

Inter-Population Variation in Hoarding Behaviour in Degus, *Octodon degus*

René Quispe*, Camila P. Villavicencio*, Arturo Cortés†‡ & Rodrigo A. Vásquez*

* Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

† Departamento de Biología, Facultad de Ciencias, Universidad de La Serena, La Serena, Chile

‡ Centro de Estudios Avanzados en Zonas Aridas, La Serena, Chile

Correspondence

Rodrigo A. Vásquez, Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile.
E-mail: rvasquez@uchile.cl

Received: July 1, 2008

Initial acceptance: October 6, 2008

Final acceptance: December 16, 2008
(D. Zeh)

doi: 10.1111/j.1439-0310.2009.01621.x

Abstract

Although foraging comprises a set of behaviours that typically vary with resource availability and/or climatic conditions, few studies have analysed how foraging, particularly food hoarding, varies across populations inhabiting different habitats. We carried out an inter-population study on foraging behaviour with the caviomorph rodent *Octodon degus* collected from two geographically separated populations in central Chile, with contrasting climates. One population was located in a mountainous zone (at 2600 m elevation) characterized by a high-altitude climate. The other population was from a low-altitude Mediterranean climate zone (450 m elevation). Under laboratory conditions, we measured population-specific differences in food consumption and hoarding by recording food utilization. We also assessed whether acclimation played a role in behavioural differences, by using two different sets of animals that had been in captivity for (1) 2 wk or (2) 6 mo, under common conditions. The results showed variation in food hoarding between populations. Individuals from the low-altitude population exclusively displayed scatter hoarding behaviour. In contrast, high-altitude animals carried out larder hoarding combined with scatter hoarding (37.4% and 62.6% respectively). There was no intra-population variation between degus with different acclimation periods under captivity, thus inter-population differences in larder hoarding were maintained despite 6 mo of acclimation to a common environment. The geographic variation observed suggests that larder hoarding is favoured under harsher environmental conditions. We discuss some probable causes for this variation. The lack of effect of acclimation suggests that inter-population differences in larder hoarding might be the result of local adaptation or, less likely, it corresponds to an ontogenetically acquired irreversible behaviour.

Introduction

One of the most effective methods to assess the adaptive value of phenotypes has been the quantification of trait variation through comparisons between populations occurring in contrasting ecological conditions (Endler 1986; Foster & Endler 1999). Species inhabiting large geographical areas covering

various habitat types must cope with diverse ecological conditions, with large environmental differences across their range (see e.g. Oswald 1998; Foster & Endler 1999; D'Anatro & Lessa 2006; Ferguson & Higdon 2006; Wingfield et al. 2007). Each population may experience selective pressures different from those experienced in populations elsewhere, resulting in differences in phenotypic traits (e.g.

Solick & Barclay 2006; for reviews, see also Endler 1986; Foster & Endler 1999; Mosseau et al. 2000). Such phenotypic traits include behavioural traits, which can be quantified under laboratory conditions (e.g. Tannenbaum 1987; Thompson 1990; Haim 1991). The study of the geographical variation of behaviour can be an important tool allowing the inference of the environmental factors influencing the evolution of behaviour (Endler 1986; Foster & Endler 1999), and can provide valuable insights into the process of behavioural diversification across wild populations.

Among the main types of behaviours that significantly influence fitness (see Krebs & Davies 1997), food foraging directly affects the energetic balance and nutritional state of animals, which in turn influences growth, reproductive performance and other traits closely related to fitness (Ritchie 1990; Lemon 1991; see also Stephens et al. 2007). Foraging is defined as all those behaviours related to obtaining and consuming resources such as food searching, recognition, catching, manipulation, transportation, hoarding and feeding (Stephens & Krebs 1986; Hughes 1993). Moreover, foraging behaviour has important implications for the colonization of new territories and novel environments and hence it plays an essential ecological role for the species' distribution (Sol et al. 2005). Therefore, foraging represents an excellent topic for comparative studies of geographical variation in behaviour because its expression is closely related to environmental conditions and resource availability. For example, populations from colder environments, or from areas where food resources become seasonally scarce, may exhibit higher levels of food hoarding activity (Barry 1976; Vander Wall 1990; Jenkins et al. 1995).

Food hoarding is a behavioural strategy that has evolved independently in a wide range of taxa and habitats (Vander Wall 1990), suggesting that it represents an adaptation to temporally variable or unpredictable food supply due to weather, predation, competition or to fluctuations in energy demands (Vander Wall 1990; Jenkins & Peters 1992; Jenkins et al. 1995). Two major patterns of food hoarding, representing the extremes in the continuum of spatial distribution of food storage, have been identified (Vander Wall 1990; Jenkins et al. 1995). The storage of food items in a protected central location, such as a burrow or a nest, is known as larder hoarding, whereas scatter hoarding refers to the concealment of individual or small groups of food items in several locations (Vander Wall 1990). As different populations of a given species may experience distinct

environmental conditions (Foster & Endler 1999), behavioural differences in hoarding activity may occur, particularly under contrasting climatic or biotic conditions.

We carried out a study on the caviomorph rodent, *Octodon degus* (common name: degu), which occupies a wide distribution throughout north-central Chile (Fulk 1976; Le Boulengé & Fuentes 1978). *Octodon degus* is an endemic species commonly found in the Chilean matorral, a biogeographical zone characterized by hot and dry summers and cool, moist winters (Rundel 1981). It is a herbivorous diurnal rodent, with a diet composed mainly of herbs, seeds and leaves (Meserve 1981; Meserve et al. 1983). Degus are generally associated with shrub cover and variable amounts of open space where they forage (Le Boulengé & Fuentes 1978; Jaksic et al. 1981; Meserve et al. 1984; Iriarte et al. 1989). In these habitats (at low elevation), degus usually construct underground burrows and galleries that are used communally (Ebensperger et al. 2004), and which are connected above ground by a system of runways (Fulk 1976; Vasquez 1997; Vasquez et al. 2002). Despite the numerous studies of foraging in degus, detailed descriptions of hoarding behaviour are lacking. Some descriptive studies mention that degus store food in their burrows, including grasses and seeds (Woods & Boraker 1975; Fulk 1976; R. A. Vásquez, pers. obs.), and during field foraging experiments they have been observed hoarding seeds to their nests (larder hoarding) and/or to a few scatter sites digging a few (1–2) centimetres underground (R. A. Vásquez, unpubl. data). Fulk (1976) noticed that adults can transport grasses to a burrow where other subjects can consume it. There are no further studies describing food hoarding in degus.

We assessed foraging behaviour by focusing on hoarding carried out by animals captured in two geographically separated populations that experience highly contrasting winter seasons. One population was collected nearby Santiago, in a typical degu site located in the matorral of central Chile (450 m elevation; see Methods for details), which is characterized by Mediterranean-type climate. The second population was located at a high altitude in the Andes mountain range, to the east of the city of Ovalle at 2600 m elevation, in an area that undergoes long and cold winters that restrict the surface activity of degus (see Methods for details). There are no previous studies in high-altitude populations of degus.

Secondly, we conducted a laboratory-based within-population comparison between recently captured wild degus and those that had been in

captivity for 6 mo (i.e. acclimated). Quantification of behavioural phenotypes of acclimated and non-acclimated animals is a valuable technique to gain insights into the flexibility of behaviour. Plasticity studies in other taxa have demonstrated that this can be an efficient approach to understand the causes of variation in foraging behaviour (see Starck 1999; Honkoop & Bayne 2002). If acclimation to common conditions does not produce convergence in foraging behaviour among populations, then inter-population differences in behaviour might be due to local adaptation or irreversible phenotypic plasticity (see Piersma & Drent 2003; David et al. 2004).

We predicted that, in comparison with the low-altitude population, degus from the high-altitude population experiencing more restrictive weather conditions should be prone to a greater food hoarding activity as an adaptive response to seasonal variability in food availability and/or accessibility. Previous studies describe degus as being able to modify their foraging physiology and behaviour, and their daytime activity budget according to seasonal and shorter term variations (Bozinovic 1995; Bozinovic & Vasquez 1999; Bozinovic et al. 2000; Kenagy et al. 2002a,b, 2004; Vasquez et al. 2006), but only a few studies have dealt with spatial variation in the foraging ecology of degus within a broad trophic spectrum (Meserve et al. 1983, 1984; Zunino & Saiz 1991).

Materials and Methods

Subjects

We captured degus at each population using standard Sherman live traps, on sites where active burrows were observed. The low-altitude population is located at the University of Chile field station at Rinconada de Maipú ($70^{\circ}53'W$, $33^{\circ}28'S$), 30 km south-west from Santiago. This area consists of a flat topography dominated by scattered shrubs (*Proustia pungens*, *Acacia caven* and *Baccharis* spp.) and contains numerous degu burrows. Runways radiate from burrow entrances through the extensive herb cover via which degus continuously travel (for degu studies carried out in the area, see e.g. Fulk 1976; Vasquez 1997; Vasquez et al. 2002; Ebensperger et al. 2004). The second population of Río Los Molles (Bocatoma area) occurs at high altitude in the Andes range ($70^{\circ}15'W$, $30^{\circ}45'S$), 98 km east from the city of Ovalle, in the IV region in the north of Chile. In this site the ground is rocky and mostly sloped, shrubs and herbs occur at lower abundance, travel runways

are less frequent, and degus are rarely observed far outside from their burrows. The two populations are approx. 400 km apart, and there are several rivers and large valleys that separate central from north-central Chile. The captures were carried out between December 2004 and April 2005. The traps were first baited at dawn with a cereal and seed mix and checked at midday. Traps were re-baited in early afternoon and checked at dusk. Captured animals were weighed, sexed, marked with numbered ear tags (National Band & Tag Co., Newport, KY, USA) and brought into captivity. Each animal was housed in a standard metal cage ($80 \times 40 \times 35$ cm), with wood shavings, under near-natural temperature and photoperiod conditions. Captured animals were fed commercial rabbit pellets *ad libitum* (Champion S.A., Santiago, Chile), with free access to water. Individuals were maintained in captivity grouped together by their native populations. Experiments were conducted during the light period. After the trials, animals were released back to their original sites of capture.

Experimental Groups

Thirty-five wild-caught individuals were used for experiments. Nineteen individuals were caught at Rinconada de Maipú consisting of nine adult males and 10 adult non-pregnant females. Sixteen individuals were captured at Río Los Molles, including 10 adult males and six adult non-pregnant females.

To investigate the behavioural flexibility to environmental change and the reversibility of hoarding behaviour under controlled conditions, two subgroups were formed within each population group. One subgroup consisted of animals that had been acclimated to captivity over at least a period of 6 mo. The second subgroup consisted of recently caught individuals (2 wk before the commencement of the experiments). From the Rinconada de Maipú population, nine individuals (five females and four males) formed the 'non-acclimated' subgroup, and 10 animals formed the 'acclimated' subgroup (five males and five females). From Río Los Molles population, six individuals belonged to the 'non-acclimated' subgroup (one female and five males) and 10 animals in the 'acclimated' subgroup (five males and five females).

Procedure

We used four identical metallic arenas consisting of a rectangular enclosure of $1\text{ m} \times 1.5\text{ m} \times 80\text{ cm}$

(width × length × height). We poured sand into each arena to a depth of 3 cm. One nest box of galvanized metal measuring 25 × 25 × 10 cm was placed in a corner of each arena; each individual had its own artificial nest box burrow during the experiment. We examined the foraging and food hoarding behaviour of subjects by providing an artificial seed patch into the arena at the far side of the nest box. This patch consisted in a metallic tray of 20 × 20 cm filled with a mixture of 200 sunflower seeds (weighing a total of 22.0 g) and fine sand, following the method used by Vasquez (1996). Previous studies have demonstrated that degus use these seeds (see Vasquez et al. 2006). The distance from the burrow to the food patch was 1 m.

Prior to each experiment, individuals were allowed to become accustomed to their artificial burrow and to the experimental food over a 4-d period. To stimulate foraging activity during the experiments, we enforced a fasting period, only with access to water, for a 24-h period before the commencement of an experiment. The trials were carried out during the southern hemisphere fall season between March and June 2005. We began a trial by randomly placing animals of each population inside their own artificial burrow in one arena. Each trial lasted 18–19 h, beginning at about 17:00 h and ending at midday of the next day, encompassing with the period of highest activity in this species (Kenagy et al. 2002a,b). This length of time allowed subjects to become accustomed, explore and forage in the arenas (see e.g. Vasquez 1996). After each trial, we counted the number of seeds larder hoarded in the burrow, and then drained the sand with a manual sieve to count the number of hoarded seeds that had been buried throughout the arena. We also assessed the unharvested seeds remaining on the food tray to calculate seed consumption (see Vasquez 1994, 1996). Each animal was tested individually and only once. After each trial each arena was cleaned and sand smoothed for next time.

Statistical Analysis

Given that body mass might affect several energy intake variables, we first compared the body mass between the two populations using a two-way ANOVA incorporating native population and acclimation subgroup as factors. We used two-way factorial ANCOVAs for the three response variables: seeds consumption, total seeds hoarded and seeds scatter hoarded. Original population and acclimation level were included as factors, and individual weight as a covariate. Data

were transformed when appropriate to meet the assumptions of each analysis (see Sokal & Rohlf 1995). There was no need to carry out a statistical analysis in order to demonstrate differences in larder hoarding because only subjects from the high-altitude population stored seeds inside the burrow. For the analysis of the effect of acclimation within populations we used a nonparametric Wilcoxon signed rank test, due to the lack of normality of data. To test whether the number of seeds larder hoarded differed from seeds scatter hoarded within populations we used a paired t-test.

Results

Because body mass might directly affect foraging, we first analysed these data. Thereafter, body mass was used as a covariate for inter-population comparisons. There was a significant effect of the population's origin and acclimation level on body mass. Degus originating from the population at Rinconada de Maipú had a larger body mass compared with animals from Rio Los Molles (animals from the low-altitude population were 52.3% and 37.2% heavier, for non-acclimated and acclimated animals respectively; see Fig. 1), while within each population, individuals acclimated to captivity were heavier than those that were not (two-way ANOVA, population: $F_{3,31} = 85.4$, $p < 0.001$; acclimation: $F_{3,31} = 69.4$, $p < 0.001$; Fig. 1). There was no effect of the interaction between population and acclimation level ($F_{3,31} = 0.04$, $p = 0.83$; Fig. 1).

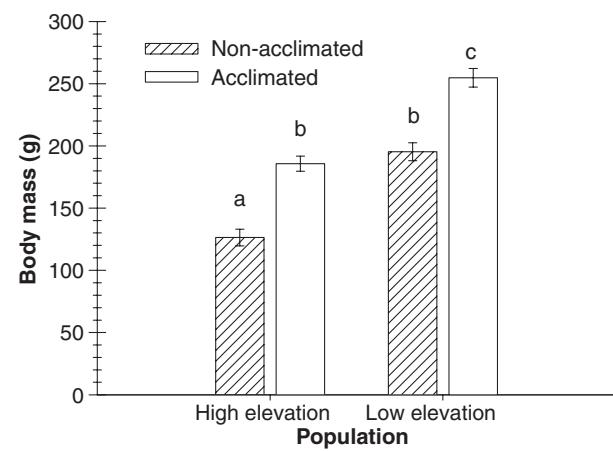


Fig. 1: Body mass of degus originating from the two studied populations and with different levels of acclimation to captivity. Values are means ± SE. Different letters represent statistically significant differences between groups, determined using Tukey's post hoc test.

There was no difference in the number of seeds consumed during each trial between both populations, nor among individuals that differed in acclimation level (two-way ANCOVA with body mass as a covariate, population: $F_{3,31} = 0.00008$, $p = 0.992$; acclimation: $F_{3,31} = 0.054$, $p = 0.816$; Fig. 2a). All degus of both populations, except one individual from Rinconada de Maipú, hoarded seeds at several places in the experimental arena. The amount of seeds hoarded did not differ between populations, and no differences were observed in the total amount of seeds hoarded between the two levels of acclimation within each population (two-way ANCOVA with body mass as a covariate, population:

$F_{3,31} = 3.105$, $p = 0.088$, power = 0.42; acclimation: $F_{3,31} = 0.347$, $p = 0.559$; Fig. 2b).

No significant differences were found between populations in the number of seeds that were scatter hoarded (i.e. in the sand outside the burrow). There was no effect of geographical population and of acclimation group on amount of seeds scatter hoarded (two-way ANCOVA with body mass as a covariate, population: $F_{3,31} = 0.514$, $p = 0.478$; acclimation: $F_{3,31} = 0.955$, $p = 0.336$; Fig. 3a).

No individual from the Rinconada de Maipú population stored seeds in their burrows. In contrast, individuals from the high-altitude population, in addition to scatter hoarding, also frequently stored

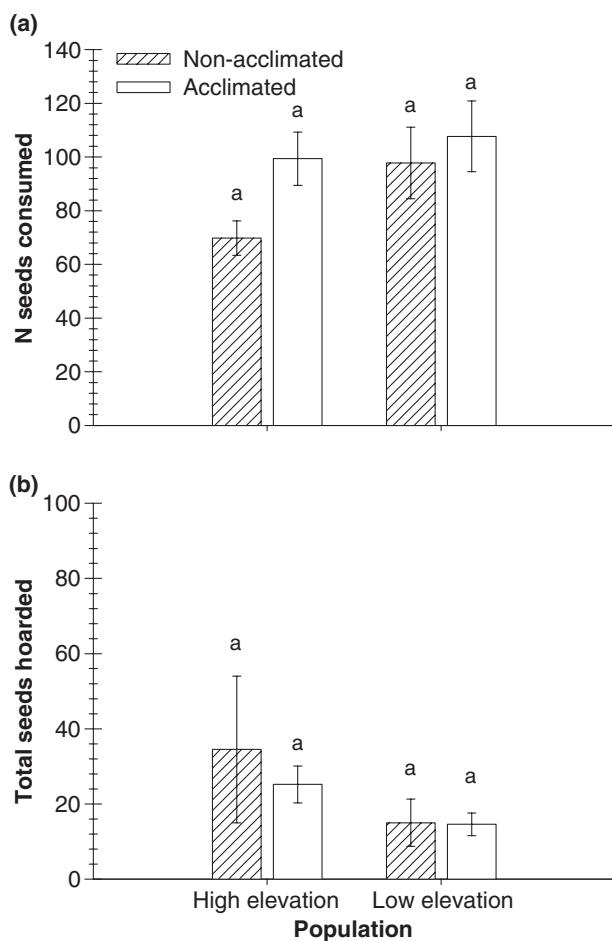


Fig. 2: (a) Total number of seeds consumed during the trials by degus originating from two populations, and belonging to different groups of acclimation time. (b) Total number of seeds hoarded during the trials by degus originating from two populations, and belonging to different groups of acclimation time to captivity within each population. Values are means \pm SE. The same letters represent no statistically significant differences between groups, determined using Tukey's post hoc test.

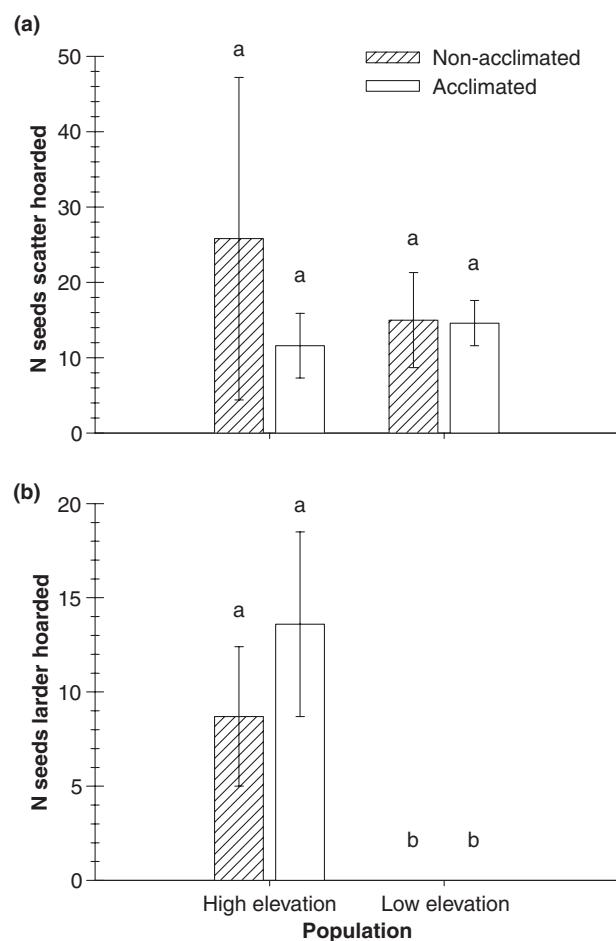


Fig. 3: (a) Number of seeds scatter hoarded throughout the arena during the trials by degus originating from two populations, and belonging to different groups of acclimation time. (b) Number of seeds larder hoarded inside the burrow during the trials by individuals originating from two populations, and belonging to different groups of acclimation time to captivity within each population. Values are means \pm SE. The same letters represent no statistically significant differences between groups, determined using Tukey's post hoc test.

seeds inside the burrow (9 of 16 animals larder hoarded; Fig. 3b). Subjects from the Rio Los Molles population did not show a significant difference between the number of seeds scatter and larder hoarded (paired t-test: $p > 0.05$).

There was no significant difference in the number of seeds that were larder hoarded between acclimated and non-acclimated subjects coming from the high-altitude population (Wilcoxon signed rank test, $p > 0.05$; Fig. 3b).

Discussion

Comparison Between Populations

Nearly all individuals displayed seed hoarding behaviour. Therefore, our results suggest that hoarding behaviour occurs as a fundamental component of foraging activity of this species. Degus appear to allocate a significant amount of energy to hoarding activities during foraging, and animals from both populations often appear to hoard food given the opportunity. This finding is important because there is not previous information about hoarding in degus. Furthermore, although no significant differences were found in the total amount of seeds hoarded between populations, we observed that degus from the high-altitude population tended to hoard a greater amount of seeds compared with the low-altitude population (see Fig. 2b). Further studies in degus could confirm this tendency, as it is known that other species of small mammals modify their behaviour in response to temperature, environmental condition and season, frequently hoarding greater quantities of food under colder environmental conditions (e.g. Schwaibold & Pillay 2006).

There was no difference in the total food intake of individuals between the two populations. This result may be due to similar energetic requirements for all degus under common controlled conditions, when food consumption is standardized to individual body mass (i.e. with individual body weight as a covariate). It should be noted that in the laboratory individuals experienced similar conditions in terms of space availability, thermoregulatory costs and food supply.

One prominent finding was that degus from the low-elevation population exclusively scatter hoarded, while degus originating from the high-altitude population larder and scatter hoarded. This inter-population difference is related to contrasting ecological conditions. It is well known that the environment in which animals inhabit can have a strong

impact on the development and evolution of behavioural patterns (Foster & Endler 1999; Brown & Braithwaite 2004). Even though we compare only two contrasting populations, a difference between them is sufficient to reject homogeneity in hoarding behaviour (i.e. lack of geographical variation) among populations (see e.g. Bell 2005). We think that the observed inter-population differences were due to intrinsic abiotic and/or biotic features differing between the studied populations, and that those differences are not idiosyncratic, and they emphasize the constraint of ecological conditions for shaping foraging behaviour in degus. In this vein, there are several factors (or a combination of them) that could have driven the variation in hoarding strategies observed between the two populations, and below we briefly discuss the most evident.

First, the high-altitude population at Rio Los Molles is located within the Andes mountain range, and it is characterized by low annual temperatures, long and cold winters with strong winds, storm presence, rain and snow cover during winter time. Feeding underground in cold weather may decrease the time that degus are exposed to lethal above-ground environmental conditions. Therefore, food storage chambers in the degu burrow system might be favoured in high-altitude populations, where food is hoarded during clear days in preparation for periods when above ground food is not accessible (e.g. cold nights, rainy days, snow cover days). In contrast, at low-altitude localities with milder weather, degus could hoard outside their burrows because individuals are able to recover the hoarded food free from restrictive climatic conditions. Other mammal species can modulate their foraging with other activities depending on environmental temperature; for example, rats can trade food for warmth under generally cold conditions (Schultz et al. 1999).

Previous research with Chilean rodents has revealed changes in foraging behaviour due to predation risk cues (Vasquez 1994, 1996; Vasquez et al. 2002; Ebensperger et al. 2006). The high-altitude population of Río Los Molles is characterized by lower availability of vegetation cover, a very rocky and sloped topography and the presence of snow during the winter. These factors could hinder the movements of degus and could also increase the conspicuousness to predators due to a higher contrast between the prey and background. These aspects might have favoured a more cautious foraging behaviour (for a review, see Caro 2005), resulting in degus directing their caches towards a

unique underground hidden point (i.e. they show larder hoarding).

The travel cost to patch resources and the risk of pilferage losses of the cached food are important factors that can affect hoarding behaviour as well (Daly et al. 1992; Jenkins & Peters 1992; Jenkins et al. 1995; Tsurim & Abramsky 2004). The low-altitude population has extensive meadows with larger and more widespread vegetation. Individuals of this population travel longer distances as revealed by long marked runways between burrow entrances and shrubs (see Vasquez et al. 2002), and particularly during the breeding season they can be highly territorial (Soto-Gamboa et al. 2005). In contrast, degus at the high-altitude population commonly build their burrows near shrub trunks (R.A. Vásquez, unpubl. data), in shorter zones mostly limited to moist areas associated with water run-offs or spring waters. These restricted areas could favour larder hoarding, suggesting that travel cost and pilferage risk could be lower. The high-altitude population seem to be less abundant and dense favouring a lower pilferage risk as well. Although Fulk's (1976) observation that degus in a low-altitude population can share food items with burrow mates challenges that idea. Furthermore, given that degus nest communally (Ebensperger et al. 2004), and that they can recognize some level of genetic relatedness via familiarity and kinship (Jesseau et al. 2008, Villavicencio et al. in press), possibly pilferage occurs mainly among non-relatives.

On the other hand, we found that degus originating from the low-altitude population had larger body mass than those from high elevation. The observed difference was maintained between acclimated subjects despite the similar period of time that each group experienced controlled captive conditions. We stress that this is the first study reporting body size differences between degu populations. Although it is difficult to pinpoint the precise factors driving this difference, possibly, smaller animals can cope better with seasonal environments than larger individuals because they are more likely to find enough food during the lean season (see e.g. Lehman et al. 2005).

From an evolutionary perspective, the intraspecific differences reported here may be explained in at least two ways. First, these differences may represent local adaptations and reflect genetic divergence, with behavioural types well suited to the environmental conditions (see e.g. Arnold 1981; Mosseau et al. 2000). On the other hand, the behavioural patterns may reflect environmentally triggered phenotypic

variation (Stearns 1989; Pigliucci 2001). As a first step to understand the source of this variation, we assessed flexibility in the hoarding behaviour by comparing individuals within each population under two different levels of acclimation (see next section).

Comparison Within Populations

Several aspects of phenotypic flexibility deserve attention because they influence the direction of the organism–environment interaction, and subsequently can alter its ecological impact. These include the time lag between changes in environmental cues and plastic responses, reversibility of responses and the shape of reaction norms with respect to environmental gradients (see Pigliucci 2001; Piersma & Drent 2003; David et al. 2004; Miner et al. 2005). Our results show that there was no convergence in the hoarding patterns between the two populations living under captivity-controlled conditions. In other words, the behavioural difference observed between populations was maintained after 6 mo under common conditions. Given that most behaviours, including foraging, are reversible or flexible, the maintenance of the hoarding patterns shown by experimental animals suggests that it might be due to genetic differentiation, thus supporting an explanation based on local adaptation. This idea is also supported by the long distance that separates both studied populations. Therefore, further studies will be needed to determine whether this hoarding response is a consequence of local adaptation to contrasting environments, or the result of a developmental genotype–environment interaction.

In addition, we found a significant body mass difference within each population between the two acclimated groups. The acclimated groups had larger body masses than newly captured animals in both populations. The longer captivity care, which included *ad libitum* food availability, controlled temperature, less space and therefore lower energetic requirements, seems to be the principal cause influencing the greater body mass of acclimated subjects. However, these captivity environmental factors did not influence the behavioural response expressed by subjects from each population.

Although behaviour is frequently thought as the most plastic or flexible phenotypic trait, our results have shown that between two degu populations, hoarding behaviour differs and it was not modified after a long period of common conditions. Therefore, larder hoarding seems to confer an adaptive advantage to degus inhabiting high-altitude habitats.

Acknowledgements

We thank M.C. Cecchi, I.N. Márquez, D. Parra, A. Rivera, W. van Dongen and R. Zúñiga for their valuable assistance. ENDESA-Chile (Los Molles hydro-electrical power station) kindly allowed us to conduct fieldwork in its property. Research was conducted under permit no. 5193 issued by the Servicio Agrícola y Ganadero, Chile, with the supervision of the Ethics Committee of the Faculty of Sciences, Universidad de Chile, and was funded by FONDECYT-1060186 to R.A.V., the Institute of Ecology and Biodiversity ICM-P05-002, and PFB-23-CONICYT.

Literature Cited

- Arnold, S. J. 1981: Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. *Evolution* **35**, 489–509.
- Barry, W. J. 1976: Environmental effects on food hoarding in deer mice (*Peromyscus*). *J. Mammal.* **57**, 731–746.
- Bell, A. M. 2005: Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J. Evol. Biol.* **18**, 463–474.
- Bozinovic, F. 1995: Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fiber. *J. Mammal.* **76**, 627–637.
- Bozinovic, F. & Vasquez, R. A. 1999: Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. *Funct. Ecol.* **13**, 602–610.
- Bozinovic, F., Lagos, J. A., Vasquez, R. A. & Kenagy, G. J. 2000: Time and energy use under thermoregulatory constraints in a diurnal rodent. *J. Therm. Biol.* **25**, 251–256.
- Brown, C. & Braithwaite, V. A. 2004: Size matters: a test of boldness in eight populations of the poeciliid *Brachyrhaphis episopi*. *Anim. Behav.* **68**, 1325–1329.
- Caro, T. 2005: Antipredator Defenses in Birds and Mammals. Univ. Chicago Press, Chicago, IL.
- D'Anatro, A. & Lessa, E. P. 2006: Geometric morphometric analysis of geographic variation in the Río Negro tuco-tuco, *Ctenomys rionegrensis* (Rodentia: Ctenomyidae). *Mamm. Biol.* **71**, 288–298.
- Daly, M., Jacobs, L. F., Wilson, M. I. & Behrends, P. R. 1992: Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. *Behav. Ecol.* **3**, 102–111.
- David, J. R., Gibert, P. & Moreteau, B. 2004: Evolution of reaction norms. In: Phenotypic Plasticity: Functional and Conceptual Approaches (De Witt, T. J. & Scheiner, S. M., eds). Oxford Univ. Press, New York, pp. 50–63.
- Ebensperger, L. A., Hurtado, M. J., Soto-Gamboa, M., Lacey, E. A. & Chang, A. T. 2004: Communal nesting and kinship in degus (*Octodon degus*). *Naturwissenschaften* **91**, 391–395.
- Ebensperger, L. A., Hurtado, M. A. J. & Ramos-Jiliberto, R. 2006: Vigilance and collective detection of predators in degus (*Octodon degus*). *Ethology* **112**, 879–887.
- Endler, J. A. 1986: Natural Selection in the Wild. Princeton Univ. Press, Princeton, NJ.
- Ferguson, S. H. & Higdon, J. W. 2006: How seals divide up the world: environment, life history, and conservation. *Oecologia* **150**, 318–329.
- Foster, S. A. & Endler, J. A. 1999: Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms and Adaptive Functions. Oxford Univ. Press, New York, NY.
- Fulk, G. W. 1976: Notes on the activity, reproduction and social behavior of *Octodon degus*. *J. Mammal.* **57**, 495–505.
- Haim, A. 1991: Behavior patterns of cold-resistant golden spiny mouse *Acomys russatus*. *Physiol. Behav.* **50**, 641–643.
- Honkoop, P. J. C. & Bayne, B. L. 2002: Stocking density and growth of the Pacific oyster (*Crassostrea gigas*) and the Sydney rock oyster (*Saccostrea glomerata*) in Port Stephens, Australia. *Aquaculture* **213**, 171–186.
- Hughes, R. N. 1993: Diet Selection: An Interdisciplinary Approach to Foraging Behavior. Blackwell Scientific Publications, Oxford.
- Iriarte, J. A., Contreras, L. C. & Jaksic, F. M. 1989: A long-term study of a small-mammal assemblage in the central Chilean matorral. *J. Mammal.* **70**, 79–87.
- Jaksic, F. M., Yáñez, J. L. & Fuentes, E. R. 1981: Assessing a small mammal community in central Chile. *J. Mammal.* **62**, 391–396.
- Jenkins, S. H. & Peters, R. A. 1992: Spatial patterns of food storage by Merriam kangaroo rats. *Behav. Ecol.* **3**, 60–65.
- Jenkins, S. H., Rothstein, A. & Green, W. C. H. 1995: Food hoarding by Merriam's kangaroo rats – a test of alternative hypotheses. *Ecology* **76**, 2470–2481.
- Jesseau, S. A., Holmes, W. G. & Lee, T. M. 2008: Mother-offspring recognition in communally nesting degus, *Octodon degus*. *Anim. Behav.* **75**, 573–582.
- Kenagy, G. J., Vasquez, R. A., Nespolo, R. F. & Bozinovic, F. 2002a: A time-energy analysis of daytime surface activity in degus, *Octodon degus*. *Rev. Chil. Hist. Nat.* **75**, 149–156.
- Kenagy, G. J., Nespolo, R. F., Vasquez, R. A. & Bozinovic, F. 2002b: Daily and seasonal limits of time and temperature to activity of degus. *Rev. Chil. Hist. Nat.* **75**, 567–581.
- Kenagy, G. J., Vasquez, R. A., Barnes, B. M. & Bozinovic, F. 2004: Microstructure of summer activity bouts of degus in a thermally heterogeneous habitat. *J. Mammal.* **85**, 260–267.

- Krebs, J. R. & Davies, N. B. 1997: *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific Publications, Oxford.
- Le Boulegé, E. & Fuentes, E. R. 1978: Quelques données sur la dynamique de population chez *Octodon degus* (Rongeur Hystricomorphe) du Chili central. *La Terre et la Vie* **32**, 326–341.
- Lehman, S. M., Mayor, M. & Wright, P. C. 2005: Ecogeographic size variations in sifakas: a test of the resource seasonality and resource quality hypotheses. *Am. J. Phys. Anthropol.* **126**, 318–328.
- Lemon, W. C. 1991: Fitness consequences of foraging behaviour in the zebra finch. *Nature* **352**, 153–155.
- Meserve, P. L. 1981: Trophic relationships among small mammals in a Chilean semiarid thorn shrub community. *J. Mammal.* **62**, 304–317.
- Meserve, P. L., Martin, R. E. & Rodriguez, J. 1983: Feeding ecology of two Chilean caviomorphs in a central Mediterranean savanna. *J. Mammal.* **64**, 322–325.
- Meserve, P. L., Martin, R. & Rodríguez, J. 1984: Comparative ecology of the caviomorph rodent *Octodon degus* in two Chilean mediterranean-type communities. *Rev. Chil. Hist. Nat.* **57**, 79–89.
- Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K. & Relyea, R. A. 2005: Ecological consequences of phenotypic plasticity. *Trends Ecol. Evol.* **20**, 685–692.
- Mosseau, T. A., Sinervo, B. & Endler, J. 2000: *Adaptive Genetic Variation in the Wild*. Oxford Univ. Press, New York.
- Oswald, C. 1998: Geographic variation and plasticity in renal function in the white-footed mouse, *Peromyscus leucopus*. *J. Mammal.* **79**, 1103–1110.
- Piersma, T. & Drent, J. 2003: Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* **18**, 228–233.
- Pigliucci, M. 2001: *Phenotypic Plasticity: Beyond nature and nurture*. Johns Hopkins University Press, Baltimore, MD.
- Ritchie, M. E. 1990: Optimal foraging and fitness in Columbian ground squirrels. *Oecologia* **82**, 56–67.
- Rundel, P. W. 1981: The matorral zone of central Chile. In: *Mediterranean Type Shrublands* (Di Castri, F., Goodall, D. W. & Specht, R. L., eds). Elsevier, Amsterdam, pp. 175–201.
- Schultz, L. A., Collier, G. & Johnson, D. F. 1999: Behavioral strategies in the cold: effects of feeding and nesting costs. *Physiol. Behav.* **67**, 107–115.
- Schwaibold, U. & Pillay, N. 2006: Behavioral strategies of the African ice rat *Otomys sloggetti robertsi* in the cold. *Physiol. Behav.* **88**, 567–574.
- Sokal, R. R. & Rohlf, F. J. 1995: *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edn. W.H. Freeman and Company, New York.
- Sol, D., Stirling, D. G. & Lefebvre, L. 2005: Behavioral drive or behavioral inhibition in evolution: subspecific diversification in holarctic passerines. *Evolution* **59**, 2669–2677.
- Solick, D. I. & Barclay, R. M. R. 2006: Morphological differences among western long-eared myotis (*Myotis evotis*) populations in different environments. *J. Mammal.* **87**, 1020–1026.
- Soto-Gamboa, M., Villalón, M. & Bozinovic, F. 2005: Social cues and hormone levels in male *Octodon degus* (Rodentia): a field test of the Challenge hypothesis. *Horm. Behav.* **47**, 311–318.
- Starck, J. M. 1999: Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Biol.* **202**, 3171–3179.
- Stearns, S. C. 1989: Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259–268.
- Stephens, D. W. & Krebs, J. R. 1986: *Foraging Theory*. Princeton Univ. Press, Princeton, NJ.
- Stephens, D. W., Brown, J. S. & Ydenberg, R. C. 2007: *Foraging: Behavior and Ecology*. Univ. Chicago Press, Chicago, IL.
- Tannenbaum, M. G. 1987: Variation in hoarding behaviour in south-eastern *Peromyscus*. *Anim. Behav.* **35**, 297–299.
- Thompson, D. B. 1990: Different spatial scales of adaptation in the climbing behavior of *Peromyscus maniculatus*: geographic variation, natural selection, and gene flow. *Evolution* **44**, 952–965.
- Tsurim, I. & Abramsky, Z. 2004: The effect of travel costs on food hoarding in gerbils. *J. Mammal.* **85**, 67–71.
- Vander Wall, S. B. 1990: *Food Hoarding in Animals*. Univ. Chicago Press, Chicago, IL.
- Vasquez, R. A. 1994: Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. *Behav. Ecol. Sociobiol.* **34**, 375–381.
- Vasquez, R. A. 1996: Patch utilization by three species of Chilean rodents differing in body size and mode of locomotion. *Ecology* **77**, 2343–2351.
- Vasquez, R. A. 1997: Vigilance and social foraging in *Octodon degus* (Rodentia, Octodontidae) in central Chile. *Rev. Chil. Hist. Nat.* **70**, 557–563.
- Vasquez, R. A., Ebensperger, L. A. & Bozinovic, F. 2002: The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behav. Ecol.* **13**, 182–187.
- Vasquez, R. A., Grossi, B. & Marquez, I. N. 2006: On the value of information: studying changes in patch assessment abilities through learning. *Oikos* **112**, 298–310.
- Villavicencio, C. P., Márquez, I. N., Quispe, R. & Vásquez, R. A. 2009: Familiarity and phenotypic similarity influence kin discrimination in the social rodent *Octodon degus*. *Anim. Behav.* (In press).

- Wingfield, J. C., Meddle, S. L., Moore, I., Busch, S., Wacker, D., Lynn, S., Clark, A., Vasquez, R. A. & Addis, E. 2007: Endocrine responsiveness to social challenges in northern and southern hemisphere populations of *Zonotrichia*. *J. Ornithol.* **148**, S435—S441.
- Woods, C. A. & Boraker, D. K. 1975: *Octodon degus*. *Mamm. Species* **67**, 1—5.
- Zunino, S. & Saiz, F. 1991: Structure and density of population of *Octodon degus* mol. *Stud. Neotrop. Fauna Environ.* **26**, 143—148.