Time and energy use under thermoregulatory constraints in a diurnal rodent

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Abstract

(1) This study was designed to understand how thermoregulatory constraints affect the timing of foraging bouts and amount of food obtained from a feeding station that was subject to an intense heat load. (2) The degu, *Octodon degus*, is a diurnal rodent inhabiting hot arid environments in Chile. Two-hour trials were run in a laboratory experimental arena to determine time allocation between a food station located under a heavy radiant heat source (2500 W/m^2) and the rest of the arena, including a cool burrow. A video camera recorded the animal's movements during the trial, and tapes were analyzed afterwards for seven degus with a heated food site and seven degus with a normal, unheated food station. (3) Degus with a food patch exposed to heat spent less time foraging and harvested less food than animals with no heat load. Over a two hour period time use of the food patch was significantly less when heated than when not heated (0.65 ± 0.59 vs 4.90 ± 1.73 min, respectively). Thus the degus subjected to heat above their food source minimized time exposure to a physiologically stressful condition by decreasing their visits to the heated food source, thereby reducing food (=energy) intake. (4) Oxygen consumption (VO$_2$), evaporative water loss (EWL) and body temperature (T_b) at air temperatures (T_{air}) of 33–34, 36–37, and 39–40°C were also determined. The metabolic response to rising T_{air} amounted to a doubling of VO$_2$ and a five-fold increase of EWL at T_{air} 39–40°C, compared with 25°C; and T_b rose above 42°C. (5) Using data from these metabolic measurements together with a theoretical heating model, heating curves were obtained that suggested that degus can exploit patches of food for only about 3 min at 60°C and 8 min at 50°C. These simulations are in agreement with our observations that degus reduced their time spent feeding when there was a thermal constraint on foraging. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Environmental temperature is one of the most important constraints on the energy and time budgets of organisms. In this respect thermal physiology is a significant element in determining foraging success of animals (Caraco et al., 1990). This is particularly important for diurnal endotherms that live in hot environments, because when foraging, these animals must move around and select different food patches and dietary items, while at the same time attempting

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to avoid predators and adjusting their location to seek suitable environmental conditions. To do this, animals may compensate or adjust their behavior and/or physiology, for instance, changing the duration and/or frequency of exposures to stressful conditions.

Recognizing that physiological and behavioral traits are a significant component of foraging ecology (Bautista et al., 1998; Bozinovic and Martínez del Río, 1996), we have examined the influence of thermoregulatory constraints on time and energy use in the degu, *Octodon degus*, in the laboratory. The degu is a diurnally active semi-fossorial herbivorous rodent inhabiting the semiarid environments of central Chile. This region is characterized by hot and dry summers. Previous studies have shown that the activity patterns and foraging sites of degus are constrained by their limited thermal tolerance (Torres-Contreras and Bozinovic, 1997) as well by other ecological factors such as food distribution and quality and predation risk (Jaksic, 1986; Lagos et al., 1995; Vásquez, 1997). Degus are efficient in water conservation (Cortés et al., 1990) and a low capability for evaporative cooling (Rosenmann, 1977). Degus food items (e.g., the dominant grass *Poa pratensis*) are normally more abundant in open microhabitats with no shrubs (Simonetti, 1989). During summer open microhabitats reach operative temperatures of up to 50°C. Our aim is to evaluate behavioral plasticity and thermal tolerance in an extreme experimental system. Specifically, to understand how thermoregulatory constraints affect the timing and duration of foraging bouts and amount of food obtained from a feeding station that was subjected to an intense heat load. The characteristics of this system suggests that appropriate timing between food patch and the rest of the arena could reduce thermal stress.

2. Material and methods

Non-reproductive degus, all captured in Quebrada de la Plata, central Chile (70°50′W, 33°31′S). We used 14 individuals (four females and ten males) with a mean body mass (m_b) of 200.6 ± 27.6 g (SD). They were maintained on commercial rabbit pellets and water, a photoperiod LD = 12:12 and air temperature of 20°C, and later randomly assigned (seven individuals per group) to different treatments.

Trials of two hours (1030–1230 h) were conducted to determine time allocation between a cool site lacking food and a hot site containing food. Trials were conducted in an experimental arena 160 by 96 by 150 cm, with a water bottle offered ad libitum in the middle of the arena. The arena was maintained at an air temperature (T_{air}) of 20°C. The floor of the arena was covered with soil to a depth of 30 cm. A food

source of sunflower seeds was offered on a metallic tray (30 by 30 cm) maintained under a 1000-W radiant electric heater located 40 cm above the food patch and delivering a radiant heat of 2500 W/m^2 measured at the surface. A cool burrow was provided at one end in front of the food patch, which was made of a clay cylinder (diameter = 12 cm, length = 15 cm) and covered with three frozen gel packs. In practice the degus did not enter the cool burrow during trials, and thus the design, effectively, turned out to allow for assessing brief appearances at the heated feeder which alternated with time spent throughout the unheated remainder of the arena.

A video camera (Sony CCD-TR413 NTSC) placed above the experimental arena and connected to a TV-VHS allowed us to record the animals movements without observers present in the room. We measured frequency and duration of patch visits and events of food collection by inspection of the video records. The operative temperatures (T_e) in the arena were in the range of 50–60°C similar to the range that we recorded in open areas of the natural habitat of *O. degus* in summer when they are ceased their foraging activity (Kenagy et al., unpublished). In addition, the temperatures of the food patch, open space and cool burrow were measured and adjusted through measurements of operative temperature (T_e) by use of hollow mounted skins or "thermal mannequins" (Bakken, 1992) that contained an internal thermocouple. Temperatures were recorded with a Digi-Sense instrument and Copper–constantan thermocouples and with a Li-Cor datalogger (LI-1400). Food in the hot site was offered, randomly distributed in the patch, mixed with the sand. A total of 8–9 seeds (=0.5 g or 15.1 kJ/g) were offered in each trial representing 25% of the daytime energy requirements of degus (Bozinovic, 1995). Treatments were presented in random order to each subject.

To determine the metabolic response to overheating, oxygen consumption (VO$_2$) was measured in a computerized (Datacan V) open-flow respirometry system (Sable Systems) in metabolic chambers of 900 ml at different air temperatures (T_{air}) above the upper limit of the thermoneutral zone of degus (*ca* 33°C, Rosenmann, 1977). The metabolic chamber received dried air at a rate of 900 ml min^{-1}, from mass flow controllers (Sierra Instruments). Before and after the chamber, air was passed through CO$_2$ absorbent granules of Baralyme [Ba(OH)$_2$] and H$_2$O absorbent granules of Drierite [CaSO$_4$] and was monitored every 5 s by an Applied Electrochemistry O$_2$ analyzer model S-3A/I (Ametek). Ambient temperature was held constant within ± 0.5°C by maintaining the metabolic chamber in an incubator water bath. Oxygen consumption values were calculated by Eq. (4a) (Withers, 1977). Body mass (m_b) and body temperature (T_b)
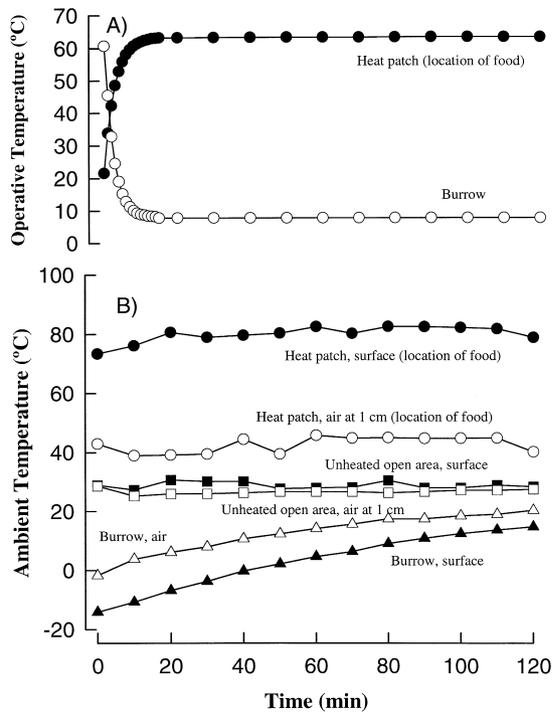
Fig. 1. (A) Heating and cooling curves of a thermal manne-quin with initial T_e of 20°C in the heat patch (where food was also located in experiments with live degus); and cooling curve of a mennequin with initial T_e of 60°C placed in the cold burrow. (B) Various ambient temperature measurements in the experimental arena over the course of the usual 2-h ex-perimental period. All temperatures remained stable except for the burrow temperatures, which rose slowly due to ad-dition of environmental heat to the ice packs associated with the cold burrow.

were measured before and after each metabolic trial with an electronic balance and a digital thermometer with Copper–constantan thermocouples, respectively. In conjunction with the VO$_2$ records, evaporative water loss (EWL) was also measured (Hainsworth, 1968). Because of the probability of killing some ani-mals by hyperthermia, we used only two representative individuals with a m_b of 237.1 ± 17.1 g. The exper-imental protocol was: acclimation to the metabolic chamber for 30 min at 33°C followed by VO$_2$ and EWL records of 30 min. Then a progressive increase of T_{air} from 36–37°C to 39–40°C was carried out fol-lowed by continuous 30 min recordings of VO$_2$ and EWL. Animals were observed continuously during all the measurements.

Statistical analyses were performed using STATISTICA® (1997) statistical package for Windows® 95 program. Data were analyzed by a MANOVA and the a posteriori Tukey tests ($\alpha = 0.05$).
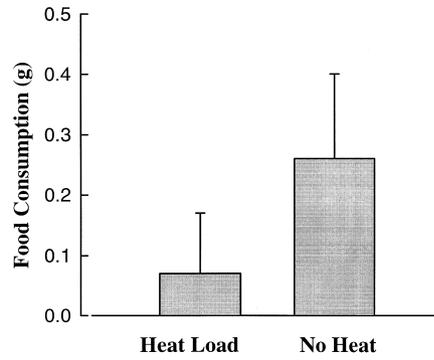

Fig. 2. Food consumption by *O. degus* during a 2-h test period in the arena under two different experimental regimes: with food available under a heat lamp (left) and with food available at an unheated location (right).

Data fulfilled the assumptions of the tests. Results are reported as mean $\pm$ 1 standard error.

3. Results

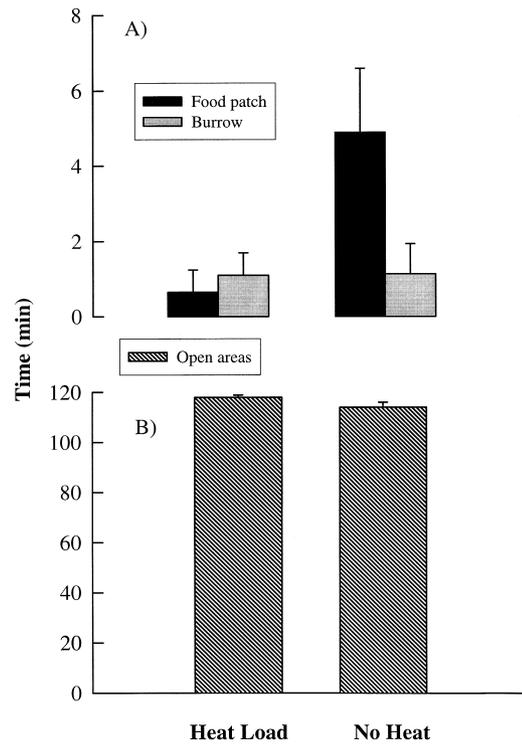Ambient temperatures (air and surface $= T_a$) of

Fig. 3. Time spent by *Octodon degus* in different areas of the arena during a 2-h experimental run. Symbols as in Fig. 2.
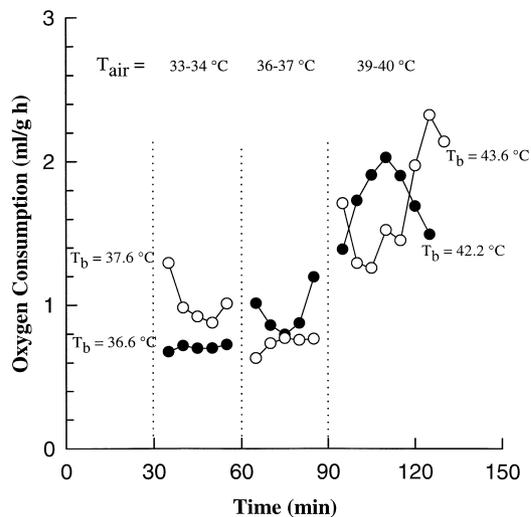
Fig. 4. Oxygen consumption as a function of time at different air temperatures (T_{air}) in two individual of degus. Body temperature (T_b) before and after the experiment are indicated.

patches in which heat was provided as well as T_e's in the patch and in the burrow, are shown in Fig. 1. Over a period of about 8 min, T_e of a thermal mannequin placed under the heat patch rose from 20°C to nearly 60°C, where it achieved equilibrium. An equilibrated mannequin at $T_e = 60$°C, when placed in the cold burrow, reached a level of about 10°C within 8 min.

Food consumption was significantly higher in the animals foraging in the unheated arena than in degus tested under the heat load (one-way ANOVA, F(1,12) = 8.309, P = 0.014, Fig. 2) Time use in the areas was influenced by the presence or absence of heat (MANOVA, Wilks lambda = 0.244, P = 0.002, Fig. 3). The a posteriori Tukey test revealed that time use of the heat patch for obtaining food was significantly lower (P = 0.0002) than time use for feeding in the absence of heat (Fig. 3). Nevertheless, time use of the cool burrow was not significantly affected by the presence of heat or absence of heat on the surface (P = 0.924, Fig. 3). Time use of the intermediate T_a's associated with most of the arena space was significantly higher under heat load than without it, due to the greater amount of time spent at the food patch in the unheated treatment (P = 0.0004, see Fig. 3). Of course this difference disappears if we add the time at the food patch to the time in the open area for the unheated treatment, in which case the temperature is the same at the food patch as in the rest of the arena. The total number of patch visits in 2 h was significantly affected by our treatments (MANOVA, Wilks lambda = 0.183, P = 0.0009). The a posteriori Tukey test indicated that the frequency of visits to the food patch was significantly lower under heat load

(5.29 ± 2.69) than without heat (19.00 ± 4.61) (P = 0.0002). As with total time, the number of visits to the cool burrow did not differ according to presence or absence of heat above ground (12.43 ± 8.22 vs 16.14 ± 10.21 respectively, P = 0.468).

Oxygen consumption increased from a basal value of 0.78 ± 0.11 ml/g h at 33°C to 2.18 ± 0.15 ml/g h at 39–40°C (Fig. 4). The basal value is within the range of previous reports of basal metabolic rate in degus (e.g., Bozinovic, 1995; Rosenmann, 1977; Veloso and Bozinovic, 1993). In addition, after 135 min at different T_{air}, we observed that T_b increased from 37.1 ± 0.7°C to 42.9 ± 0.9°C (Fig. 4). Evaporative water loss increased to 5.1 ± 0.5 mg/g h at 39–40°C which is about five times higher than the rate reported by Cortés et al. (1990) at 25°C. By using the equation $C = VO_2/(T_b - T_{air})$, McNab (1980), where C = thermal conductance in mlO_2/g h°C, we calculated the increase in C as a function of the increase in T_{air}. At 33°C, C was 0.225 ± 0.034 mlO_2/g h°C and at 40°C we calculated a C value equal to 0.783 ± 0.139 mlO_2/g h°C. Rosenmann (1977) reported that below the thermoneutral zone minimum C is 0.069 mlO_2/g h°C for degus of 195 g. These physiological data were obtained and used to calculate thermal tolerance under field conditions (see Discussion).

4. Discussion

In this paper we evaluated behavioral plasticity and thermal tolerance, in an extreme experimental system. Movements among various thermal dimensions of the environment have been described, mainly in desert dwelling ground squirrels. These movements within the environment occur between areas used for feeding (exposed to a high T_a) and cooling (burrow and/or shade at lower T_a's). Different authors (e.g., Bennett et al., 1984; Chappell and Bartholomew, 1981a,b; Van Heerden and Dauth, 1987; Vispo and Bakken, 1993) have suggested that the regulation of body temperature of squirrels imposes a constraint on the time these organisms can spend foraging in thermally costly areas, determining a behavioral pattern of shuttling between hot and cold (cooling) patches.

Our results indicate a role for "shuttling" behavior in degus, with adjustments in timing and frequency of foraging. Challenged with a patch that poses a potential thermal stress, similar to extremes found in the field during the hot season, degus in the laboratory changed the time relationships between foraging time (FT) and time not foraging (NFT) in an area where there is no food, with $FT/FT + NFT$ = 0.005 under heat load and 0.04 under no heat. That is, degus minimized time exposure to physiologically costly conditions by nearly one order of magnitude by
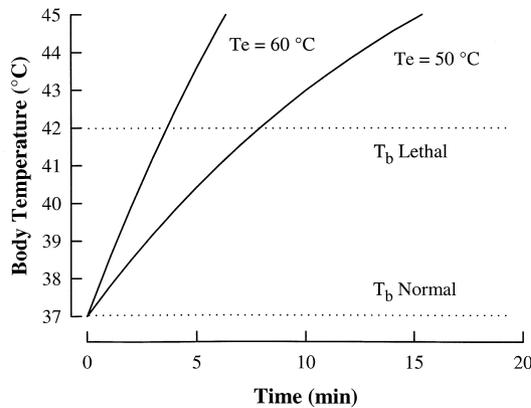
Fig. 5. Computed heating curves showing the increase in body temperature at two operative temperatures (T_e) for degus. Normal and lethal body temperatures (T_b) are indicated (see text for equations).

decreasing their visits to a hot food patch, and as a consequence, degus reduced energy intake.

We predicted periodic locomotory movements between patches characterized by different thermal conditions and that is what they did. Degus were able to maintain heat balance without retreating to the extremely cold artificial burrow. Interestingly under the presence of a heat load degus did not select the burrow, which is at lower T_{air}, but rather an intermediate one that was widely available throughout the space of the arena, which comprised most of the space available to them. Apparently degus did not allow body temperature to increase and they did this by moving out of the thermally stressful patches, despite compromising their energy intake.

In an attempt to extrapolate our laboratory measurements of energetics and thermal tolerance to field conditions, we used the heating model proposed by Hainsworth (1995) to calculate changes in T_b over time under different simulations of the thermal environment. In short, the model is an integration of the Newton Law of Cooling, that is:

$$\log(T_b - T_e) = \log E + \frac{C(t)}{K}(\log e) \qquad (1)$$

where E is $(T_b - T_e)$ when $t = 0$, e is the base of the natural logarithm, C (J/g min °C) is the thermal conductance measured by us at different T_{air} under laboratory conditions and K is the specific heat of rodents = 3.431 J/g °C (Hainsworth, 1995). We used the equivalent of 20.1 J/mlO$_2$ (Schmidt-Nielsen, 1987) for the transformation of C and VO$_2$ values. Thus, heating at field T_e's of 50 and 60°C were calculated according to:

$$T_b = T_e + [E - 0.2(t)](e)^{-0.076(t)} \qquad (2)$$

where 0.2 represents our records of metabolic rate (Fig. 4) divided by K, and 0.076 is C/K at 40°C. Based on our laboratory measurements and this model, we obtained the heating curves plotted in Fig. 5. It is clear that degus can exploit patches of food for only approximately 3 min at 60°C and 8 min at 50°C. These simulations are in agreement with our records of spatial movements in the experimental arena (Fig. 3).

During periods of high temperatures degus used food patches during shorter bouts of time than predicted by our simulations. It is probable that degus defend their T_b from exceeding lethal or even sublethal limits by evaporative cooling but compromising their water economy because EWL is substantial (Fig. 5). The interaction between these factors should be reflected in a trade-off between thermoregulatory risk, activity and foraging. Hypothetically, if degus are maximizing energy intake, then we predict that the energy saved from thermoregulation would at least balance the decrease in energy intake caused by a reduction in foraging time. Certainly, our findings need to be tested under field conditions to determine whether our conclusions apply to this and other systems.

Acknowledgements

References

Bakken, G.S., 1992. Measurement and application of operative and standard operative temperatures in ecology. Am. Zool. 32, 191–216.

Bautista, L.M., Tinbergen, J., Wiersma, P., Kacelnik, A., 1998. Optimal foraging and beyond: how starlings cope with changes in food availability. Am. Nat. 152, 543–561.

Bennett, A.F., Huey, R.B., John-Alder, H., Nagy, K.A., 1984. The parasol tail and thermoregulatory behaviour of the Cape ground squirrel *Xerus inauris*. Physiol. Zool. 57, 57–62.

Bozinovic, F., 1995. Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fibre. J. Mamm. 76, 627–637.

Bozinovic, F., Martínez del Río, C., 1996. Animals eat what they should not: why do they reject our foraging models? Rev. Chil. Hist. Nat. 69, 15–20.

Caraco, T., Blanckenhorn, W.U., Gregory, G.M., Newman, J.A., Recer, G.R., Zwicker, S.M., 1990. Risk-sensitivity: ambient temperature affects foraging choice. Anim. Behav. 39, 338–345.

Chappell, M.A., Bartholomew, G.A., 1981a. Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. Physiol. Zool. 54, 215–223.

Chappell, M.A., Bartholomew, G.A., 1981b. Standard operative temperatures and thermal energetics of the antelope ground squirrel *Ammospermophilus leucurus*. Physiol. Zool. 54, 81–93.

Cortés, A., Rosenmann, M., Baez, C., 1990. Función del riñón y del pasaje nasal en la conservación de agua corporal en roedores simpátridos de Chile central. Rev. Chil. Hist. Nat. 63, 279–291.

Hainsworth, F.R., 1968. Evaporative water loss from rats in the heat. Am. J. Physiol. 214, 979–982.

Hainsworth, F.R., 1995. Optimal body temperatures with shuttling: desert antelope ground squirrels. Anim. Behav. 49, 107–116.

Jaksic, F.M., 1986. Predation upon small mammals on shrublands and grasslands of southern South America: ecological correlates and presumable consequences. Rev. Chil. Hist. Nat. 59, 209–211.

Lagos, V.O., Contreras, L.C., Meserve, P.L., Gutiérrez, J.R., Jaksic, F.M., 1995. Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. Oikos 74, 259–264.

McNab, B.K., 1980. On estimating thermal conductance in endotherms. Physiol. Zool. 53, 145–156.

Rosenmann, M., 1977. Regulación térmica en *Octodon degus*. Medio Ambiente (Chile) 3, 127–131.

Schmidt-Nielsen, K., 1987. Animal Physiology: Adaptation and Environment. Cambridge University Press, p. 602.

Simonetti, J.A., 1989. Microhabitat use by small mammals in central Chile. Oikos 56, 309–318.

Statistica®, 1997. STATISTICA release 5 (Quick Reference) for the Windows 95 operating system, 3rd ed. StatSoft, Tulsa, Oklahoma.

Torres-Contreras, H., Bozinovic, F., 1997. Food selection in an herbivorous rodent: balancing nutrition with thermoregulation. Ecology 78, 2230–2237.

Vásquez, R.A., 1997. Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. Rev. Chil. Hist. Nat. 70, 557–563.

Van Heerden, J., Dauth, J., 1987. Aspects of adaptation to an arid environment in free-living squirrels *Xerus inauris*. J. Arid Env. 13, 83–89.

Veloso, C., Bozinovic, F., 1993. Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecology 74, 2003–2010.

Vispo, C.R., Bakken, G.S., 1993. The influence of thermal conditions on the surface activity of thirteenlined ground squirrels. Ecology 74, 377–389.

Withers, P.C., 1977. Measurements of VO_2, VCO_2, and evaporative water loss with a flow through mask. J. Appl. Physiol. 42, 120–123.