Cost of living in free-ranging degus (*Octodon degus*): seasonal dynamics of energy expenditure

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Abstract

Animals process and allocate energy at different seasons at variable rates, depending on their breeding season and changes in environmental conditions and resulting physiological demands. Overall total energy expenditure, in turn, should either increase in some seasons due to special added demands (e.g. reproduction) or it could simply remain at about the same level, in which case the animals must show compensatory rebalancing of other expenditures that can be reduced. To test for the alternative hypotheses of seasonal variability or compensation, we measured total daily energy expenditure (DEE) in free-living degus (*Octodon degus*) at four seasons and followed this with determinations of basal metabolic rate (BMR) in the laboratory in the same individuals. DEE varied seasonally but was only significantly different (lower) in summer (non-breeding season), with a DEE:BMR ratio of only 1.6, whereas autumn, winter and spring DEE values were statistically indistinguishable from one another and showed DEE:BMR ratios ranging from 1.9 to 2.2. Our values of DEE in the field fall within the broad range of allometric expectation for herbivorous mammals in general, but the ratios of DEE:BMR are lower than expected. This, together with the lack of strong major shifts in total levels of DEE, suggests that degus are showing compensatory shifts among various categories of energy expenditure that allow them to manage their overall energy balance by minimizing total expenditure.
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1. Introduction

Many of the spatial and temporal variations in the activities of animals are centered on how to obtain, allocate and conserve energy. The balance between acquisition and expenditure of energy is critical to survival and reproductive success. This balance depends on the interplay among intake of matter and energy, digestive processing, allocation to alternative functions such as thermoregulation, growth, reproduction and others (Karasov, 1986; Bacigalupe and Bozinovic, 2002). Indeed, animals can face spatial and temporal unpredictability in the food availability in the environment as well as in climatic conditions. Nevertheless the energy

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budget of an organism may change due also to constraints of its own physiological design and demands of various functions to be performed (Drent and Daan, 1980; Kirkwood, 1983; Weiner, 1992; Hammond and Diamond, 1997).

Two competing hypotheses suggest how endotherms attempt to manage their energy allocation seasonally in relation to environmental changes (e.g. Weathers and Nagy, 1980; Doherty et al., 2001). These hypotheses are the peak total demand and the reallocation hypotheses, predicting, respectively, that total energy expenditure is higher during breeding or winter, or does not vary across seasons. Recently, Nagy et al. (1999) reviewed the energetics of free-ranging mammals by summarizing information on the daily energy expenditure (DEE) of animals in the field, also known as field metabolic rate (FMR), which is typically determined by the doubly-labeled water (DLW) method (Nagy, 1987; Speakman, 1997). FMR includes basal rate of metabolism (BMR), thermoregulation, locomotion, foraging, digestion, growth, reproduction, as well as all energy expenditures that eventually end up as heat production. Nagy et al. (1999) reported that studies of seasonal FMR in 19 species of mammals indicated a lack of seasonal differences in FMR. These studies thus appear to support the reallocation hypotheses. Berteaux (1998), however, reported that female meadow voles (*Microtus pennsylvanicus*) show both reallocation and increased energy demand, but her overall results indicate increased expenditure. Nevertheless, after reviewing the effect of seasonal changes of FMR in 16 species of small mammals, Speakman (2000) reported a variety of contradictory results and concluded that thermal acclimatization and behavioral plasticity are important mechanisms involved in the dynamics of energy allocation in free-ranging small mammals.

Food abundance and climatic conditions in nature influence the rates at which animals can acquire and expend energy (Kenagy et al., 1989; Corp et al., 1999). Environmental temperature varies in time and space at different time scales; therefore, organisms are continually challenged to maintain energetic homeostasis (Johnston and Bennett, 1996). For mammals the concomitant effects of environmental constraints associated with the availability and quality of food during pregnancy and lactation may limit the acceleration in energy expenditure and production that occurs during reproduction, which will finally affect the structure of the animal's energy budget.

The contrasting results and analyses concerning the effect of environmental conditions on the cost of living for mammals in the field, as presented by Speakman (2000), is the basis on which we designed the present study to evaluate the seasonal energetics of an herbivorous semi-fossorial rodent, the degu, *Octodon degus* (Octodontidae). The degu inhabits the seasonal semiarid Mediterranean environment of Central Chile, where summers are hot and dry and winters are cold and rainy. It appears to be limited in its spatial and temporal use of habitat by thermal conditions and predation risk (Jaksic, 1986; Lagos et al., 1995; Kenagy et al., 2002a; Vásquez et al., 2002; Bacigalupe et al., 2003). Indeed degus shift from a bimodal foraging regime in summer to a unimodal one in winter (Kenagy et al., 2002a). In the field as well as in laboratory experiments, foraging degus can be temporally and spatially constrained by thermal tolerance, food quality and predation risk (Jaksic, 1986; Bozinovic, 1995; Lagos et al., 1995; Bozinovic and Vásquez, 1999; Yunger et al., 2002). Degus are seasonal breeders and usually reproduce successfully only once a year, with parturition in early spring, followed by a non-reproductive period in summer. Degus have a lengthy gestation of 3 months, giving birth to relatively precocial young that require 3 weeks of suckling (Morales, 1982; Rojas et al., 1977).

In this study we examined the seasonal field energetics in degus. Since degus are known to behaviorally avoid harsh environmental conditions we hypothesized that DEE in free-living degus would not vary markedly among seasons (the reallocation hypothesis) similar to most other small mammals studied so far (Nagy et al., 1999). Further, we tested whether they exhibit a limit to DEE in the field at the postulated limit of four times BMR (Drent and Daan, 1980).

2. Materials and methods

2.1. Site and design of study

A seasonal sequence of four studies was conducted between winter 2001 and autumn 2002 in natural matorral habitat in the Andean foothills at San Carlos de Apoquindo (33°23′S, 70°31′W), approximately 20 km east of Santiago, at a study site with elevation approximately 1100 m. We

used the field-station property of the Estación de Investigaciones Ecológicas Mediterráneas (EDIEM) of the Universidad Católica de Chile (see www.bio.puc.cl/ediem/). Climate and habitat are described in detail at www.bio.puc.cl/sca/, and weather data were obtained from a computerized weather station at EDIEM. The vegetation at the study site is sclerophyllous, described physiognomically as evergreen scrub, and more specifically known as matorral. The climate is Mediterranean, with an annual mean precipitation of 376 mm, concentrated 65% in winter, from June to August. Precipitation is minimal from December to March, with only 3% of the annual total. Temperatures are highest from December to March, corresponding to the austral summer, and lowest from June to August, the austral winter. On average, the mean minimum temperature is approximately 6 °C below the mean temperature, while the maximum mean lies approximately 6 °C above. The broadest daily range (from mean maximum to mean minimum) of air temperatures (T_a) is observed from December to February (16–17 °C), and the narrowest from May to August (9–10 °C). The combination of high temperatures and low precipitation from December to March thus represents the typical summer drought of this Mediterranean climate.

The dates, in sequence, of the four seasonal sampling periods were winter (6–8 August), spring (1–3 October), summer (18–20 and 25–27 January), and autumn (21–23 May). Recorded standard average air temperatures (2 m height) during the four seasonal sampling periods were: winter: 9.3 ± 7.1 °C (range: 0.8–22.8 °C), spring: 13.4 ± 8.6 °C (range: 4.8–23.8 °C), summer: 19.1 ± 7.9 °C (range: 9.7–26.9 °C) and autumn: 11.8 ± 9.2 °C (range: 1.9–17 °C).

We selected a rectangular study plot of 70×50 m at EDIEM because of its open space and relatively sparse shrub and tree cover. To enhance recapture success of degus, we constructed an enclosure of this rectangle with 1.8 m high wire grid fencing (2.5 cm squares), additionally burying galvanized sheet-metal barriers to a depth of 40 cm. The open microhabitat was comprised >90% of a cover of grasses and small herbs, and the shrubs and small trees amounted to approximately 15% cover, comprised of *Baccharis linearis*, *Lithrea caustica* and *Acacia caven*.

In July 2001 we released an initial cohort of 23 adult degus (eight males, 15 females), which we captured from adjacent habitat, into the enclosure. The degus were initially provided with artificial below-ground shelters that we constructed with bricks and boards. Within several weeks the animals made their own tunnels and burrow openings in the soil surrounding the artificial burrows. In order to offset the effects of natural adult mortality (which included effects of aerial but not large terrestrial predators) we introduced an additional 20 degus (six males, 14 females) at subsequent intervals in order to maintain sample sizes for the metabolic measurements. During the course of the study adult females showed signs of pregnancy in August and September and of lactation in September and October; juveniles appeared above ground in October, but these were not included in the metabolic measurements. Adults in January were no longer in reproductive condition, and in May the adults were entering into breeding condition.

Degus are social and colonial, and occupy very small home ranges, estimated as small as 0.04 ha (Agüero and Simonetti, 1989) or ranging 0.05–0.71 ha (Zunino et al., 1992).

2.2. Measurements of field and basal energy expenditure

Daily energy expenditure in the field was measured at the four specified seasonal time intervals using the doubly labeled water (DLW) method with a water mixture enriched with ^{2}H and ^{18}O provided by the Center for Isotope Research (CIO) at the University of Groningen, The Netherlands (www.cio.phys.rug.nl). We otherwise used the protocol of Kenagy et al. (1989) and injected 0.8 ml DLW. After 1 h equilibration we obtained an initial blood sample, under light ether anesthesia, from the orbital sinus with an 80 µl heparinized capillary tube; individual 15 µl aliquots of blood were flame-sealed with a fine-pointed propane torch and stored at 5 °C pending analysis. Degus were weighed with a portable electronic Sartorius™ balance (±0.01 g). Although retrapping of degus after 48 h was facilitated by the study enclosure, we did not recapture all individuals, and we report only the final numbers of samples for DLW analysis that were recaptured after approximately 48 h. Time of sampling was recorded to the nearest minute and metabolic rates expressed as 24 h, daily rates. Samples were sent to the CIO for analysis of isotope concentrations by isotope ratio mass spectrometry. We converted ml CO_2 to kJ

Table 1
Seasonal pattern body mass (m_b), basal metabolic rate (BMR), daily energy expenditure (DEE) and the ratio DEE:BMR in *Octodon degus*

	Summer	Autumn	Winter	Spring	*P*
Number of animals	9	5	7	7	
Body mass (g)	182.17 ± 13.3	206.52 ± 17.8	184.31 ± 15.0	181.20 ± 15.0	0.682
Basal metabolic rate (kJ/day)	77.9 ± 6.5	76.6 ± 8.7	72.7 ± 7.4	71.6 ± 7.4	0.906
Percent[1]	170.0	150.98	157.08	156.72	
Daily energy expenditure (kJ/day)	125.0 ± 5.8	142.0 ± 7.8	150.4 ± 6.6	155.9 ± 6.6	0.008
Percent[2]	57.8	60.6	69.1	72.4	
DEE:BMR	1.6	1.9	2.1	2.2	
Percent[3]	66.7	78.6	86.5	90.6	

Values are mean $\pm$ S.E.M. *P* values after an ANCOVA test using m_b as a covariate are indicated; Percent[1] $=$ BMR/(BMR in J/h $= 29.87\ m_b^{0.799}$), equation of McNab (1988); Percent[2] $=$ FMR or DEE /(FMR in kJ/d $= 7.94\ m_b^{0.646}$), equation of Nagy et al. (1999); Percent[3] $=$ DEE/(DEE:BMR $= 4.79\ m_b^{0.133}$), equation of Degen and Kam (1995).

assuming 21.7 J/ml CO_2. At each season background samples were obtained from uninjected degus inhabiting the same enclosure. Fluxes were calculated for each individual, on the basis of the individual-specific size of the body water pool (based on the plateau value of the ^{2}H dilution; Bozinovic et al., 2003), and the individual-specific fractional ^{2}H turnover rate. We took isotope fractionation effects into account, assuming that 50% of the water efflux was lost through evaporative pathways, following Kenagy et al. (1989). In three animals, the sizes of their body water pools could not be assessed due to minor leakage of the DLW dose. In these cases, we used the average percentage of body water to estimate the individual-specific sizes of the body water pool.

To determine BMR at each season we transferred the individuals recaptured at 48 h to the laboratory and housed them individually in plastic cages ($60 \times 60 \times 20$ cm), lined with approximately 3 cm of wood chips, and fed them carrots ad libitum. Temperature and photoperiod were held constant at 22 ± 2 °C and 12L: 12D. Animals were held for 2 days prior to BMR measurements and then fasted for 6 h immediately before placement in 1000 ml steel chambers, at air temperature (T_a) 30.0 ± 0.5 °C, which is within the thermoneutral zone for this species (Rosenmann, 1977; Veloso and Bozinovic, 1993). BMR was determined according to the following protocol for measurements collected over a 3-h period during mid-morning. Oxygen consumption (V_{O_2}) was measured in a computerized (Datacan V™) open-flow respirometry system (Sable Systems, Henderson, NV, USA). The metabolic chamber received dried air at a rate of 800 ml/min from thermal-mass flow-controllers (Sierra Instruments™, Monterey, CA, USA), which ensured adequate mixing in the chamber. Air passed through CO_2-absorbent granules of Baralyme™ and Drierite™ before and after passing through the chamber and was monitored every 5 s by an applied electrochemistry O_2-analyzer, model S-3A/I (Ametek™, Pittsburgh, PA, USA). Oxygen consumption values were calculated using equation 4a of Withers (1977): p. 122). We converted ml O_2 to kJ assuming 20.1 J/ ml O_2. All degus were returned to the field enclosure within a week. Observed BMR was compared against standard BMR values predicted for small burrowing grazers (McNab, 1988), i.e. BMR (J/h) $= 29.87\ m_b^{0.799}$, where $m_b =$ body mass. In the same manner observed DEE in the field (FMR) was compared against standard FMR values predicted for herbivorous mammals (Nagy et al. 1999), i.e. FMR (kJ/d) $= 7.94\ m_b^{0.646}$. Finally, the allometric equation for the FMR:BMR ratio in relation to m_b for eutherian mammals (Degen and Kam, 1995), i.e. FMR:BMR $= 4.79\ m_b^{-0.133}$, was also used as a standard reference.

2.3. Statistics

Statistical analyses were performed using the STATISTICA (2001) statistical package for Windows operating system. Data were analyzed by ANCOVA and Tukey tests for multiple comparisons using m_b as a covariable. Data fulfilled the assumptions of the ANCOVA. Results are reported as mean ± 1 S.E.M.

3. Results

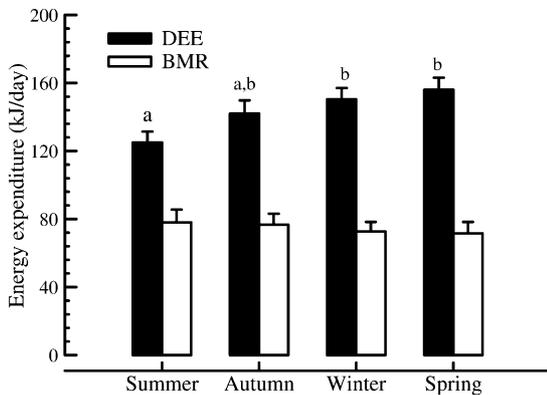Body mass of the free-living degus did not differ significantly in relation to season (Table 1,

Fig. 1. Seasonal pattern of variation in daily energy expenditure (DEE) of free-living *Octodon degus* and basal metabolic rate (BMR) of the same individuals measured in the laboratory. Values are mean ± 1 S.E.M. Same letters indicate non-significant differences among seasons by post-hoc Tukey test (see text). Sample size and further details in Table 1.

d.f. = 3,24, $F = 0.505$, $P = 0.682$). Similarly basal metabolic rate (BMR) did not vary significantly by season (Fig. 1, d.f. = 3,23, $F = 0.184$, $P = 0.906$).

Daily energy expenditure (DEE) varied significantly over the seasons (Fig. 1, d.f. = 3,23, $F = 8.295$, $P = 0.0006$). The outstanding difference, revealed by Tukey post-hoc test, was that summer DEE was lower than that of winter and spring ($P = 0.010$ and 0.002, respectively) though not significantly different from autumn ($P = 0.227$). However, among themselves, autumn, winter, and spring, DEE did not differ significantly ($P = 0.227$, 0.764 and 0.391, respectively). No significant differences were observed between males and females in any season of the year (d.f. = 3,23, $F = 0.632$, $P = 0.601$). All of our DEE values fall within the 95% confidence limits of the allometric prediction of Nagy et al. (1999) for herbivorous mammals, which show an enormous range of 54–421% of the predicted DEE value.

4. Discussion

In the semiarid environment of degus, thermal opportunities for activity shift seasonally, along with the quality and availability of food. We have previously suggested that flexibility in the behavioral timing of surface activity allows degus to maintain thermal homeostasis and energy balance throughout the year under these conditions (Kenagy et al., 2002a). Degus remain active on the

surface under a much narrower range or 'window' of thermal conditions than those that occur over the entire range of the day and year. Furthermore degus exhibit a low net allocation of time and energy to locomotion, suggesting further that their daily activities are not limited by the extreme environmental conditions of the summer solstice (Kenagy et al., 2002b; Bacigalupe et al., 2003). Their total energy intake requirements can be met by as little as 4.5 h of surface activity for foraging per day. The small impact of locomotion on the total energy budget is thus a further economy of the behavior of these animals.

We have attempted to understand how small endotherms manage their energy allocation as a function of environmental seasonality by testing the peak demand and the reallocation hypotheses in *O. degus* living under field conditions. Several values of DEE obtained from captive degus (on ad libitum food and water) provide interesting comparisons. Using the laboratory metabolic data of Rosenmann (1977), continuous 24 h exposure to 10 °C air would produce a DEE of 178 kJ/day, and to 20 °C air a DEE of 112 kJ/day (at a body mass of 183 g, as per Table 1). These two values lie, respectively, above and below, our four seasonal field values of DEE, and thus, due only to laboratory thermoregulatory costs associated with existence on ad libitum food and water, we find rates of laboratory DEE that can exceed the annual range observed in the field. This kind of comparison suggests both that life in the laboratory may be extravagant when ad libitum food and water are available, and however, that in nature the animals practice more parsimonious economies. Looking further at energetics of female degus in the laboratory the values obtained by Veloso and Bozinovic (2000), for individuals on ad libitum food and water and with a body mass of 200 g, amount to DEE as great as 264 kJ/day. Such levels of DEE exceed by far the rates we measured in the field (Fig. 1; Table 1). Again this suggests that expenditures in captivity may be extravagantly high, and that field conditions seem to yield rather modest rates of overall energy expenditure.

Our values of field DEE support neither the reallocation nor the peak demand original hypotheses. In part the potential of such a demonstration is limited because the DLW method of measuring DEE determines only the total of all expenditures. It does not provide a determination of the internal adjustments of allocations that could lead, for

example, to compensatory decrease in one category to balance an increase in another. It is clear, however, from our field data that seasonal variation in DEE is generally modest. Nevertheless, a caution note is necessary because both hypotheses have been developed with regards to reproductive investment of females, and not to males. Despite that the hypotheses could be adapted to make predictions about male investment, the predicted patterns of seasonal change in DEE would not be the same for males and females because male investment (access to females) occurs before peak female investment (lactation). Nevertheless, because we found no differences in DEE or in BMR between sexes, we pooled the data, and we adapted and generalized both hypotheses to both sexes.

In light of the modest variation in overall DEE, we can point out one component of the energy budget that apparently can show a surprising economy in winter. Field observations of winter activity behavior (at the season when shaded air temperatures and soil temperatures are at a minimum), revealed that the above-ground component of daily existence may occur exclusively under exposure to direct solar radiation (Kenagy et al., 2002a). Because winter solar radiation is mild and tolerable to degus, it means that they encounter operative environmental temperatures that allow them to exist in thermal neutrality (no thermoregulatory costs) while active on the surface. This feature of degu physiology and environment apparently contributes to the moderate winter value of DEE (Fig. 1), which closely approximates those of autumn and spring. Indeed, we (Kenagy et al., 2002a,b) presented an analysis of behavioral flexibility in a day-active caviomorph rodent, the degu, in response to temporal (daily, seasonal), spatial and thermal heterogeneity of its environment. We quantified activity and foraging behavior in a population, together with thermal conditions, in an extremely open habitat in the seasonally hot and arid matorral of Central Chile. We observed that summer activity was bimodal, with a gap of more than 8 h between the morning bout of 2.5 h of intensive foraging and the afternoon bout of 2 h. More than half of this surface activity occurred in the shade of early-morning or late-afternoon provided when the sun was below the local skyline. Autumn and spring activity were also bimodal, but with greater proportions of the activity occurring under direct solar radiation, and with shorter mid-

day gaps between the two major bouts. Winter activity was unimodal and all occurred under direct solar radiation. In summer, autumn and spring the activity of degus was curtailed as operative temperature moved above 40 °C. At the winter solstice (June) operative temperature generally remained below 30 °C, which means that heat load could not drive body temperature above normal; consequently degus remained in the open throughout the middle of the day. Assessing time budgets in summer, we found that individual degus spent approximately 2/3 of their above-ground time foraging; they remained stationary approximately 88% of the time, walked around slowly approximately 10%, and ran rapidly from one point to another only approximately 2% of the time. Net locomotion costs were computed at only 2.2% of daily energy expenditure; this taken together with abundant distribution of plant food over an extremely small home range leads us to conclude that time, space, thermal tolerances and food processing do not constrain the performance of degus under normal conditions. Energy demands can be met by as little as 4.5 h surface activity per day. Finally, we concluded that flexibility of timing allows degus to maintain thermal homeostasis and energy balance throughout the year. This is consistent with the interpretation of Garland (1983) that small mammals in general allocate only approximately 1% of DEE to net costs of locomotion. Speakman (2000) has also pointed out that thermal acclimatization and behavioral plasticity are important mechanisms for allocating energy expenditure in free-ranging small mammals. Indeed, the environmental modification of the organism's physiology in the field, or acclimatization, is often hypothesized to allow organisms to adjust to changing biotic and abiotic environmental conditions through increases in performance.

Our results with field DEE seem to support our interpretation of energy minimization previously suggested with regard to the time management of degus (Kenagy et al., 2002a), and thus we are able to identify a novel behavioral and physiological strategy. These animals appear to decrease their activity and foraging strategy depending on summer thermoregulatory and feeding costs, thus maintaining a lower DEE during the hot, dry season. This avoidance behavior depends on the total thermal demands, the supply and distribution of food and the total amount of time available for access to the food.

Our previous observations of activity timing (Kenagy et al., 2002a,b) can be further interpreted with the observation that degus can supplement food and water intake by passing fecal pellets through the digestive tract a second time, i.e. the practice of coprophagy (Kenagy et al., 1999). Nonetheless our assessment of time use by degus suggests that they have adequate time available throughout the day at any time of year for the few hours of foraging they require to survive on their generalist herbivore diet. Although individual components of their energy demands must be accelerated at times, for example during reproduction (Veloso and Bozinovic, 2000), we were unable to detect an increase in overall DEE during reproduction in the field. Further studies are needed, with larger sample size and explicit design to examine males and females separately and at more closely specified stages of the annual cycle, in order to pinpoint significant natural biological variation over the course of the year.

Our observed values of DEE in the field fall within the broad range of allometric expectation for herbivorous mammals in general, but the ratios of DEE:BMR are lower than expected. Indeed, Speakman's (2000) comprehensive review of DEE:BMR ratios in 62 species of small mammals reported that the modal class of ratios was centered on 2.5, with a median of 3.1 and a mean of 3.4. Degus exhibit a DEE:BMR ratio near 2 (Table 1), which is much lower than the theoretical limit of four times BMR postulated by Drent and Daan (1980), however, degus do fall within the modal class for small mammals. This, together with the lack of strong major shifts in total levels of DEE, suggests that degus are showing compensatory shifts among various categories of energy expenditure that allow them to manage their overall energy balance by minimizing expenditure, which suggest they are reallocating activity and energy expenditures, not as originally stated by the reallocation hypothesis—i.e. not during breeding and winter, but during summer.

Acknowledgments

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