studies of growth patterns and body mass dynamics in natural populations are important to understand how life history processes affect population dynamics. Because of the relationships between body mass, survival, and reproduction, it is reasonable to incorporate body mass as a variable in demographic models (see Caswell 1989). Also, the study of body

* to whom all correspondence should be sent

mass dynamics is important because it allows an integration between the energetics of individuals and demography, which arises from the metabolic implications of body mass changes on population energy use (Marquet *et al.* 1995, Medel *et al.* 1995).

For small mammals, there is abundant information concerning body mass changes and field growth rates (Merritt 1984, and references therein). Several authors have observed that small mammals exhibit seasonal variation in mean body mass, being smaller during winter periods (Pucek 1970, Iverson and Turner 1974, Cameron and Spencer 1983, Merritt 1984, Slade *et al.* 1984, Zeng and Brown 1987, Bozinovic *et al.* 1990). Thus, a decrease of individual body mass causes a decrease in populational body mass during periods of low food availability and/or quality (Wunder *et al.* 1977, Merritt 1984, Karasov 1989, Bozinovic *et al.* 1990). The same pattern may arise from processes such as emigration of old individuals, differential mortality, and recruitment of young individuals (Iverson and Turner 1974). Consequently, determination of field growth rates may shed light on the mechanisms involved in changes of population mass structure (Cameron and Spencer 1983, Slade *et al.* 1984). Although several short-term studies of this phenomenon have been conducted among neotropical small mammals (O'Connell 1986), we are not aware of any long-term analysis of the population ecology of a neotropical rodent. Such long-term studies are needed to quantify body mass dynamics and growth patterns, in an attempt to gauge how these traits respond to variation in the environment and in population density.

In this paper we describe the body mass dynamics, sex-specific growth curves, mass, sex, habitat and season-specific body mass, and field growth rates, based on eight years of data from a population of the cricetid rodent *Phyllotis darwini* (Waterhouse, 1837) inhabiting a semi-arid region of Chile. The leaf-eared mouse *P. darwini* exhibits periodic outbreaks (up to 100 individuals/ha) which are triggered by unusually high rainfall and subsequent pulses in plant growth (Jiménez *et al.* 1992, Jaksic *et al.* 1996). Consequently, we analyze the relationships between body mass dynamics and field growth rates concerning population density and rainfall regimes.

Material and methods

Field and laboratory studies

The study was conducted in Las Chinchillas National Reserve, at Aucó (31°30'S, 71°06'W), 300 km north of Santiago. The Reserve has a rugged relief with many ridges dissected by deep ravines and few flat areas. The climate is semi-arid, with scarce rainfall concentrated in winter months. The vegetation is a thorn-scrub, with species composition and cover depending on solar exposure (see Jiménez *et al.* 1992). Slopes that face to the equator receive high solar radiation and are dry, whereas slopes that face to the pole receive less radiation and are more mesic.

Life history data on *P. darwini* were collected through mark-recapture procedures on two opposite-facing slopes in each of two creeks 2 km apart within the Reserve from October 1987 to January

1992, alternating creeks every month. Four trapping grids were used: two in opposite facing slopes of El Grillo creek, and two in El Cobre creek. Each 7 by 7 trapping grid had stations separated by 15 m, thus covering an area of 105 by 105 m considering an influence boundary strip. We equipped grids with one Sherman trap at each station; trapping sessions occurred every other month in each creek, with traps activated simultaneously on the equatorial- and polar-facing slopes during 5 consecutive nights. Traps were baited with rolled oats, and checked every morning. Each individual was marked with a metal ear tag and the species, body mass, reproductive condition, and sex were determined. From January 1992 to July 1996 only El Cobre creek was monitored, on a seasonal (quarterly) basis.

To analyze growth patterns during the first days of life, adult individuals of *P. darwini* were captured near Santiago (La Plata creek, 33°28'S, 70°54'W) and transported to the laboratory. We assigned animals in pairs of both sexes to plastic cages (40 × 40 cm) with wood shavings as bedding or nest material, and rabbit food pellets and water *ad lib*. We maintained animals at natural photo periods and ambient temperatures. When females gave birth, males were removed and we recorded body mass of offspring (± 0.01 g) during the first 40 days of life on a weekly basis.

Data analysis

Field growth rates were calculated by subtracting body mass of an individual during trapping period *I* from its mass in trapping period *I+1*, dividing by the number of days elapsed during each period, and then multiplying by 7 to yield a growth rate in g/week (see Slade *et al.* 1983). We calculated field growth rates for individuals segregated by sex, season, slope exposure (equatorial and polar facing slopes), and mass class. We defined seasons as winter (June–August), spring (September–November), summer (December–February), and fall (March–May). In this study, animals were assigned to seasons according to the season in which the last of successive captures occurred. We assigned mass classes as juveniles (< 40 g) or adults (> 40 g), and body mass at first capture defined mass class between successive periods of trapping. Because some animals that we recaptured during a given trapping bout experienced mass loss, we only used the first capture of each seasonal trapping period. To test growth rates for differences in sex, season, slope exposure, and mass class, we used a four-way ANOVA. In this analysis we used two consecutive captures for a single individual. When an individual was recaptured several times, we only used the first two consecutive captures, so that mass changes represent independent samples.

To test body mass for differences in sex, season, and slope exposure, we used a three-way ANOVA. We analyzed the relationships of body mass and growth rates with population density and rainfall using the cross-correlation function (Chatfield 1989) and least-squares procedures. In this study, we used the seasonal pattern of precipitation for the interval of time considered (1987–1996). We related the precipitation that fell during the previous season with growth rates observed the subsequent season. We excluded pregnant females when we analyzed body mass data, but not when we analyzed growth rates.

Curves for age-specific growth patterns of body mass in both sexes were calculated using data from the field and laboratory. We estimated age-specific growth patterns of body mass from individuals born in the laboratory by means of regression analysis during the first 40 days of life. We used this relationship to estimate age (days) of individuals captured for the first time in the field and with body mass lower than 30 g for females, and 35 g for males. *P. darwini* began to appear in the traps at 15–25 g of body mass, which probably corresponds to time of weaning. In the laboratory, individuals reached that body mass at the age of 20 days approximately. This way, we avoided inclusion of adult animals that suffered loss of body mass. Then, we fitted a growth equation for each sex using data for changes in mass between successive captures of the same-aged individuals. In this analysis we excluded pregnant females. Data were fitted to von Bertalanffy's model by the least-squares procedure.

Results

We analyzed body mass data from 2614 captures (1361 of males and 1253 of females), and individual growth rates data from 631 captures (269 of males and 362 of females), which corresponded to 408 different individuals (193 males and 215 females). Body mass varied temporally in both sexes, with *P. darwini* reaching a peak in body mass in winter and a decrease in fall (Fig. 1). Nevertheless, there was a large temporal variability in body mass in both sexes.

The three-way ANOVA revealed significant effects of sex on body mass ($F = 441.99$, $df = 1$, 2608 , $p = 0.0001$), with males being larger than females (mean \pm SD: 53.03 ± 14.6 and 42.42 ± 11.5 g, respectively). Also, we found significant effects of seasons on body mass ($F = 37.03$, $df = 3$, 2608 , $p = 0.0001$), highest body masses occurring during winter (53.76 ± 0.75 g), intermediate in spring and fall (48.78 ± 0.51 g and 46.83 ± 0.54 g, respectively), and lowest during summer (45.66 ± 0.48 g). In addition, there was a significant effect of slope exposure on body mass ($F = 17.84$, $df = 1$, 2608 , $p = 0.0001$), with equatorial-exposure subpopulations being heavier than polar ones (48.68 ± 0.35 g and 46.59 ± 0.46 g, respectively). These patterns of change probably reflect responses due to variations in growth, mortality, and recruitment. We did not find any effects of population density on body mass in either sex (males: $R^2 = 0.024$, $df = 1$, 32 , $F = 0.77$, $p = 0.39$; females: $R^2 = 0.021$, $df = 1$, 32 , $F = 0.70$, $p = 0.41$) or of rainfall (males: $R^2 = 0.008$, $df = 1,28$, $F = 0.23$, $p = 0.64$; females: $R^2 = 0.0001$, $df = 1$, 29 , $F = 0.01$, $p = 0.92$).

Growth rates in both sexes also showed a large temporal variability (Fig. 2). Seasonal growth rates of males and rainfall showed a significant peak of CCF at

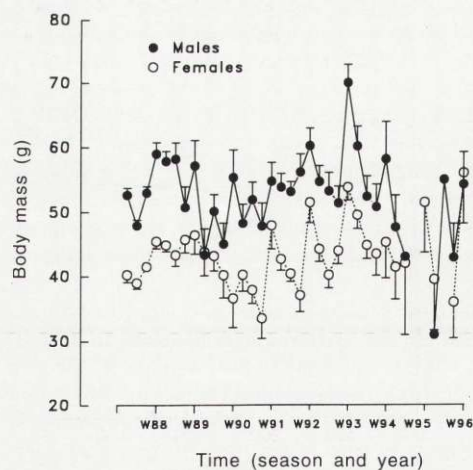


Fig. 1. Relationship between body mass (g) and season during consecutive years in males (closed dots and solid lines) and females (open dots and broken lines) of *Phyllotis darwini*. W – winter, vertical bars – one standard error.

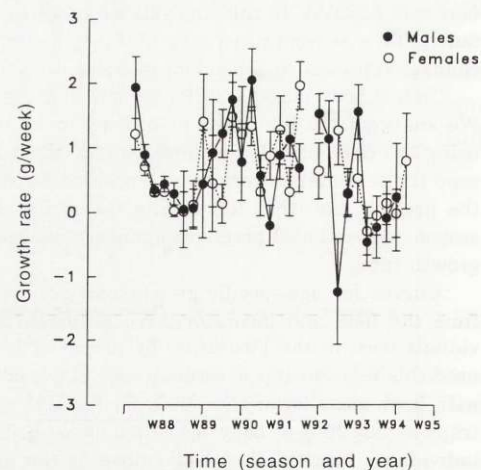


Fig. 2. Relationship between growth rate (g/week) and season during consecutive years in males and females of *Phyllotis darwini*. Explanations as in Fig. 1.

lag 0 (Fig. 3), which corresponds to the precipitation that fell the previous season. Therefore, changes of body mass of males were positively associated with rainfall levels. Consequently, we fitted a power curve ($y = a + bx^c$) for the relationship between growth rates of males and rainfall (Fig. 4), and the model fitted explained 70% of the variance. If we removed the outlier located at 450 mm of rainfall in the graph, the correlation between growth rates and precipitations decreased to $R^2 = 0.20$, but the relationship was still significant ($df = 1, 21, F = 5.24, p = 0.033$).

We tested the growth rates of 408 different individuals for differences in sex, season, slope exposure, and body mass class. The ANOVA revealed a significant difference between growth rates of males and females ($F = 10.54, df = 1, 395, p = 0.0001$), with males growing 0.62 g/week (SD = 0.07) and females 0.51 g/week (SD = 0.06). There was a significant difference in growth rates between mass classes ($F = 64.38, df = 1, 395, p = 0.0001$), juveniles (< 40 g) showing higher growth rates than adults (1.04 ± 0.08 g/week and 0.36 ± 0.05 , respectively). We did not find any effect of slope exposure on individual growth rates ($F = 1.23, df = 1, 395, p = 0.27$). Nevertheless, we found significant differences between seasons ($F = 9.54, df = 3, 395, p = 0.001$), highest total growth rates occurring during spring (0.83 ± 0.11 g/week), and summer (0.76 ± 0.10), intermediate during winter (0.57 ± 0.09), and lowest during fall (0.35 ± 0.07). Also, there was a marginal significant interaction term between mass class and seasons ($F = 2.41, df = 3, 395, p = 0.07$), suggesting that juveniles and adults had different patterns of seasonal variations in body mass change. Consequently, we repeated the same analysis but with juveniles and adults separate. The three-way ANOVA for adult data revealed significant effects of seasons ($F = 2.81, df = 3, 272, p = 0.04$), highest growth rates occurring during

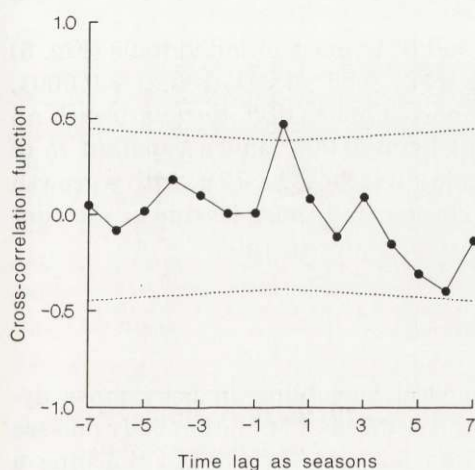


Fig. 3. Cross-correlation function between growth rates of males of *Phyllotis darwini* and rainfall during the previous season. Dotted lines indicate Bartlett's band. Seasons as time lags.

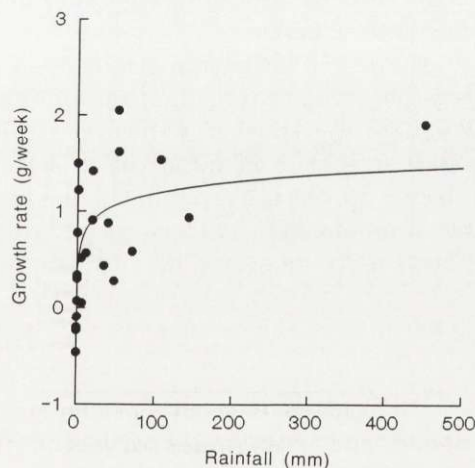


Fig. 4. Relationship between growth rate (g/week) of males of *Phyllotis darwini* and rainfall (mm) during the previous season. The fitted curve was a power function ($y = 0.24 + 0.25x^{0.3}$, $R^2 = 0.70$).

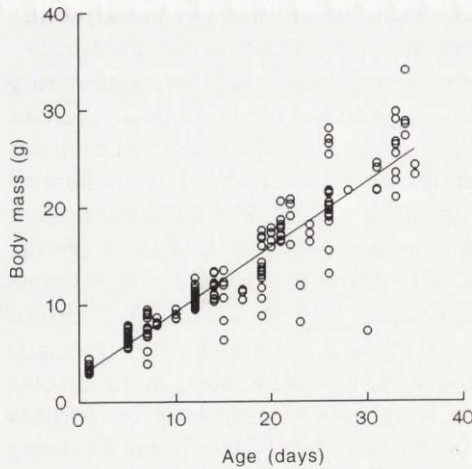


Fig. 5. Relationship between body mass (g) and age (days) for both sexes of *Phyllotis darwini* held in captivity during the first 40 days of life. Body mass = $2.62 + 0.66 \text{ Age (days)}$, $R^2 = 0.85$.

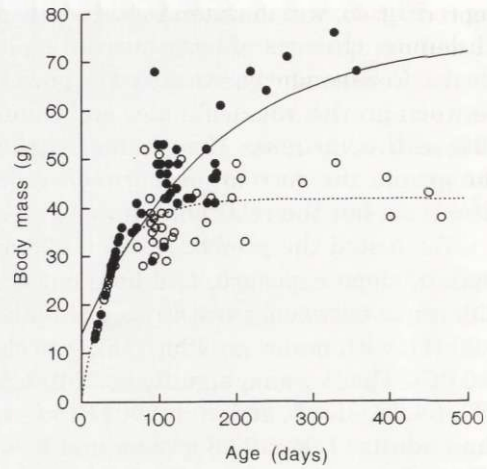


Fig. 6. Relationship between body mass (g) and age (days) in males (closed dots and solid line) and females (open dots and broken line) of *Phyllotis darwini* in the field. Growth curves were fitted by von Bertalanffy's model. Males: Body mass = $75.07[1 - e^{-0.006(\text{Age} + 33.86)}]$. Females: Body mass = $41.72 [1 - e^{-0.025 (\text{Age} + 0.576)}]$.

spring ($0.63 \pm 0.12 \text{ g/week}$), intermediate during winter and summer (0.46 ± 0.10 and 0.33 ± 0.12 , respectively), and lowest during fall (0.14 ± 0.084). Juveniles showed highest growth rates during spring and summer (1.68 ± 0.24 and 1.43 ± 0.14 , respectively), intermediate during winter (0.99 ± 0.18), and lowest during fall (0.67 ± 0.11).

A linear relationship between age (days) and body mass of individuals (Fig. 5) was observed during the first 40 days of life ($R^2 = 0.85$, $df = 1$, 185 , $p = 0.0001$, $n = 186$). We show growth curves in Fig. 6, wherein males of *P. darwini* reach an adult weight of 75.07 g, the growth constant being 0.006, and a constant t_0 of -33.86 . On the other hand, females reach an adult weight of 41.72 g, with a growth constant of 0.025, and a constant t_0 of -0.58 . These results suggest that *P. darwini* shows a strong sexual dimorphism in body size and growth rates.

Discussion

The leaf-eared mouse presents large temporal variability in body mass dynamics and growth rates, with important seasonal effects. Population body masses are smallest during summer, increasing during fall and spring, and reaching a peak in winter. Different processes operating at inter-annual and intra-annual time scales may underlie the observed body mass dynamics. At an intra-annual scale, body mass dynamics reflects the allocation of energy of individuals to

reproduction and maintenance during different seasons, and likely the variability in demographic parameters such as mortality, recruitment, and reproduction.

Our results showed that *P. darwini* reaches the largest mean body mass during winter and the smallest during summer. Several processes may explain changes in mean body mass, for instance recruitment of light-weight individuals, differential mortality, or changes in individual body mass (growth rates). Loss of body mass during fall and summer may be related to energetic costs associated with a period of low food availability and quality. In close agreement, we found that juveniles and adult individuals showed their lowest growth rates between summer and fall. In our study site, precipitation was concentrated during winter months (Jaksic *et al.* 1996) and was associated with the season of vegetation growth and reproduction. Thus, during summer and fall there was an important decrease in herbage available for rodent consumption, and this may represent a nutritional bottleneck for this species (*sensu* Karasov 1989). Even if rodents may compensate for low availability of food items by behavioral and physiological mechanisms, Karasov (1989) showed a clear effect of food quality and availability on free-living woodrats *Neotoma lepida* during a seasonal nutritional bottleneck in the Mojave Desert. He detected body mass reduction and nutrient imbalances, with important consequences on survival and population mass dynamics.

Growth rates of *P. darwini* varied temporally in both sexes. The existence of seasonal effects on growth rates provides some evidence that the body mass dynamics observed in this population may be a result of changes in individual body mass. Similarly, several authors have reported seasonal effects on growth rates in other small-mammal species (Cameron and Spencer 1983, Merritt 1984, Slade *et al.* 1984). The existence of low growth rates throughout summer and fall supports the hypothesis that these seasons represent a period of low food availability. As expected, juveniles showed higher growth rates than adults.

The body mass dynamics observed may be a consequence of the different seasonal effects on growth rates of juveniles and adults, and the recruitment of light-weight individuals. Our opinion is that most changes in body mass dynamics may be accounted for the recruitment of light-weight individuals in summer, and the existence during winter of old individuals and young individuals that attain their adult body size. The same pattern was documented in other rodent species (Iverson and Turner 1974, Slade *et al.* 1984). In addition, we found significant effects of slope exposure on population body masses, but not on individual growth rates. Consequently, body mass differences between solar exposures may be the result of demographic processes, such as differential mortality, or differential recruitment in these two habitat types. It is important to consign here that differences in population density, extinction and colonization rates, have been recorded between slope exposures (Jiménez *et al.* 1992, Lima *et al.* 1996). Thus, we think that spatial structure influences some demographic traits in *P. darwini*.

Because we did not find any relationship between body mass and population density or rainfall in either sex, body mass dynamics may be the result of several

demographic processes such as growth, survival, recruitment, and reproduction. Therefore, if tradeoffs exist among these life history traits, or they relate in different ways to population density and rainfall, then any relationship between body mass and population density and rainfall may have been masked. Contrary to body mass, growth rates of males showed a positive relationship with rainfall, and therefore precipitation may determine the energy available for somatic growth in males. This correlation reflects the seasonal changes found in growth rates and the seasonal variability of the rainfall at this mediterranean-type locality. In addition, this correlation may help explain the outbreaks reported for this population (Jiménez *et al.* 1992, Jaksic *et al.* 1996). For example, the increase of energy available for somatic growth may directly influence survival and reproductive probabilities, thus providing a plausible mechanism underlying outbreaks of *P. darwini*. Changes of individual body mass may determine survival and reproductive probabilities, especially during periods of nutritional imbalances (Karasov 1989). Thus, mass-based demography can be an important tool for understanding the implications of individual-level processes such as changes in body mass, on population-level patterns. Mass-based demographic studies have been conducted in some rodent populations (Sauer and Slade 1985, 1986, 1987), and these authors pointed out the importance of body mass for population processes.

We found strong sexual dimorphism in body mass and growth rates. Growth rates of males were higher than those of females, with males reaching a larger adult body mass than females. This pattern was also evident in the growth curves. Marked sexual differences in body size and age-specific growth suggest that *P. darwini* has some important differences in life history features between sexes. For example, females attain their maximum weight at 100 days, while males reach their maximum body mass past 200 days. This difference suggests that females attain sexual maturity younger than males, which is a common feature of species with polygynous mating systems, with strong male-male competition for mates (Emlen and Oring 1977). Sexual dimorphism in body size has been reported for other rodent species (Cameron and Spencer 1983, Zeng and Brown 1987, Heske and Ostfeld 1990 and references therein). According to Heske and Ostfeld (1990), Ostfeld and Heske (1993), Boonstra *et al.* (1993), and Wolff *et al.* (1994), sexual dimorphism in body size is expected to vary as a function of mating systems in microtine rodents. Heske and Ostfeld (1990) argued that sexual dimorphism in body size results from sexual selection, and that the difference in body size between sexes is higher in the most polygynous species (Ostfeld and Heske 1993). Based on our observed growth curves, we hypothesize that *P. darwini* has a polygynous mating behavior, with males competing for mates and territories during the breeding season, and females selecting larger males. In the laboratory, we observed strong aggressive interactions between males during the mating period, resulting in body injuries and sometimes death. If *P. darwini* has a polygynous mating behavior, then we can predict that males should present lower survival rates,

larger variances in reproductive success, and larger territories than females. Although results of sexual dimorphism in body size are strongly suggestive in this species, further studies concerning mating and social behavior are needed, and we cannot reject the hypothesis of a promiscuous mating behavior of the females.

Acknowledgments: This study was supported by Fondo Nacional de Ciencia y Tecnología grants FONDECYT 296-0034 to ML, 195-0394 to FB, and 196-0319 to FMJ, and was conducted during the graduate program of ML. FMJ acknowledges the support of the President's Endowed Chair in Science. We thank two anonymous reviewers for their valuable comments on the manuscript.

References

- Boonstra R., Gilbert B. S. and Krebs C. J. 1993. Mating systems and sexual dimorphism in mass in microtines. *Journal of Mammalogy* 74: 224–229.
- Bozinovic F., Novoa F. F. and Veloso C. 1990. Seasonal changes in energy expenditure and digestive tract of *Abrothrix andinus* (Cricetidae) in the Andes range. *Physiological Zoology* 63: 1216–1231.
- Cameron G. N. and Spencer S. R. 1983. Field growth rates and dynamics of body mass for rodents on the Texas coastal prairie. *Journal of Mammalogy* 64: 656–665.
- Caswell H. 1989. *Matrix population models*. Sinauer, Sunderland, Massachusetts: 1–328.
- Chatfield C. 1989. *The analysis of time series*. Chapman and Hall, New York: 1–241.
- Emlen S. T. and Oring L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215–223.
- Heske E. J. and Ostfeld R. S. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *Journal of Mammalogy* 71: 510–519.
- Iverson S. L. and Turner B. N. 1974. Winter weight dynamics in *Microtus pennsylvanicus*. *Ecology* 55: 1030–1041.
- Jaksic F. M., Feinsinger P. and Jiménez J. E. 1996. Ecological redundancy and long-term dynamics of vertebrate predators in semiarid Chile. *Conservation Biology* 10: 252–262.
- Jiménez J. E., Feinsinger P. and Jaksic F. M. 1992. Spatiotemporal patterns of an irruption and decline of small mammals in Northcentral Chile. *Journal of Mammalogy* 73: 356–364.
- Karasov W. H. 1989. Nutritional bottleneck in a herbivore, the desert wood rat (*Neotoma lepida*). *Physiological Zoology* 62: 1351–1382.
- Lima M., Marquet P. A. and Jaksic F. M. 1996. Extinction and colonization processes in subpopulations of five neotropical small mammal species. *Oecologia* 107: 197–203.
- Marquet P. A., Navarrete S. A. and Castilla J. C. 1995. Body size, population density, and the energetic equivalence rule. *Journal of Animal Ecology* 64: 325–332.
- Medel R. G., Bozinovic F. and Novoa F. F. 1995. The mass exponent in population energy use: the fallacy of averages reconsidered. *American Naturalist* 145: 155–162.
- Merritt J. F. 1984. Winter ecology of small mammals. Special Publication of the Carnegie Museum of Natural History, Pittsburgh: 1–380.
- O'Connell M. A. 1986. Population variability of Neotropical rodents: influence of body size, habitat, and food habits. *Revista Chilena de Historia Natural* 59: 169–178.
- Ostfeld R. S. and Heske E. J. 1993. Sexual dimorphism and mating systems in voles. *Journal of Mammalogy* 74: 230–233.
- Pucek Z. 1970. Seasonal and age change in shrews as an adaptive process. *Symposia of the Zoological Society of London* 26: 189–207.
- Roff D. A. 1992. *The evolution of life histories. Theory and analysis*. Chapman and Hall, New York: 1–535.
- Sauer J. R. and Slade N. A. 1985. Mass-based demography of a hispid cotton rat (*Sigmodon hispidus*) population. *Journal of Mammalogy* 66: 316–328.

- Sauer J. R. and Slade N. A. 1986. Size-dependent population dynamics of *Microtus ochrogaster*. *American Naturalist* 127: 902–908.
- Sauer J. R. and Slade N. A. 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? *Ecology* 68: 642–650.
- Slade N. A., Sauer J. R. and Glass G. E. 1984. Seasonal variation in field-determined growth rates of the hispid cotton rat (*Sigmodon hispidus*). *Journal of Mammalogy* 65: 263–270.
- Wolff J. O., Edge W. D. and Bentley R. 1994. Reproductive and behavioral biology of the gray-tailed vole. *Journal of Mammalogy* 75: 873–879.
- Wunder B. A., Dobkin D. S. and Gettinger E. R. 1977. Shifts of thermogenesis in the prairie vole (*Microtus ochrogaster*): strategies for survival in a seasonal environment. *Oecologia* 33: 273–281.
- Zeng Z. and Brown J. H. 1987. Population ecology of a desert rodent: *Dypodomys merriami* in the Chihuahuan desert. *Ecology* 68: 1328–1340.

Received 16 July 1996, accepted 8 November 1996.