Journal of Mammalogy, 85(2):260–267, 2004

MICROSTRUCTURE OF SUMMER ACTIVITY BOUTS OF DEGUS IN A THERMALLY HETEROGENEOUS HABITAT

G. J. KENAGY,* RODRIGO A. VÁSQUEZ, BRIAN M. BARNES, AND FRANCISCO BOZINOVIC

Department of Biology and Burke Museum, University of Washington, Seattle, WA 98195, USA (GJK)
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile (RAV)
Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA (BMB)
Centro de Estudios Avanzados en Ecología & Biodiversidad and Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago 651-3677, Chile (FB)

Small day-active endotherms living in hot environments maintain heat balance and avoid overheating by behavioral adjustments of their time budgets. We examined the temporal and spatial microstructure of surface activity bouts in the degu (*Octodon degus*) under maximal, summertime environmental heat load in a thermally complex habitat mosaic of sun and shade. The degu is the only native small mammal regularly active during the day in central Chile. We recorded thermal environmental data and activity of individuals with video cameras to quantify time spent in open sun as compared to shade. We predicted that individuals would adjust activity ''microbouts'' (successive momentary movements in and out of shade cover) in response to increasing heat load. As heat load increased toward end of morning, the proportion of total surface time spent in shade increased and approached 100%. Likewise, direct exposures to solar radiation decreased from almost 8 min in early morning to less than 1 min by late morning. Field measurements of body temperature remained within a 24-h range of 36–38°C (mean 36.7°C), suggesting an intolerance of increases above this range. The low heat tolerance of the degu seems to be a physiological limitation associated with its nocturnal family lineage. Because daytime activity is exceptional within this lineage, the degu has used behavioral adjustments to become the only regularly day-active native small mammal in its environment.

Key words: behavioral decisions, Chile, habitat complexity, *Octodon degus*, space use, temperature regulation, thermal ecology, time budget

The way in which mobile animals use their habitat results in consequences for the balance of thermal energy exchanged between animals and their environment. This is especially relevant for small animals in spatially complex terrestrial environments. Although small animals have the disadvantage of rapid potential thermal change compared to large animals, they do have access to a full range of spatially diverse microenvironmental conditions. These important aspects of thermal conditions for both ectothermic and endothermic animals have been emphasized in a number of overviews (Gates 1980; Huey 1991; Johnston and Bennett 1996; Partridge 1978; Tracy and Christian 1986). The movements of mobile animals within their habitat result from decisions among activity options that are based on interactions between the animal's internal state, often represented by energy balance, and the environment. Such decisions are often expressed as trade-offs between competing activities with alternative consequences for each (Clark and Mangel 2000; Houston and McNamara 1999). This aspect of behavior lies at the interface of ecology and physiology.

The responses of small endothermic animals to the spatial and temporal variability of hot and arid environments are particularly interesting because of the extreme environmental conditions and the behavioral flexibility of these animals (Bartholomew 1964). Among the most broadly distributed and successful of small mammals that are active during the daytime and that occur in hot, arid environments are rodents of the squirrel family, Sciuridae. The thermally relevant behavior and ecophysiology of squirrels in hot environments have been investigated in a variety of species (Bakko et al. 1988; Bennett et al. 1984; Chappell and Bartholomew 1981a, 1981b; Melcher et al. 1990; Sharpe and Van Horne 1999; Vispo and Bakken 1993). These studies illustrate trade-offs between activity functions, including foraging, and the avoidance of excess heat load by appropriate repositioning within the range of coarse-scale natural microclimatic conditions found in the habitat.

* *Correspondent: kenagy@u.washington.edu*

In the present study, we compare the behavior and physiology of an exceptional day-active rodent belonging to a lineage of South American rodents in which other members are nocturnal. We examined the spatial and temporal microstructure of activity in the degu (*Octodon degus*; Family Octodontidae) under maximal, summertime environmental heat loads in a complex habitat mosaic of low woody perennial vegetation and rocky substrate. The spatial scale of variation between sun and shade formed by the small plants and rocks characteristic of the habitat represents a finer scale of analysis of habitat structure than that of any previous study of a small day-active mammal (cited previously). Our measurement of time intervals to the nearest second also represents a more precise time scale. Our general hypothesis was that the animals should be able to exploit these extremely small scales of space and time. We specifically predicted that the frequency and duration of activity microbouts (defined here as successive short-term movements in and out of shade cover provided by small plants and rocks) would be adjusted to increasing heat load by an overall decrease in exposure of degus to open sun. A random distribution of activity between sun and shade, on the other hand, would indicate independence of activity from the thermal and habitat dimensions at the selected microscales. We conducted this study in the hottest and driest season of the year, following the breeding season and recruitment of juveniles into the population, which occurred about 3 months prior to our fieldwork.

The degu is the only native small mammal regularly active during the daytime in central Chile. Degus are broadly herbivorous, and adults weigh ~160–200 g. An earlier field study revealed the general sensitivity of degus to solar radiation and identified the importance of shade on a large scale (as provided by trees and shrubs) for maintaining thermal homeostasis (Lagos et al. 1995). We undertook an analysis on much smaller scales of space and time and focused on fine-scale activity movements during the major early morning period of degu summer activity. In summer, degu activity is distinctly bimodal, consisting of major early morning and late afternoon bouts (Kenagy et al. 2002a).

Materials and Methods

This study was conducted about 30 km west of Santiago, Chile, in Quebrada de la Plata, a field station of the Universidad de Chile, at 33°28′S, 70°53′W and elevation 445 m. The general habitat was typical of central Chilean matorral, but we selected a small area containing a particular kind of habitat consisting of rolling topography with rocky substrate, lacking in large shrubs and trees, and containing extensive patches of small woody perennial vegetation (30–60 cm high). The evergreen woody perennial composite *Senecio adenotrichius* was dominant; it provides cover, shade, and food for the degus. Two 20-m transects (using the methods of Bullock 1996) revealed an average cover of 27.5% by woody perennials. The complexity of the substrate was also enhanced by small rocks scattered over the surface, some as big as 10–40 cm in height and only a few greater than 40 cm; the rocks also contributed shaded refuge for the degus. Two 20-m transects had an average coverage of 7.5% by these larger rocks. The overall maximal area of our general observations was about 200 × 200 m, amounting to about 4 ha. In a previous study of seasonal variation in patterns of degu activity at this same field station, we selected a different and completely open study area covered principally by grasses and herbs (Kenagy et al. 2002a). Despite the greater structural complexity of the habitat in the present study, it was open enough that degus could be readily observed from selected vantage points.

During each morning activity period over 5 consecutive days, 26–30 January 1999, we recorded direct visual observations of the activity level of the population as a whole. We also made corresponding observations during the 2nd major bout of activity, in late afternoon, on three days: 27 and 30 January and 1 February. From these records, we summarized the general overall bimodal pattern of population activity, using the methods of a previous study (Kenagy et al. 2002a). All times are reported as Chilean Standard Time.

We used video cameras (Sony models CCD-TRV65 or CCD-TR413) to record as many observation bouts of surface activity of individuals as possible over the 5 mornings. Successful observation bouts contained continuous sequences of movements of individual degus. We defined periods of observation for each observer as observation bouts. Although some individuals had been previously marked externally with individually recognizable patterns of black hair dye, not all the degus could be identified individually. However, each successful bout of recording was distinguished by clear association with a single individual that was continuously followed visually. We used the camera screen clock for timing activity microstructure during each recording bout and narrated the filming to facilitate further data input concerning each individual. We obtained a total of 42 observation bouts by 3 individual observers. Thirty-eight observation bouts were records of partial bouts of aboveground activity, beginning when we observed an animal and ending when our continuous focus on the individual was interrupted. We set a minimum threshold of 10-min duration for such a bout to be included in our data set. Mean bout duration was 26.45 min (range 10–84 min). We also included 4 additional bouts <10-min duration that were complete and undisturbed natural bouts of emergence, surface activity, and return to the burrow. The total data set of 42 observation bouts amounted to 1,015.82 min of continuous observation of degus during morning activity. We defined individual periods of presence of degus on the surface as activity bouts. The microstructure within these activity bouts was, in turn, differentiated for our analysis into microbouts belonging to 2 different categories: presence in the open and exposed to solar radiation or presence in the shade cover of small woody perennials or rocks.

Each videotaped observational bout was reviewed afterward in the laboratory. We characterized all surface activity in terms of microbouts representing events for each of 2 microhabitat conditions: open and under direct solar radiation or shaded and under cover of small woody perennials or rocks. We selected the particular study area for these observations because it contained a habitat that provided this spatial complexity and corresponding thermal heterogeneity.

To obtain a concurrent measure of the range of thermal conditions reflecting the spatial heterogeneity (sun compared to shade) of the study area, we recorded global solar radiation (W/m^2) in the open using a LI-COR LI-200SA pyranometer (LI-COR, Inc., Lincoln, Nebraska) and shaded air temperature at 40 cm above the surface with a thermocouple in a shaded white hood. These 2 variables were recorded continuously during our presence on the study area with a LI-1400 data logger (LI-COR). We also recorded operative environmental temperature (T_e) from a thermocouple inside a thermal mannequin (Bennett et al. 1984; Chappell and Bartholomew 1981b; Kenagy et al. 2002a). Our thermal mannequin was a hollow skin of a degu mounted over a wire frame that was covered with aluminum foil and arranged in the typical quadrupedal posture (after Bennett et al. 1984). To standardize and maximize the influence of solar heat load on T_e, we used a single

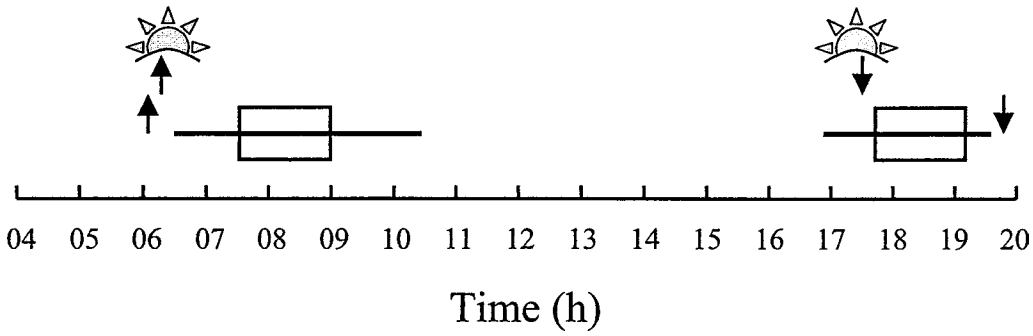

FIG. 1.—Summary of bimodal daily activity patterns in the degu population observed in Chile in late January (austral summer). The 2 rectangles represent average morning and afternoon periods of intense population activity, and horizontal lines cover extremes from earliest to latest individuals. Sunrise (0600 h) and sunset (1949 h) with respect to the 0° horizon, according to almanac, are indicated by the 1st and 4th arrows (extreme left and right); 2nd and 3rd arrows, respectively, and adjacent to solar symbols indicate appearance (0619 h) and disappearance (1729 h) of the sun at the local skyline associated with the profile of hills to the east and west of the study area.

mannequin maintained in a fully open location, reoriented at intervals to maintain perpendicularity to direct solar radiation. The T_e was read manually from a Sensortek telethermometer (Sensortek, Costa Mesa, California) at 15–20-min intervals; readings were plotted and interpolated to give continuous values as needed. We also obtained daily maximum and minimum air temperatures for general reference from the nearby Pudahuel station of the Chilean Meteorological Service.

We subdivided activity behavior recorded by video camera according to the microstructural subdivision of open as opposed to shaded microhabitat, and then we combined these data with the measurements of operative temperature. We grouped records of T_e by 5° intervals (10–15°C, 15–20°C, and so on), with corresponding beginning and ending times of each interval on the basis of the daily curve of increase in T_e. The presence of degus in sun as opposed to shade is presented in relation to these 5° intervals.

We obtained a continuous measurement of internal, abdominal T_b in a single degu under free-living conditions at the field site using a surgically implanted miniature device consisting of a thermistor, battery, and data logger programmed to record every 24 s. The unit (weighing about 10 g) was a modified Tidbit logger (Onset, Pocasset, Massachusetts—Boyer and Barnes 1999). The sensor was calibrated against a glass calibration thermometer in a water bath. The animal was captured in a Sherman (Tallahassee, Florida) large folding aluminum live trap in the late afternoon of 27 January, and the data logger was implanted intraperitoneally during a 5-min procedure (according to Boyer and Barnes 1999) under ether anesthesia at about 2000 h. The degu was held in the laboratory overnight and released into a burrow at the study site on 28 January at about 0600 h. It was recaptured on 1 February in late afternoon and held in the laboratory at 25°C beginning about 2030 h for recording of T_b until 1900 h on 2 February, at which time the implanted device was removed. Results are presented as mean ± 1 *SD*.

RESULTS

Activity and foraging were concentrated in 2 daily periods, early morning and late afternoon, with the greatest intensity from about 0730–0900 h and 1745–1915 h (Fig. 1). The ranges of morning activity were about 0630 to 1030 h, and those of afternoon activity were about 1655 to 1930 h. Typically we saw 4–8 animals simultaneously on the surface during the most intensely active periods. The few individuals occasionally active at the end of the morning period were no longer foraging and were generally resting in the shade of large rocks. Distribution of activity in morning and afternoon was not symmetrical with respect to times of sunrise and sunset (Fig. 1). This can be related to local topography and its effect on the time the sun appeared above or disappeared below the local skyline (as distinct from almanac times of sunrise and sunset, which refer to the unobstructed, 0° horizon). Topography to the east consisted of low and distant hills (allowing the sun to appear shortly after passing above the 0° horizon), while to the west nearby hills rose steeply over the area (blocking the sun for a considerable time before it passed below the 0° horizon). As a result of this temporal asymmetry, the morning activity period occurred entirely after the emergence of the sun above the local skyline, whereas the late afternoon activity occurred almost entirely after the sun had dropped below the skyline (i.e., under shaded conditions). By concentrating our study of activity microbouts in the morning, we obtained a detailed analysis of movements of animals between open sun and shade, both of which remained available over a small spatial scale during the entire morning activity period.

Over the 5 days of video observation, mean minimum air temperature was 12.0 ± 1.0°C, and maximum was 29.1 ± 0.8°C. During the morning activity period, we also obtained records of increases in solar radiation and environmental temperature (Fig. 2). Although the 1st day began with heavy ground fog, the sky cleared after 0830 h (Fig. 2; 26 January); the following 4 mornings were essentially completely clear and highly uniform thermally (Fig. 2; e.g., 30 January).

The relationship between direct solar radiation (Fig. 2A) and operative environmental temperature (Fig. 2C) is described by the linear regression $y = 0.041x + 16.6$ ($R^2 = 0.91$, $n = 46$, $P < 0.001$), where y is operative temperature (T_e) in °C and x is solar radiation in W/m^2. From this relationship, T_e of 40°C, just above mammalian body temperature, corresponds to a solar input of 570 W/m^2.

During the earliest part of morning activity, when T_e remained below 40°C (solar radiation <570 W/m^2) and shaded air temperatures was less than 18°C (Fig. 2), degus generally

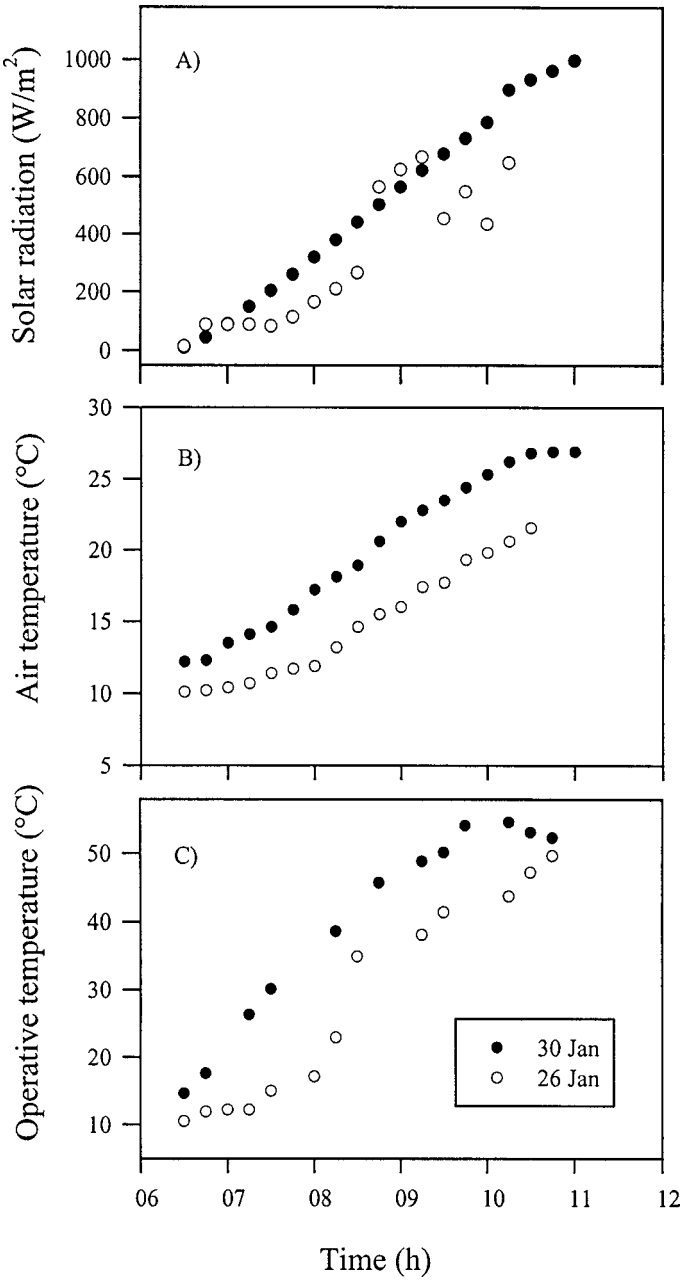

FIG. 2.—A) Solar radiation, B) shaded air temperature, and C) operative environmental temperature, T_e, recorded on 2 of the 5 mornings when behavioral observations were made. Solid circles, data for 30 January (with a clear sky); open circles, data for 26 January (morning with early ground fog). Records of 27–29 January were nearly identical to those of 30 January and are not shown.

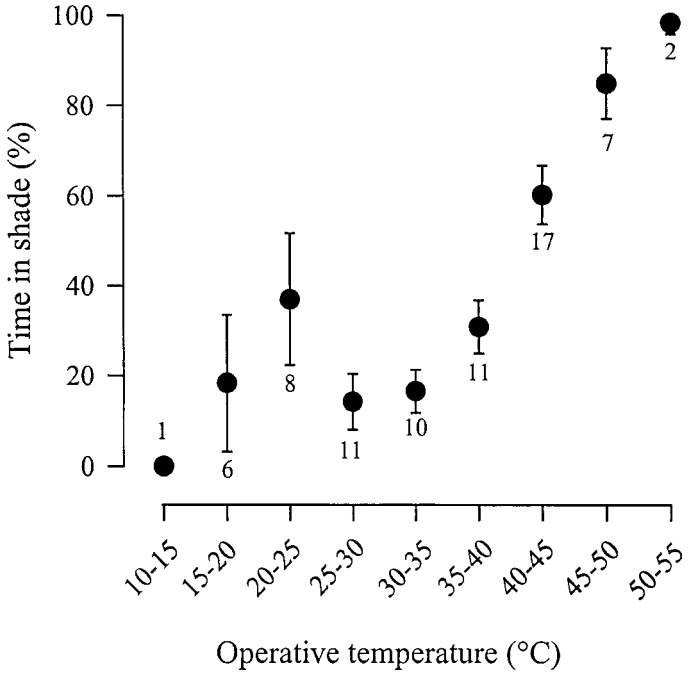

FIG. 3.—Time (%) spent by degus in the shade (mean ± *SE*) during 73 bouts of activity recorded 26–30 January in relation to operative environmental temperature. Increase in mean time in the shade with temperature is significant (Spearman exact rank correlation test, $r_s = 0.82$, $P = 0.0054$).

spent less than one-third of their time in the shade (Fig. 3). As environmental heat load continued to increase later in the morning (Fig. 2), total time in the shade increased as well, significantly, and approached 100% (Fig. 3). At the end of morning activity, when only a few degus remained active and spent nearly all their time in the shade, foraging ceased. At this time the last few degus active were resting in the shade, typically next to rocks, prior to retiring to their burrows.

As temperatures increased, the relationship between solar exposure and temperature was inverse to that of time in the shade (Fig. 4). The actual duration of microbouts of activity in the sun decreased significantly from a mean of nearly 8 min in the earlier morning to <1 min by the end of morning activity (Fig. 4).

We obtained the 1st continuous recording of core body temperature (T_b) of a free-living degu (Fig. 5). Body temperature fluctuated daily over a relatively narrow range (36–38°C) with only slight excursions above 38°C. The record covered 5 daytime periods corresponding to normal surface activity by the population (Fig. 5A–B). The 1st day, which followed implantation and overnight recovery in the laboratory, showed the lowest body temperatures and suggests post-implantation hypothermia and a reduction or possible lack of surface activity. The 2nd through 5th days showed variable increases in T_b in morning and afternoon (rising to 1 or more peaks; Fig. 5), which corresponded to the 2 daily periods of population surface activity (Fig. 1). During the midday interval between the 2 major increases in T_b, T_b declined to nearly 36°C, and nocturnal T_b declined to 36–36.5°C. The overall mean field T_b for the 5 daily (24 h) means was 36.7°C ± 0.2, based on successive daily means of 36.5, 36.5, 36.9, 36.8, and 36.9°C. During a postrecapture interval of about 22.5 h, while the degu was held in the laboratory at 25°C (Figs. 5B and 5C), its T_b ranged within ± 0.5°C of 37°C, with a mean of 37.2°C, remaining fairly flat by comparison to the field T_b over the previous days.

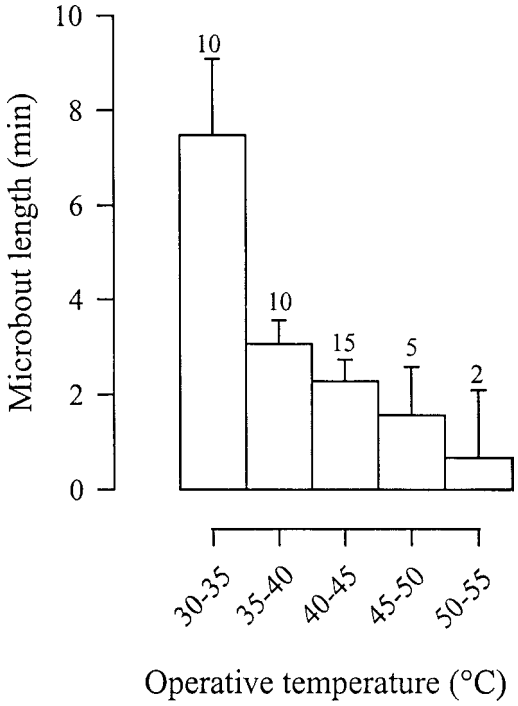

FIG. 4.—Length of exposure to solar radiation (mean ± *SE*) in relation to 5° incremental intervals of operative environmental temperature, as shown by duration of 42 individual activity microbouts. Pattern of decrease in mean sun exposure with temperature is significant (Spearman exact rank correlation test, $r_s = 1.0$, $P = 0.0083$).

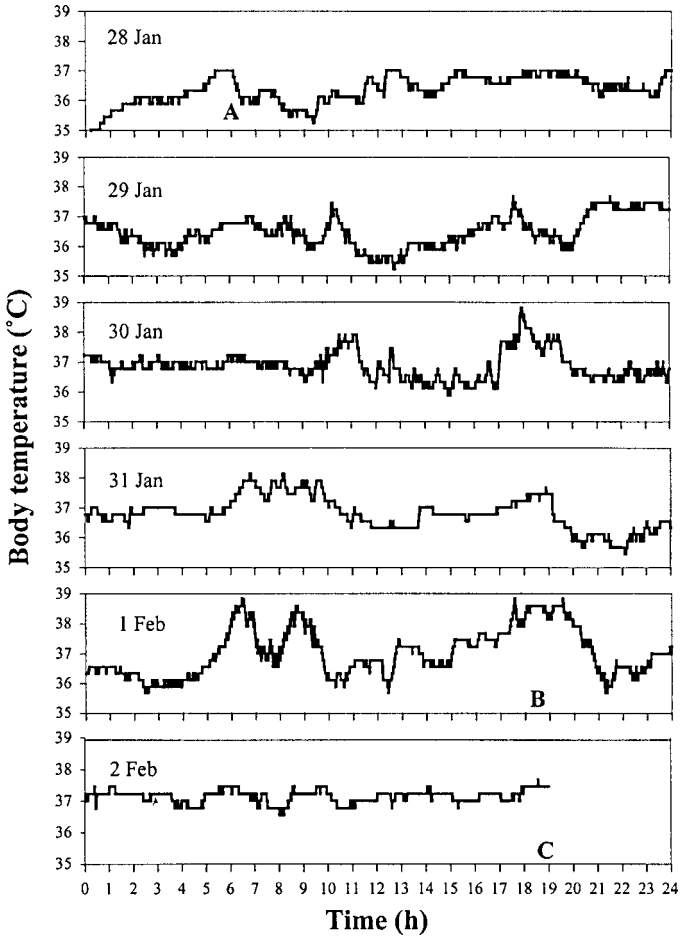

FIG. 5.—Continuous 6-day record of body temperature of a degu, as measured with a data logger 28 January–2 February. A) Release of animal in the field following implant, 28 January. B) Recapture of animal, followed by retention in laboratory beginning at 2030 h, 1 February. C) Removal of implant. Animal was 1st captured 27 January in late afternoon, implanted with data logger shortly thereafter, and held in laboratory overnight before release at 0600 h on 28 January at the site of capture.

DISCUSSION

We have demonstrated for the 1st time the interaction of activity and habitat use at extremely small scales of space and time in a small mammal in a hot, arid environment. Our use of video cameras facilitated the timing of microbouts of activity to the nearest second and the discrimination of small, degu-sized patches of shade associated with small woody perennial vegetation and small rocks. The analysis showed a systematic increase in proportion of time spent in shade as environmental temperature increased. Microbouts of solar exposure decreased to less than 1 min each shortly before conditions became completely intolerable for surface activity. Previous studies of the activity of squirrels in hot environments (Bakko et al. 1988; Bennett et al. 1984; Chappell and Bartholomew 1981a, 1981b; Melcher et al. 1990; Sharpe and Van Horne 1999; Vispo and Bakken 1993) did not resolve the spatial and temporal refuge from heat to the extent observed in the present study.

We have conducted other studies that cover a range of habitat structure scales for provision of shade as a refuge from solar radiation. In a previous study (Kenagy et al. 2002a), we specifically worked with degus in extremely open habitat that lacked trees, shrubs, or small perennials. Under these conditions, the only spatial refuge for the degus was escape from the surface into burrows, whereas escape in time was possible by being active early and late in the day, when the sun was below the local skyline. However, if cover is available, degus seek the shade of trees and large shrubs associated with the matorral vegetation (Lagos et al. 1995). We reexamined the selection of such heavily shaded large areas in a more recent study (Bacigalupe et al. 2003) and further validated the observation that large (tree-generated) patches of shade allow activity to continue at times when activity under direct solar radiation would be impossible. In the present study, we selected an extremely small scale of habitat heterogeneity, namely, that of tiny pieces of shade about the same size as a degu, that are generated in a complex mosaic by small woody perennial shrubs and rocks. For this assessment, we also needed to work on a small scale of time intervals. This overall series of studies illustrates a full range of spatial scales of thermally relevant habitat selection (Huey 1991; Partridge 1978) along with a range of temporal scales from seconds and minutes to days and seasons.

The intermittent and diverse nature of animal movement patterns is of interest to both ethologists and physiologists. An overall activity pattern must accommodate trade-offs among

a variety of behavioral and physiological functions. Few animals move continuously for long, and pauses are thus a regular feature of activity, whether they fall between short bursts of rapid movement or simply between longer periods of slow movement (Pennisi 2000). Depending on an animal's position in the food chain, pauses may serve for detection of prey or predators, and for all species they serve for general vigilance, orientation to the environment, and social awareness of conspecifics (Dyer 1998; Gendron and Staddon 1983; McAdam and Kramer 1998; O'Brien et al. 1990). Pauses between bursts of rapid locomotion also provide for physiological recovery from intense exertion (Kenagy and Hoyt 1989). The temporal scale of our observations in the present study encompassed mostly resting and intermittent slow movement (walking, at <0.5 m/s), simply because rapid movement (running, $\sim$2–4 m/s) occupies so little time for degus (Kenagy et al. 2002b). When moving slowly, degus were seeking food, which they found abundantly because the leaves of the most common woody perennial, *Senecio adenotrichius*, were desirable food. Pauses included time to harvest and ingest leaves and to maintain vigilant watch for predators, both aerial and terrestrial. Further analysis of time and energy use by degus has demonstrated temporal trade-offs among the diverse behaviors in the degu's repertoire (Kenagy et al. 2002b; Vásquez et al. 2002). Many functions are included in the behavioral routines of small animals, and our analysis of activity patterns with respect to environmental heat load and avoidance of overheating includes only part of the overall suite of functions that must be optimized in the time allocation of these animals.

Our observations raise questions about the physiological capacity of degus to endure exposure to daytime environmental conditions. Previous measurements of thermal physiology and body temperature (T_b) of degus are limited to laboratory study. Rosenmann (1977) reported a mean T_b in thermal neutrality of 37.2°C and a thermal neutral zone of 24–32°C. Refinetti (1996) reported a mean T_b of 36.8°C, with a daily amplitude of about 2.6°C and a range that remained essentially between 36 and 38°C. From the standpoint of animals under the extreme thermal challenges of natural summer daytime heat loads, it is surprising that our lengthy continuous field recording of T_b (Fig. 5) also remained essentially in the same range, 36–38°C, as Refinetti's (1996) laboratory T_b telemetry records and that our mean T_b of 36.7°C lies slightly below the means reported for captive animals. Thus, a degu exposed to natural extreme summer heat loads (Fig. 2) was able to avoid excessive T_b elevation above the range shown in the laboratory. Thus, the degu relies on behavior to adjust its exposure to aboveground conditions both on small temporal and spatial scales and over the broad range of seasonal changes in timing of daily activity (Kenagy et al. 2002a). Therefore, it avoids levels of T_b that would exceed its conservative homeostatic range. Degu activity is curtailed as operative environmental temperature (T_e) rises above 40°C; temperatures higher than this are tolerated only briefly (Kenagy et al. 2002a).

Thermal physiology and tolerances of the North American, desert-dwelling antelope ground squirrel, *Ammospermophilus leucurus*, have been well studied (Chappell and Bartholomew 1981a, 1981b). Telemetric measurements of T_b in summer showed a mean maximum of 40.2°C, with an extreme of 43.6°C and a mean minimum of 38.0°C. These values clearly all lie above the T_b levels of the degu. In addition to *A. leucurus*, other rodents of the squirrel family (Sciuridae) also show indications of tolerating increases in T_b that are greater than the tolerable range of the degu (Bakko et al. 1988; Bennett et al. 1984; Melcher et al. 1990; Sharpe and Van Horne 1999; Vispo and Bakken 1993). The tolerances of these sciurid rodents thus have a phylogenetic basis, but the physiological processes behind these patterns represent an integration of heat flow between animal and environment as well as the additional avenue of endogenous heat production associated with locomotion.

The daytime activity of *Octodon degus*, which promotes exposure to solar radiation, is a behavioral pattern that is apparently recently derived. Two other species of *Octodon* and the remainder of the family Octodontidae are all considered to be nocturnal (Contreras et al. 1987). We suggest that the lack of physiological tolerance for higher body temperatures in degus, by comparison to sciurid rodents, is a result of the degu's recent derivation of daytime activity. The solution for the degu's survival and success results from the nature of the behavior itself, which allows degus to select those moments and hours and the particular locations in their environment that allow them to escape in space and time from the most thermally demanding conditions. This escape nonetheless allows them to occupy a daytime temporal niche into which they have moved in only recent evolutionary time.

Daytime activity by small endotherms, rodents in particular, in hot, arid environments represents a pattern of success that is not phylogenetically widespread in mammals. The rodents living in this temporal niche are almost exclusively members of the Sciuridae, a family that lacks any representatives in the region of southern South America containing Chile. Despite the evolution of some apparent physiological abilities for specialization to at least a modest degree, the role of behavior remains fundamental in allowing the success of degus. Small endotherms can readily seek the refuge of small microenvironmental spaces, and they can come and go in short intervals of time. This is especially important, in ways that we have demonstrated here, in the special case of daytime activity in hot, arid environments.

Resumen

Los endotermos pequeños y diurnos que viven en ambientes cálidos mantienen su balance calórico y evaden el sobrecalentamiento a través de ajustes conductuales en sus presupuestos de tiempo para actividad y alimentación. Examinamos los eventos de actividad temporal y microestructura espacial de actividad en superficie en el degu (*Octodon degus*) bajo carga térmica ambiental máxima en verano y en un hábitat térmicamente complejo de sol y sombra. El degu es el ùnico mamífero pequeño nativo que es activo durante el día en Chile central. Obtuvimos datos ambientales y registramos la actividad de los individuos con cámaras de video y cuantifi-

camos el tiempo gastado en exposición al sol en comparación a exposición a sombra. Nuestra predicción fue que los individuos ajustarían la frecuencia y duración de los ''micro-eventos'' de actividad (movimientos sucesivos momentáneos de entrada y salida de la sombra) en respuesta a un incremento en la carga calórica. Nuestros resultados muestran que a medida que la carga calórica aumenta, la proporción de tiempo en superficie gastado en la sombra también incrementa y se aproxima al 100% al final de período de actividad matinal. Del mismo modo, la duración en la exposición a radiación solar decrece desde casi 8 min de exposición directa en la mañana a menos de un minuto al final de la misma. Las mediciones de temperatura corporal del degu en el campo, en un rango de 24-h, varían entre 36–38°C (media 36.7°C), sugiriendo ausencia de tolerancia a incrementos ambientales sobre ese rango. La baja tolerancia térmica del degu parece ser una limitación fisiológica resultante de un linaje familar generalmente nocturno. Debido a que la actividad diurnal es excepcional dentro de este linaje, el degu muestra ajustes conductuales que le permiten ser el ùnico pequeño mamífero de su ambiente regularmente activo durante el día.

Acknowledgments

Support for this research was provided by the U.S. National Science foundation (INT 9600578) for cooperative research in Chile, by the Fondo de Desarrollo Cientifico (1950394) to G.J. Kenagy and F. Bozinovic, and by Fondo de Desarrollo de Areas Prioritarias 1501-001 to F. Bozinovic. Animal care and use procedures followed American Society of Mammalogists Guidelines and were conducted under protocols of the University of Washington and Pontificia Universidad Católica de Chile. Thanks to Ray Huey for advice with data analysis.

Literature Cited

Bacigalupe, L. D., E. L. Rezende, G. J. Kenagy, and F. Bozinovic. 2003. Activity and space use by degus: a trade-off between thermal conditions and food availability. Journal of Mammalogy 84: 311–318.

Bakko, E. B., W. P. Porter, and B. A. Wunder. 1988. Body temperature patterns in black-tailed prairie dogs in the field. Canadian Journal of Zoology 66:1783–1789.

Bartholomew, G. A. 1964. The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. Symposia of the Society of Experimental Biology 18:7–29.

Bennett, A. F., R. B. Huey, H. John-Alder, and K. A. Nagy. 1984. The parasol tail and thermoregulatory behavior of the cape ground squirrel, *Xerus inauris*. Physiological Zoology 57:57–62.

Boyer, B. B., and B. M. Barnes. 1999. Molecular and metabolic aspects of mammalian hibernation. BioScience 49:713–723.

Bullock, J. 1996. Plants. Pp. 111–138 in Ecological census techniques (W. J. Sutherland, ed.). Cambridge University Press, Cambridge, United Kingdom.

Chappell, M. A., and G. A. Bartholomew. 1981a. Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus*. Physiological Zoology 54:215–223.

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

Clark, C. W., and M. Mangel. 2000. Dynamic state variable models in ecology: methods and applications. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, United Kingdom.

Contreras, L. C., J. C. Torres-Mura, and J. L. Yáñez. 1987. Biogeography of octodontid rodents: an eco-evolutionary hypothesis. Fieldiana Zoology, New Series 39:401–411.

Dyer, F. C. 1998. Cognitive ecology of navigation. Pp. 201–260 in Cognitive ecology (R. Dukas, ed.). University of Chicago Press, Chicago, Illinois.

Gates, D. M. 1980. Biophysical ecology. Springer-Verlag, Berlin, Germany.

Gendron, R. P., and J. E. R. Staddon. 1983. Searching for cryptic prey: the effect of search rate. American Naturalist 121:172–186.

Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behaviour; an approach based on state. Cambridge University Press, Cambridge, United Kingdom.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91–S115.

Johnston, I. A., and A. F. Bennett (eds.). 1996. Animals and temperature: phenotypic and evolutionary adaptation. Society for Experimental Biology, Seminar Series 59, Cambridge University Press, Cambridge, United Kingdom.

Kenagy, G. J., and D. F. Hoyt. 1989. Speed and time-energy budget for locomotion in golden-mantled ground squirrels. Ecology 70: 1834–1839.

Kenagy, G. J., R. F. Nespolo, R. A. Vásquez, and F. Bozinovic. 2002a. Daily and seasonal limits of time and temperature to activity of degus. Revista Chilena de Historia Natural 75:567–581.

Kenagy, G. J., R. A. Vásquez, R. F. Nespolo, and F. Bozinovic. 2002b. A time-energy analysis of daytime surface activity in degus, *Octodon degus*. Revista Chilena de Historia Natural 75:149–156.

Lagos, V. O., F. Bozinovic, and L. C. 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.

McAdam, A. G., and D. L. Kramer. 1998. Vigilance as a benefit of intermittent locomotion in small mammals. Animal Behaviour 55:109–117.

Melcher, J. C., K. B. Armitage, and W. P. Porter. 1990. Thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*). Physiological Zoology 63:803–820.

O'Brien, J. W., H. I. Browman, and B. I. Evans. 1990. Search strategies of foraging animals. American Scientist 78:152–160.

Partridge, L. 1978. Habitat selection. Pp. 351–376 in Behavioural ecology: an evolutionary approach (J. R. Krebs and N. B. Davies, eds.). Blackwell, Oxford, United Kingdom.

Pennisi, E. 2000. In nature, animals that stop and start win the race. Science 288:83–85.

Refinetti, R. 1996. Comparison of the body temperature rhythms of diurnal and nocturnal rodents. Journal of Experimental Zoology 275:67–70.

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

Sharpe, P. B., and B. Van Horne. 1999. Relationships between the thermal environment and activity of Piute ground squirrels (*Spermophilus mollis*). Journal of Thermal Biology 24:265–278.

TRACY, C. R., AND K. A. CHRISTIAN. 1986. Ecological relations among space, time, and thermal niche axes. Ecology 67:609–615.

VÁSQUEZ, R. A., L. A. EBENSPERGER, AND F. BOZINOVIC. 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. Behavioral Ecology 13: 182–187.

VISPO, C. R., AND G. S. BAKKEN. 1993. The influence of thermal conditions on the surface activity of thirteen-lined ground squirrels. Ecology 74:377–389.

Submitted 19 September 2002. Accepted 17 April 2003.

Associate Editor was Penny S. Reynolds.