

A time-energy analysis of daytime surface activity in degus, *Octodon degus*

Análisis del uso de tiempo y energía en la actividad superficial diaria en degus,
Octodon degus

G.J. KENAGY¹, RODRIGO A. VÁSQUEZ², ROBERTO F. NESPOLO³ & FRANCISCO BOZINOVIC³

¹Department of Zoology and Burke Museum, University of Washington,
Seattle, Washington 98195, U.S.A.

²Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile,
Santiago, Chile

³Centro de Estudios Avanzados en Ecología & Biodiversidad, Departamento de Ecología,
P. Universidad Católica de Chile, Santiago, Chile; e-mail: fbozinov@genes.bio.puc.cl

ABSTRACT

We present an analysis of time and energy allocation in a day-active caviomorph rodent, the degu, *Octodon degus*, in central Chile. We quantified components of surface activity in the field on a daily basis in individual degus near the time of the summer solstice, when conditions of heat and aridity were also at a seasonal extreme, in order to answer the following questions. Does the absolute time available for surface activity limit performance? Does the allocation of time and energy for locomotion place a functionally significant limitation on overall energy balance and performance? Degus spent about 2/3 of their above-ground time foraging; they remained stationary about 88 % of the time, walked around slowly about 10 %, and were running rapidly from one point to another only about 2 % of the time. Net locomotion costs (for walking and running combined) were computed to be only 2.2 % of total daily energy expenditure. This low net allocation of time and energy to locomotion, taken together with abundant distribution of plant food over the extremely small home range, suggests that the daily performance of degus is not limited by the absolute amount of time available under normal conditions at the summer solstice (seasonal extreme of day length, heat, and aridity). Total energy demands can be met by as little as 4.5 h surface activity per day. Our empirical observations, together with a simple computational model of time and energy expenditure, provide a useful validation of the impact of activity on the overall energy balance of a free-living rodent. The small impact of locomotion on the total energy budget is an economy of the behavior of these animals, and the rapid mode of locomotion allows them to minimize predation risks. We believe that this kind of quantitative analysis of energy expenditure associated with behavior in the field can contribute a useful basis for theoretically based time-energy modeling.

Key words: time, energy, activity, central Chile.

RESUMEN

Presentamos un análisis de la asignación de tiempo y energía en un roedor caviomorfo diurno el degu, *Octodon degus*, en Chile central. Cuantificamos los componentes de actividad superficial en el campo sobre una base diaria durante el solsticio de verano en condiciones de calor y aridez extrema, para contestar la siguiente pregunta: ¿el tiempo absoluto disponible para la actividad superficial limita el rendimiento? ¿la asignación de tiempo y energía a locomoción juega un limitación funcional significativa en el presupuesto de energía total y en el rendimiento? Los degus permanecen forrajeando cerca de 2/3 de su tiempo fuera de las cuevas; están estacionarios cerca de 88 % del tiempo, caminan cerca del 10 %, y corren rápidamente de un punto a otro solamente un 2 % del tiempo. Los costos netos de locomoción (caminando y corriendo) fueron calculados en 2,2 % del gasto energético total. Esta baja asignación neta de tiempo y energía a locomoción, junto a la abundante distribución de alimento en un ámbito de hogar pequeño, sugieren que el rendimiento diario de los degus no está limitado por el tiempo absoluto disponible bajo condiciones normales en el solsticio de verano (extremo estacional de largo del día, calor y aridez). Las demandas de energía totales se lograrían con 4,5 h de actividad superficial por día. Las observaciones empíricas, junto a un modelo simple de gasto de energía y tiempo entregan una validación simple de la actividad del balance de energía total en roedores de vida libre. El bajo impacto de la locomoción sobre el presupuesto de energía total representa una economía en la conducta de estos animales, los rápidos modos de locomoción minimizarían el riesgo de predación. Postulamos que estos análisis cuantitativos de gasto de energía asociados con la conducta de campo contribuirían a la modelación teórica del uso de tiempo y energía.

Palabras clave: tiempo, energía, actividad, Chile central.

INTRODUCTION

The cumulative use of time and energy by an animal moving around and foraging in its environment results from a sequence of behavioral switches among a variety of different functions. The election of particular behaviors is time-dependent, and these "decisions" are integrated responses to the environment (e.g., distribution of food, temperature) and the internal state (e.g., energy balance) of the animal (Mangel & Clark 1988, Krebs & Kacelnik 1991).

We present here an analytical problem in ecology and ethology involving such decisions as to when and how much an animal will be moving, resting, or foraging. Our investigation is empirical and descriptive, and it offers an approach to understanding time and energy allocation (Houston & McNamara 1985, Houston 1995). We address the general question of whether absolute amount of time, taken together with requirements for space and food processing, can limit daily performance as reflected in the state of energy balance.

Our analysis is based on a summertime field study of energetically definable components of surface activity in the degu (*Octodon degus*). Degus are herbivorous caviomorph rodents that inhabit the matorral environment of central Chile, which is hot and dry in summer. They are fairly generalized looking brownish rodents, with adult mass ~160-200 g, and they are the only endemic small mammals of central Chile that are routinely active in the daytime. They remain in subterranean burrows at night and at intervals during the day. The general activity of degus and their reliance on shrub cover as a refuge from heat and predators have been previously described (Fulk 1976, Yáñez & Jaksic 1978, Iriarte et al. 1989, Lagos et al. 1995). Habitat analyses indicate that degus are generally associated with shrub cover and variable amounts of intervening open space (Le Boulengé & Fuentes 1978, Jaksic et al. 1981, Meserve et al. 1984, Iriarte et al. 1989). In addition, Bozinovic et al. (2000) reported a role for shuttling behavior in degus, with adjustments in timing and frequency of foraging. Degus minimized time exposure to physiologically risky conditions in nearly one order of magnitude by decreasing their visits to a hot food patch and as a consequence, degus reduced energy intake. Based on measurements of oxygen consumption, evaporative water loss and body temperature, as well as on a theoretical model of temperature regulation, these authors obtained heating curves and showed that degus can exploit patches of food only during approximately 3 min at 60 °C and 8 min at 50 °C. These simulations are in agreement with records of shuttling in an experimental arena (Bozinovic et al. 2000). This

processes of activity may explain why degus changed their seasonal timing of foraging from a bimodal regime in summer to an unimodal activity in winter (G.J. Kenagy et al. unpublished results). On the other hand, Torres-Contreras & Bozinovic (1997) reported a series of diet selection experiments conducted in an experimental arena under variable food quality and thermal regimes. They found that degus preferred items of high quality (low-fibre) but that selection was influenced by seasonal and spatial changes in food quality and environmental temperatures, coupled with feeding time, digestive processing, and thermoregulatory risk.

Our goal was to obtain measurements of time use for a time budget of above-ground activity that could be further translated to estimate energy expenditure for locomotion and general activity. We used the analysis to address two questions: does the absolute time available for surface activity limit performance? does the allocation of time and energy for locomotion place a functionally significant limitation on overall energy balance and performance of daily activity? Empirical and descriptive studies such as this are necessary to validate the functional significance of parameters that are the frequent subjects of theoretical considerations of physiologically relevant behavior. We selected a study site that was extremely open, with almost no shrub cover, which allowed us to maximize our direct observation of the behavior of individuals. The observational data were combined with further computations to provide an overall context of daily energy expenditure, against which we evaluated the potential limits to energy balance.

MATERIAL AND METHODS

The study was conducted about 30 km west of Santiago in Quebrada de La Plata, at 33° 29' S, 70° 56' W and elevation 800 m. The general habitat was typical of central Chilean matorral, but we selected the particular study area because of its extensive open space and sparse shrub and tree cover. The area was dotted with numerous degu burrows, with runways radiating from burrow entrances throughout the extensive cover of grasses and herbs.

We quantified components of the above-ground time budget of 72 individual non-reproductive degus near the time of the summer solstice, on 11-16 December 1996, by recording specific activities during continuous bouts of observation. We defined activity by four categories: (1) sitting (stationary position, lack of locomotion); (2) walking (slow movement, often while searching for and gathering food); (3) running (rapid move-

ment, usually within runways, and for longer distances); (4) foraging (searching for, harvesting, or ingesting food). Foraging (4) can be done, by definition, by an animal in state (1) or (2), whereas categories 1-3 are mutually exclusive of one another. Teams of two observers (one spotting and verbally identifying behavior; the other recording and timing the data, using a continuously running stopwatch and data form) obtained records of 23 activity bouts of continuously observed individuals (range 4 to 98 min; mean duration 20 min) totaling 7.54 h. We measured and recorded (to the nearest second) the duration of each successive change of state (sitting, walking, running) and also the time engaged in foraging during rest and walking, following methods of Kenagy et al. (1989).

On other occasions in November and December we quantified the speeds of walking and running gaits, following methods of Kenagy & Hoyt (1988), by observing the spontaneous locomotion of individuals immediately upon release from live traps. This consisted of timing a short but steady burst of locomotion for which the path of

movement could be visually distinguished (start and stop points) and then measured, to the nearest centimeter, following departure of the animal. The degus were not individually marked. Although multiple measures of same individuals were included in the data, I minimized the probability of biasing the results through recording the behavior of some individuals more than others during each observation session.

RESULTS

Time allocation to three states of movement

We assigned all of the continuously observed above-ground behavior to three states, which provides a simple time budget that can readily be translated into an energy budget (see Kenagy et al. 1989).

(1) Sitting. The animals remained stationary and were either completely still or showed only small motor actions such as harvesting or ingesting food, grooming, or changing posture.

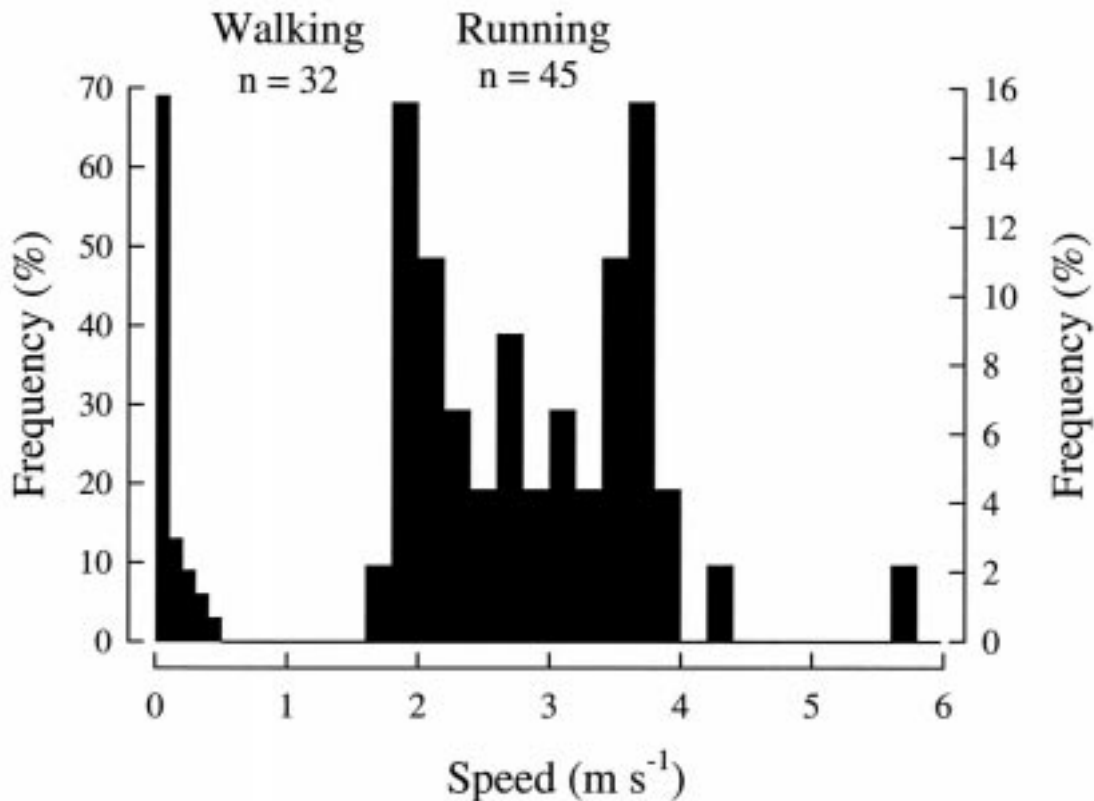


Fig. 1: Frequency distribution of speeds for two different modes of locomotion in degus observed in the field — walking (left axis and data, mean \pm SD = 0.11 ± 0.11 m s⁻¹) and running (right axis and data, 2.85 ± 0.83 m s⁻¹).

Distribución de frecuencia de velocidades para dos modos de locomoción en degus observados en el campo—caminando (eje izquierdo y datos, media = $0,11 \pm 0,11$ m s⁻¹) y corriendo (eje derecho y datos, $2,85 \pm 0,83$ m s⁻¹).

(2) Walking. The animals moved very slowly, showing exploratory behaviors, searching for food, harvesting and even intermittently ingesting food. The walking gait included momentary pauses, and its range of speeds was less than 0.5 m s^{-1} (Fig. 1). Our observation of walking also included occasional very short, rapid movements, of $< 1 \text{ s}$ duration; but these did not entail movement over significant distances and were interspersed among the routine movements and foraging that characterized walking in general.

(3) Running. The animals moved rapidly, with a trotting or hopping gait, and galloping at the higher speeds within the range, which spanned from 1.7 to 5.7 m s^{-1} (Fig. 1). About 90 % of all running speeds were 1.8 - 4.0 m s^{-1} . Running was most frequently used for rapid commuting between two points, and occasionally it involved social chasing or escape from potential predators.

Our time-budget revealed that degus were sitting still most of the time (88.3 %), and moving around the rest of the time, either walking (9.7 %) or running (2.0 %) (Table 1). Running typically consisted of short bursts of $< 2 \text{ s}$ that covered about 3-6 m. This is based on a total of 254 running events, contained within 23 bouts of observation (Table 1); nearly half of these running events (111 out of 254) lasted 1 s each, while the mean \pm SD of all events was $2.14 \pm 1.99 \text{ s}$. At an average running speed of 2.85 m s^{-1} (Fig. 1), this means that the average distance run was about 6 m.

Time spent foraging

Time spent foraging included both harvesting and ingestion of food, and it occurred concurrently with both sitting and walking. Of all foraging,

about 90 % occurred while sitting and 10 % while walking (Table 1). Foraging amounted to 66.6 % of all time spent of the surface, and nearly the same percentages of time separately either for sitting or walking (Table 1). The broadly herbivorous foraging of degus included herbs and grasses, occasional subterranean plant parts, and seeds, which were gathered either directly from dried plants or from the ground.

DISCUSSION

Since an unknown proportion of our data set may have included repeated observations of same individuals, such data pooling may have biased the results through inflating degrees of freedom. We can not determine the extent of such potential bias, but some aspects may have decreased it to some extent. Indeed, external body marks along with simultaneous trapping of the animals revealed that at least 72 different individuals were seen in the area during the observation period.

Analyzing individual behavior—time and energy

Individual degus produce patterns of daily activity that result from a series of “decisions” (in the sense of Krebs & Kacelnik 1991) regarding election of particular activities, when and where to execute them, and for how long. These “choices” are based on processing of information on the animal’s internal state and the environment (Mangel & Clark 1988).

The most general decision for a semifossorial rodent involves the movement from the burrow onto the surface, resulting in a balance of time on

TABLE 1

Time budget summary of degu summer activity. Data derived from 453 min (= 7.54 h) of observations, summed from 23 continuous observation bouts ranging 4-98 min, mean \pm SD duration $19.7 \pm 19.3 \text{ min}$

Resumen del presupuesto de tiempo de la actividad de verano de degus. Datos derivados de 453 min (= 7,54 h) de observaciones, sumadas de 23 eventos de observación contínuos de 4-98 min, media \pm SD duración $19,7 \pm 19,3 \text{ min}$

State of movement	All activity Time (min)	Percent	Foraging ¹ Time (min)	Percent	Foraging as percent of each state ²
Sitting	399.81	88.3	271.60	90.1	67.9
Walking	44.16	9.7	29.80	9.9	67.5
Running	9.10	2.0			
Total	452.63	100.0	301.40	100.0	66.6

¹Foraging occurred only during sitting and walking; percentages expressed with respect to total foraging

²Foraging expressed with respect to time spent sitting, walking, and all activity

the surface, T_{surf} , with time in the burrow, T_{bur} , that sums to 24 h:

$$T_{surf} + T_{bur} = 24 \text{ h}$$

For degus in summer T_{surf} accumulates during two major bouts of activity each day, early morning and late afternoon, which may, nonetheless include brief intervals of T_{bur} (G.J. Kenagy, R.F. Nespolo, R.A. Vásquez & F. Bozinovic unpublished results).

Once a degu is on the surface, we have identified three simplified states of movement, for each of which we can specify a rate of energy expenditure: time spent without change of position, T_{sit} , time walking, T_{walk} , and time running, T_{run} , such that:

$$T_{surf} = T_{sit} + T_{walk} + T_{run}$$

Our best estimate for T_{surf} of an individual is the period of population foraging activity, which is an overestimate, due to T_{bur} associated with intermittent retreats below ground. From another study of population foraging activity near the time of the summer solstice, we obtained a sum of only 4.5 h day⁻¹ for T_{surf} , distributed between more-or-less equal morning and afternoon bouts (see Kenagy et al. 1999, G.J. Kenagy, R.F. Nespolo, R.A. Vásquez & F. Bozinovic unpublished results).

Our determination of time allocation on the surface in summer was 88.3 % sitting, 9.7 % walking, and 2.0 % running (Table 1), which corresponds to absolute values of $T_{sit} = 3.97$ h, $T_{walk} = 0.44$ h, and $T_{run} = 0.09$ h (Table 2). Applying the average speeds for walking and running (Fig. 1) to these values results in a total distance moved per day (DMD) of 0.18 km walking and

0.92 km running, for a total of 1.10 km surface locomotion (Table 2).

The amount of time actually foraging by an individual degu is less than our designated period of population foraging by not only the time of occasional retreats below ground, but more importantly by the amount of time spent on the surface while not foraging. Our observation of summer foraging and activity budgets showed that 2/3 of T_{surf} was spent foraging, and that essentially this same proportion of both T_{sit} and T_{walk} were allocated to foraging, which is because the absolute amount of T_{run} is so low (Table 1). Applying the value of 66.6 % (Table 1) to summer foraging translates to an absolute daily sum of 3.0 h total foraging, T_{for} , for an individual degu, consisting of 2.7 h during T_{sit} ($T_{for*sit}$) and 0.3 h during T_{walk} ($T_{for*walk}$), where:

$$T_{for} = T_{for*sit} + T_{for*walk}$$

Since the development of theory concerning the idea that animals may show a tradeoff between maximizing energy intake and minimizing time foraging (Schoener 1971), a variety of empirical results and interpretations have been applied to generalist-herbivorous rodents (Belovsky 1986, Vispo & Bakken 1993), suggesting that either or both of the two tradeoffs may occur. A significant issue here is that of limits and how they operate. It is often assumed that because thresholds (limits) to activity exist, e.g., associated with thermally intolerable conditions (e.g., Chappell & Bartholomew 1981, Lagos et al. 1995) that the total time available for activity or foraging may place a limit on the capacity of individuals to maintain energy balance and survive. This may not be the case. Animals avoid uncomfortable extremes, and they may do so by approaching but

TABLE 2

Daily time allocation for degu locomotion in summer and distance moved per day (DMD)

Asignación de tiempo diaria en locomoción en verano y distancia recorrida por día (DMD) en degus

State of movement	Time ¹ (%)	Activity total ² (hd ⁻¹)	Average speed ³ (ms ⁻¹)	DMD ⁴ (km d ⁻¹)
Sitting	88.3	3.97		
Walking	9.7	0.44	0.11	180
Runnig	2.0	0.09	2.85	920
Total	100.0	4.50		1100

¹Percent, from Table 1

²Using percentages, at left, to estimate on basis of 4.5 h above ground on summer day, from Table 1

³From Fig. 1, units converted to km h⁻¹

⁴Product of two columns to left

not entering a state of thermal stress. However, the time missed due to such a temporary limit may readily be made up at another, physically more suitable time of day. This depends on the total energetic and nutritional demands on the animal, the supply and distribution of food, and the total amount of time available for access to the food. Our observations of degus indicate that they obtain adequate food in the time available, without limitation. We also believe that the behavioral processes and timing we have observed in individuals include both risk-sensitive foraging (Caraco et al. 1990) and maximizing of energetic efficiency (Houston 1995).

Herbers (1981) has made another important point in this line of argumentation, that the foraging and activity of some animals may be modeled by alternative schemes other than those of maximizing energy or minimizing time. The criteria for such alternative models of foraging dynamics are met by herbivores that have abundant and easily accessible food and that appear to spend a great deal of time resting on the surface, i.e., apparently doing “nothing”, or being “lazy” (Herbers 1981). We believe this situation applies to degus, which, as herbivores, spend most of their time on the surface either not moving at all or moving very slowly (Table 1). Admittedly, important functions such as vigilance and digestion are being performed when animals sit still. 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. Their energy demands are accelerated at times, for example during reproduction (Veloso & Bozinovic 2000), but it remains to be shown whether they encounter ecological challenges that limit them to a level of energy intake less than that of which they are physiologically capable of ingesting.

Our assessment of degu energetics suggests that locomotion is a very small component of the overall energy budget, amounting to a net of about 2 % of daily energy expenditure (DEE) (Tables 1, 2, 3). This is consistent with the interpretation of Garland (1983), based on a literature survey and allometric analysis of physiology and behavior, that small mammals in general allocate only about 1 % of DEE to net costs of locomotion; however, it is not in agreement with alternative computational approaches by Karasov (1992) which suggest much more substantial daily energy costs for locomotion (“activity”). Our conclusion for degus, based on detailed behavioral observations and energetics computations presented below, is contrary to the results of a similar empirical study (Kenagy & Hoyt 1989) that apparently reflects a behaviorally and ecologically different species, the golden-mantled ground squirrel *Spermophilus saturatus*, which is extensively active over a large home range and shows a net cost of locomotion amounting to 13 % of DEE, or a total expenditure during locomotion of 21 % of DEE. The key field data required to differentiate species are behavioral and spatial

TABLE 3

Daily time and energy expenditure for locomotion and its relationship to total daily energy expenditure (DEE) in the field and to basal metabolic rate (BMR)

Tiempo diario y gasto de energía en locomoción y su relación al gasto de energía diario (DEE) en el campo y a la tasa metabólica basal (BMR)

	Metabolic rate ¹		Time hd ⁻¹	Daily cost kj (gd) ⁻¹		Locomotion (%DEEE) ³		Net locomotion as % BMR ⁴
	mlO ₂ (gh) ⁻¹	kJ (gh) ⁻¹		Total	Net ²	Total	Net %	
Walking	33.3	0.0669	0.44	0.029	0.012	2.5	1.0	2.6
Running	9.78	0.1966	0.09	0.018	0.014	1.6	1.2	3.0
Total			0.53	0.047	0.026	4.1	2.2	5.6

¹Using equation 2 (0.11 m s⁻¹ for walking) and equation 3 (2.85 m s⁻¹ for running) of Hoyt & Kenagy (1988) for *Spermophilus saturatus*, which is similar in body size to *O. degus*, and converting to energy expenditure at 20.1 J ml⁻¹ oxygen

²Net increase due to locomotion is obtained by subtracting metabolic rate (as oxygen consumption) of alert, nonmoving animal from the rate during locomotion. Alert MR is taken as 2 x BMR of degus (Rosenmann 1977), which approximates the relationship of alert to basal in *S. saturatus* (Kenagy et al. 1989)

³DEE is total daily energy expenditure of free-living degus, estimated as 2.5 BMR (Rosenmann 1977) = 1.153 kJ (g d)⁻¹, for nonbreeding degus, in accord with BMR multiples of Kenagy et al. (1989) and Drent & Daan (1980)

⁴Based on value of Rosenmann (1977) for basal metabolic rate of 0.461 kJ (g d)⁻¹

data. Degus are social, perhaps colonial, and in contrast to the golden-mantled ground squirrel, degus occupy very small home ranges, estimated as small as 0.04 ha (Agüero & Simonetti 1989) or ranging 0.05-0.71 ha (Zunino et al. 1992). With a daily movement distance (DMD) of only 1.1 km/d (Table 2) and an allocation of only 2 % of T_{surf} time for running and 9.7 % for walking (Table 1), degus show a total daily expenditure during all this locomotion of only 4.1 % of DEE and a net locomotion expenditure of only 2.2 % (Table 3). Clearly the use of two different major gaits contributes to the efficiency of such a low locomotion expenditure. If degus walked instead of running the distance covered during T_{run} (which is only 2 % of T_{surf} time), they would require an enormous amount of time, 2.33 h, to cover the 0.92 km that they run, on average, in a summer day (Table 2). Thus the rapid running gait is key to the overall time and energy economy of degus, as it provides quick and safe commuting around the home range; of course running is also important as the direct mechanism of escape from predators, when needed. The much greater time spent in T_{walk} , compared to T_{run} , leads to coverage of very little total distance but nonetheless meets the time need for seeking and harvesting food, which is apparently readily accomplished in the small home range of degus with its abundant food supply.

CONCLUSIONS

Despite limitations to degu activity in summer by thermal conditions, our analysis of individual activity budgets and energetics suggests that adequate time and food are available, taken together with the use of a small home range, to meet energy demands without pressing the limits of total available time. The small daily proportion of energy allocated to locomotion and the considerable amount of time for which the animals, while present on the surface, are able to sit without foraging, reflect further energetic efficiencies that contribute to the survival and success of degus. The social vigilance of degus "on watch" contributes to their antipredatory warning system (Vásquez 1997). The minimization of time and energy expenditure for locomotion also means that degus are minimizing their exposure to predators, while also remaining able to use rapid locomotion, when needed, to escape from predators. The safety margins contained in this system also allow for increased foraging when the quality of the plant food declines, thereby requiring greater intake to meet energy demands (Bozinovic 1995,

Bozinovic et al. 1997). From this standpoint, it also appears that the option of restraining daily energy expenditure below levels of maximum performance (Drent & Daan 1980) could serve as additional insurance for survival in the face of the physically and nutritionally unpredictable elements of the degu's seasonally hot and arid environment.

ACKNOWLEDGMENTS

Support for this research was provided by the U.S. National Science foundation (INT 9600578) for cooperative research in Chile and by the Fondo de Desarrollo Científico y Tecnológico (FONDECYT 1950394 and 101-0950) to G.J.K. and F.B. We thank Ray Huey, Kevin O'Brien, and Swifty Stevenson for advice on analysis and presentation, and Ned Place for field assistance. The observational methods of this research comply with current animal research laws of Chile.

LITERATURE CITED

- AGÜERO T & JA SIMONETTI (1989) Home range assessment: a comparison of five methods. *Revista Chilena de Historia Natural* 61: 223-229.
- BELOVSKY GE (1986) Generalist herbivore foraging and its role in competitive interactions. *American Zoologist* 26: 51-69.
- BOZINOVIC F (1995) Nutritional energetics and digestive responses of an herbivorous rodent, *Octodon degus* (Rodentia, Caviomorpha) to different levels of dietary fiber. *Journal of Mammalogy* 76: 627-637.
- BOZINOVIC F, FF NOVOA & P SABAT (1997) Feeding and digesting fiber and tannins by an herbivorous rodent *Octodon degus* (Rodentia: Caviomorpha). *Comparative Biochemistry and Physiology* 118A: 625-630.
- BOZINOVIC F, JA LAGOS, RA VÁSQUEZ & GJ KENAGY (2000) Time and energy use under thermoregulatory constraints in a diurnal rodent. *Journal of Thermal Biology* 25: 251-256.
- CARACO T, WU BLANCKENHORN, GM GREGORY, JA NEWMAN, GM RECER & SM ZWICKER (1990) Risk-sensitivity: ambient temperature affects foraging choice. *Animal Behaviour* 39: 338-345.
- CHAPPELL MA & GA BARTHOLOMEW (1981) Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. *Physiological Zoology* 54: 215-223.
- DRENT RH & S DAAN (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- FULK GW (1976) Notes on the activity, reproduction, and social behavior of *Octodon degus*. *Journal of Mammalogy* 57: 495-505.

- GARLAND T (1983) Scaling the ecological cost of transport to body mass in terrestrial mammals. *American Naturalist* 121: 571-587.
- HERBERS J (1981) Time resources and laziness in animals. *Oecologia* 49: 252-262.
- HOUSTON AI & JM McNAMARA (1985) The variability of behaviour and constrained optimization. *Journal of Theoretical Biology* 112: 265-273.
- HOUSTON AI (1995) Energetic constraints and foraging efficiency. *Behavioral Ecology* 6: 393-396.
- HOYT DF & GJ KENAGY (1988) Energy costs of walking and running gaits and their aerobic limits in golden-mantled ground squirrels. *Physiological Zoology* 61: 34-40.
- IRIARTE JA, LC CONTRERAS & FM JAKSIC (1989) A long-term study of a small-mammal assemblage in the central Chilean matorral. *Journal of Mammalogy* 70: 79-87.
- JAKSIC FM, JL YÁÑEZ & ER FUENTES (1981) Assessing a small mammal community in central Chile. *Journal of Mammalogy* 62: 391-396.
- KARASOV WH (1992) Daily energy expenditure and the cost of activity in mammals. *American Zoologist* 32: 238-248.
- KENAGY GJ & DF HOYT (1989) Speed and time-energy budget for locomotion in golden-mantled ground squirrels. *Ecology* 70: 1834-1839.
- KENAGY GJ, SM SHARBAUGH & KA NAGY (1989) Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia* 78: 269-282.
- KENAGY GJ, C VELOSO & F BOZINOVIC (1999) Daily rhythms of food intake and feces reingestion in the degu, an herbivorous Chilean rodent: optimizing digestion through coprophagy. *Physiological and Biochemical Zoology* 72: 78-86.
- KREBS JR & A KACELNIK (1991) Decision-making. In: Krebs JR & NB Davies (eds) *Behavioural ecology: an evolutionary approach*: 105-136. Blackwell Scientific Publications, Oxford, United Kingdom.
- LAGOS VO, F BOZINOVIC & LC CONTRERAS (1995) Microhabitat use by a small diurnal rodent (*Octodon degus*) in a semiarid environment: thermoregulatory constraints or predation risk? *Journal of Mammalogy* 76: 900-905.
- LE BOULENGÉ E & ER FUENTES (1978) Quelques données sur la dynamique de population chez *Octodon degus* (rongeur Hystricomorphe) du Chili central. *La Terre et la Vie* 32: 325-341.
- MANGEL M & CW CLARK (1988) *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, New Jersey. 308 pp.
- MESERVE PL, R MARTIN & J RODRÍGUEZ (1984) Comparative ecology of the caviomorph rodent *Octodon degus* in two Chilean mediterranean-type communities. *Revista Chilena de Historia Natural* 57: 79-89.
- ROSENMANN M (1977) Regulación térmica en *Octodon degus*. *Medio Ambiente (Chile)* 3: 127-131.
- SCHOENER TW (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-403.
- TORRES-CONTRERAS H & F BOZINOVIC (1997) Food selection in an herbivorous rodent: balancing nutrition with thermoregulation. *Ecology* 78: 2230-2237.
- VÁSQUEZ RA (1997) Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. *Revista Chilena de Historia Natural* 70: 557-563.
- VELOSO C & F BOZINOVIC (2000) Effect of food quality on the energetics of reproduction in a precocial rodent, *Octodon degus*. *Journal of Mammalogy* 81: 971-978.
- VISPO CR & GS BAKKEN (1993) The influence of thermal conditions on the surface activity of thirteen-lined ground squirrels. *Ecology* 74: 377-389.
- YÁÑEZ J & FM JAKSIC (1978) *Historia natural de Octodon degus* (Molina) (Rodentia, Octodontidae). Publicación Ocasional, Museo Nacional de Historia Natural (Chile) 27: 3-11.
- ZUNINO S, F SAIZ & LR YATES (1992) Uso del espacio, densidad de *Octodon degus* y oferta de recursos en Ocoa, Parque Nacional La Campana, Chile. *Revista Chilena de Historia Natural* 65: 343-355.

Associate Editor: F. Jaksic

Received September 26, 2001; accepted November 27, 2001