DAILY ACTIVITY OF A NEOTROPICAL RODENT (OXYMYCTERUS NASUTUS): SEASONAL CHANGES AND INFLUENCE OF ENVIRONMENTAL FACTORS

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We investigated daily activity patterns of the long-nosed mouse (Oxymycterus nasutus) in a high-elevation grassland field in southern Brazil. We censused the animals every other month from June 2001 to May 2002, determining capture time with digital timing devices attached to traps. Activity patterns were markedly diurnal and did not differ between sex or age classes. Captures were more frequent just after sunrise and just before sunset. Daily activity was strongly influenced by ambient light, with animals showing seasonal changes in their activity time according to day length but with some activity at night. Nocturnal captures were positively related with night brightness measured in log lm/m² (logistic regression; odds ratio = 1.76, P < 0.001). Temperature positively influenced the probability of capture of O. nasutus during daylight hours (quadratic regression; r² = 0.76, d.f. = 11, P < 0.001), with the highest predicted capture probability at 3–6°C and a sharp reduction above 21°C. Although diurnal activity has been reported for other Oxymycterus species this is the 1st study to rigorously quantify diurnal activity of a neotropical rodent in the field. O. nasutus apparently showed a more strictly diurnal pattern than described for other congeners.

Key words: Brazil, Campos de Altitude, daily activity patterns, high-elevation grassland, Oxymycterus nasutus, small mammals

Most animals divide their lives into 2 alternative behavioral states: rest and activity. During active periods they perform actions necessary for survival, such as foraging, exploration of new environments, searching for mates, and territory defense in the case of territorial species (Halle and Stenseth 2000). Most importantly, during their active period most small animals also are at risk of predation. Thus, the daily activity patterns of prey animals are influenced not only by physiological constraints (e.g., ambient temperature and light sensitivity), but also by ecological interactions such as competition, predator activity, and food availability.

Small mammals generally are subject to high predation pressure but require relatively high food intake. Thus, their daily activities represent a balance between potentially contradictory needs (Halle 2000a). Because the risk of being preayed upon while feeding is high, rodent species should limit their activity to time periods with reduced predation risk. For some small mammals, for instance, nocturnal activity is reduced during bright lunar phases (Bowers 1988; Julien-Laferrière 1997). Light intensity generally is thought to strongly influence small-mammal activity patterns (Bittencourt et al. 1999). Rodent activity patterns also may be influenced by seasonal changes, especially in photoperiod and temperature (Lockard 1978; Lockard and Owings 1974; Wauters 2000). Small rodents should be active at those times when temperatures are suitable, to avoid excessive loss of energy through compensation for heat loss, when ambient temperature is low (Vickery and Bider 1981), or to avoid heat stress, when ambient temperature is high (Feldhamer et al. 1999). Moreover, sex-specific evolutionary pressures may cause differences in behavior and space use between sexes (Ostfeld 1990) and may lead to intraspecific differences in daily activity patterns (Merritt and Vessey 2000).

Despite its potential ecological relevance, few studies have analyzed daily activity patterns of small rodents in the Neotropics (but see Bittencourt et al. 1999; Kravetz 1972; Priotto and Polop 1997; Vieira and Baumgarten 1995). For most species, there is only a general acknowledgement that they are nocturnal or diurnal, without detailed information on their activity time (Alho 1982; Emmons and Feer 1997).
where they generally are common, but also occur in swampy areas within forests (Alho 1982; Eisenberg and Redford 1999; Emmons and Feer 1997). In the Campos de Altitude one of us (EMV) has noted that the long-nosed mouse (Oxymycterus nasutus; Rodentia: Sigmodontinae) is the dominant small-mammal species. Similar to other species of this genus, O. nasutus is semifossorial and highly insectivorous (González 2001).

In the present study we used live traps equipped with timing devices to investigate daily activity patterns of O. nasutus in the field. We addressed the following questions: What are the general activity patterns of the species? Are there seasonal changes in such patterns? Are there sex or age-related differences? Is there any relationship between temperature and nocturnal light and activity of O. nasutus?

**Materials and Methods**

**Study area.**—We conducted this study in Aparados da Serra National Park in southern Brazil (29°10′S, 50°05′W; Fig. 1). The climate is markedly seasonal and mesothermic, with average annual temperature of 12–20°C, moderate winters, and mild, wet summers (DeForest Safford 1999), corresponding to Köppen’s (1948) Cfb zone.

From 1998 to 2000 the total annual precipitation in the region ranged from 1,700 to 2,000 mm. During this period the mean daily extreme temperatures in summer were 9.4°C and 24.6°C. In winters these values dropped to 2.5°C and 19.3°C (Auxiliar Climatological Station of Cambará do Sul, Rio Grande do Sul, Brazil, in litt.).

Aparados da Serra National Park comprises 10,250 ha ranging from 75 m to 1,000 m in elevation, and with the contiguous Serra Geral National Park forms a protected area of about 27,500 ha. The vegetation is composed of grasslands and natural patches of Araucaria forest in the higher areas, and typical Atlantic Forest in the lower parts. We conducted the study in the Campos de Altitude of the national park. The vegetation of the Campos de Altitude is highly diverse and is characterized by nonarboreal species, mainly species of Poaceae, Cyperaceae, Asteraceae, Apiaceae, Rubiaceae, Fabaceae, and Ericaceae. Tall grasses dominate, mainly Andropogon lateralis, Schizachyrium tenerum, Paspalum maculosum, and Axonopus siccus (Boldrini 1997). For more detailed information on the vegetation of the national park see Dalmagro and Vieira (2005) and Behling et al. (2004). The landscape of the area consists of flat hills, topped with permanent dry lands (i.e., without apparent water on the soil surface), and wet fields in lower areas (Fig. 2).

**Data collection.**—We conducted 7 trapping sessions (5 days each) in June and July 2001 (winter), September and November 2001 (spring), January 2002 (summer), and March and May 2002 (autumn), using standard Sherman live traps (9 × 8 × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) in 5 transects placed ≥50 m from each other. Transects were arranged to equally sample wet and dry areas and comprised 14 trap stations spaced 40 m apart, totaling 70 trap stations. Censuses were made with 60 traps; in every trapping session we randomly selected 60 stations to sample (total effort of 300 trap-nights per session). Once we captured an animal, a trap was moved to another trap station to minimize successive recaptures. We generally moved traps to unoccupied stations, but sometimes a few trap stations had 2 traps for a few days. We tried to increase the number of individuals captured and reduce number of recaptures to avoid problems with potential dependence of data caused by multiple captures of a few individuals (see “Data analysis”).
All traps were equipped with digital timers that indicated the time of capture to the nearest minute. Traps were baited with a mixture of peanut butter, cornmeal, mashed banana, commercial cod-liver oil, and vanilla essence. We examined traps and renewed bait if necessary between 0830 and 1200 h every day. We recorded species, location, capture time, sex, and weight of every captured animal. Animals were classified as young (less than one-third the maximum adult weight), subadult (one-third to two-thirds the maximum weight), and adults (greater than two-thirds the maximum weight). Animals were ear-tagged (no. 1005 Monel tags; National Band and Tag Co., Newport, Kentucky), and released at the point of capture after data collection. Trapping and handling conformed to guidelines sanctioned by the American Society of Mammalogists (Animal Care and Use Committee 1998).

We measured air temperature in the field every 15 min during the entire period of the trapping series using a Hobo data logger (Onset Corporation, Bourne, Massachusetts; −10°C to 50°C, to the nearest 0.1°C) with an external sensor placed under the dense grass cover where O. nasutus travels using runways. We also measured light intensity using a Stowaway data logger (Onset Corporation; 3.0–4.0 log lm/m², to the nearest 0.01 log lm/m²) placed in the study area 50 cm aboveground. We recorded daily sunset and sunrise times as reported by a handheld global positioning system unit (Garmin 12X; Garmin International, Inc., Olathe, Kansas).

**Data analysis.**—We quantified daily activity patterns by assessing the number of animals captured in each 2-h period. Although this method has been used for assessing activity patterns of small mammals (Bruseo and Barry 1995; Priotto and Polop 1997), it could be biased because trapped animals are not available for subsequent recapture and they occupy traps that are not available to document activity at later periods (Graipel et al. 2003). To assess the potential for such bias we estimated population size of O. nasutus using the Jolly–Seber method (Krebs 1989) to evaluate the proportion of the population that remained inside traps during each day of capture.

To reduce potential effects of capture stress, bait feeding, and time in the trap on the animal's behavior, we considered only the 1st capture of an individual within any 24-h period. For most analyses we pooled captures in 2-h periods. Because O. nasutus is markedly diurnal, we pooled nocturnal captures (e.g., from 2 h after sunset to 2 h before sunrise) in a single night period to reduce the number of empty cells (Zar 1996).

For each season we compared proportions of 1st capture of individuals and all captures of individuals for each sex and age class, using Kolmogorov–Smirnov 2-sample tests (Zar 1996). All these comparisons were nonsignificant ($P > 0.05$), except for all categories in summer, subadults in spring and autumn, and females in autumn, for which limited sample sizes precluded statistical comparisons. Based on similar distribution of individuals and captures, we assumed that all captures were independent and analyses were applied to total captures (as in Bruseo and Barry 1995).

We tested for differences between sexes and between age classes by comparing capture frequencies in different time periods using Kolmogorov–Smirnov 2-sample tests (Zar 1996). Small sample sizes for juveniles limited comparisons by age to subadult and adult categories. Comparisons were made for each season, although low capture frequencies in summer and autumn precluded analyses between age classes for those seasons.

We also compared overall capture frequencies among seasons using Kolmogorov–Smirnov 2-sample tests. These seasonal comparisons were run twice, 1st using capture frequencies grouped in regular 2-h periods without correcting for sunrise or sunset time. To compare daylight activity without considering changes caused by seasonal variation in day length, we ran the same test using 2-h periods based on sunrise and sunset times (e.g., 2 h before sunrise, sunrise hour, 2 hours after sunrise, 4 h after sunrise, and so on). Because there were marked differences in day length among seasons, the midday category (between 4 h after sunrise and 4 h before sunset) had different duration in each season, ranging from 2 h, 20 min in winter to 4 h, 55 min in summer. To reduce the effect of this variation, we corrected the number of midday captures by the length of this category, thus estimating the number of captures on a 2-h basis. The influence of this variation on the results was minor because midday was the diurnal category with the lowest capture frequencies for most seasons.

The Kolmogorov–Smirnov 2-sample test used in the present study only enables comparisons between season pairs (i.e., winter × spring, winter × autumn, winter × summer, and so on). Therefore, we proceeded to a sequential Bonferroni procedure (Holm 1979) for correction of the significance level ($\alpha$) by dividing the overall $\alpha$ (0.05) by the number of comparisons (maximum of 6), resulting in a lowest significance level of 0.008. Because this Bonferroni adjustment has been criticized for being excessively conservative (see Gotelli and Ellison 2004), we also indicate in the results the comparisons that resulted in $P$ values ranging from 0.008 to 0.05. Because the $P$ values of only 2 (16.7%) of 12 comparisons fell into this category, the influence of performing sequential Bonferroni procedures on our results was minor.

We investigated the relationship between nocturnal activity, light intensity, and temperature using multiple logistic regression. We tested the hypothesis of a linear relationship between presence and absence of captures during 1-h intervals (dependent variable) and 2 independent variables: the average of 4 measures of light intensity (log lm/m²) and average of 4 measures of temperature (°C) during this 1-h interval. The influence of 1-h intervals with multiple captures on the results was negligible, because very few 1-h intervals had more than 1 capture (<5% of the total).

For the relationship between activity and diurnal temperature we expected a nonlinear relationship, where the number of captures would be higher at intermediate temperatures. We tested this assumption by grouping 1-h intervals in classes of temperature of 3°C and estimating the proportion of successful periods (i.e., those periods with captures) within each class. We used a standard arcsine–square-root transformation on the values expressed in proportions to meet assumptions of normality (Zar 1996). Then we used these transformed...
values as the dependent variables, which were regressed against temperature using the polynomial curve fitting described in Zar (1996).

 RESULTS

We recorded 303 captures of 139 individuals of *O. nasutus* with 1,981 trap-days of effort, resulting in a capture success of 15.3%. Most animals were captured only a few times (\( \bar{X} = 2.18 \) captures per individual; median = 1 capture per individual), indicating a similar contribution of most individuals to the observed activity patterns. The estimated population size of *O. nasutus* ranged from 48 to 109 individuals, with a mean percentage of the population kept inside traps of about 11% per day. These results indicated that we were not retaining a large proportion of the trappable animals.

In addition to *O. nasutus*, we also captured the didelphid marsupial *Monodelphis cf. brevicaudis* (31 individuals) and the sigmodontine rodents *Akodon* sp. nov. (80 individuals), *Akodon azarae* (35 individuals), *Oligoryzomys flavescens* (6 individuals), *Scapteromys* sp. nov. (5 individuals), *Oligoryzomys nigripes* (2 individuals), and *Akodon montensis* (2 individuals), resulting in an overall trapping success of 26.4%. Thus, on average more than 73% of traps were available at the end of any sampling night.

For seasons with appropriate sample sizes, captures of *O. nasutus* did not differ significantly between sexes (winter, 0.9; spring, 0.9; summer, 0.7; autumn, 0.9) or ages (winter, 0.9; spring, 0.9). Therefore, we pooled the data for subsequent analyses.

*Oxymycterus nasutus* showed a markedly diurnal activity pattern with 2 daily peaks in all seasons (Fig. 3). We documented high activity peaks just after sunrise and again, but less intense, just before sunset. Activity rapidly declined after about 0800 h to a minimum during the middle of the day. Comparisons between seasons indicated that daily activity patterns varied significantly when grouped by regular 2-h classes, for 3 of 6 comparisons (winter × spring, 0.9; winter × summer, 0.9; summer × autumn, 0.9; spring × autumn, 0.046; and for the other 2 comparisons, 0.250). In contrast, when captures were grouped in 2-h classes bracketing sunrise and sunset we did not detect significant differences between any season pair (P = 0.025 for autumn × summer, and P = 0.260 for the other 5 comparisons; Fig. 3).

Although primarily diurnal, *O. nasutus* showed some nocturnal activity (Fig. 3). The logistic model indicated that only the effect of nocturnal light on the probability of animals being captured, holding temperature constant, was significant (odds ratio = 1.76, 95% confidence interval = 1.56 to 1.99, 0.001; logit \( P = -0.1370 + 0.5660x \), where \( x = \) light intensity in log lm/m²).

Mean hourly temperatures during the day ranged from \(-0.3^\circ C\) to \(38.8^\circ C\); in this period 191 of 379 1-h intervals yielded captures. The mean number of 1-h intervals per 3°C temperature class was 31.3 (range: 6–70). The highest temperature class, between 36°C and 39°C, was not considered for analysis because there were only three 1-h periods (all of them nonsuccessful) in that class. A quadratic model provided the best fit to the relationship between diurnal temperature and proportion of successful 1-h intervals (\( y = 0.96100 + 0.03890x - 0.00087x^2 \), where \( x = \) temperature; adjusted \( r^2 = 0.76, \) df = 11, 0.001; Fig. 4). The highest probability of captures (70.4%) was predicted to occur at an ambient temperature of 3–6°C.

 DISCUSSION

Field studies are the best means of studying ecological aspects of animal behavior (Halle and Weinert 2000). The method of assessing time of capture by using timing devices...
attached to traps is relatively inexpensive and provides information that could not be easily obtained otherwise. The alternative method of checking and resetting traps at 1- to 4-h intervals to assess daily activity patterns (as used by Vieira and Baumgarten 1995) has the disadvantage of potentially interfering with animal activity by checking traps several times during a 24-h period. Additionally, it does not indicate the exact time of capture, as does the method used here. However, both methods provide information only about foraging activity, and are not useful for investigating other activity aspects, such as searching for mates.

Graipel et al. (2003) and Vieira and Baumgarten (1995) noted that daily activity patterns determined by the frequency of animals entering traps might be influenced by the effect of the reduction in the number of animals available for trapping during a 24-h period. Hicks et al. (1998) also criticized the method of timing devices used in the present study, suggesting that only 1 trap checking per day could produce an artificial increase in capture frequency in the 1st hours after setting traps. This increase would be an artifact caused by the reduction in the number of traps available for the rest of the population through the 24-h period. In our study, trap arrangement and capture rates resulted in a low proportion of the population retained in traps per day, and most traps were available throughout the entire sampling period. Thus, the effects of reducing the trappable population and number of available traps were negligible. Moreover, the activity peak that we detected (between 0600 and 0800 h) occurred just before trap checking, when traps had been available for >20 h. These observations indicate that our results reflected real activity patterns.

Diurnal and crepuscular small mammal species are influenced by photoperiod (Halle 2000a). Bartness and Albers (2000) affirmed that biphasic activity patterns generally are characterized by a distribution of activity in the transitional periods between light and dark phases. Our results support this pattern, because sunlight seemed to establish the beginning and the end of daily activity for O. nasutus. In contrast to microtine rodents (e.g., lemmings) and shrews (Soricidae), which have polyphasic activity phases throughout the day (Halle 2000b; Merritt and Vessey 2000), murid rodents generally show circadian components in their activity patterns; that is, they present only 1 long phase of activity during a 24-h period (Bruseo and Barry 1995; Eccard et al. 2004; Ryan et al. 1993; Stokes et al. 2001). This pattern appears to hold for most neotropical sigmodontine rodents, such as species of Oryzomys (Bittencourt et al. 1999; Graipel et al. 2003), Nectomys squamipes (Bittencourt et al. 1999), and species of Calomys (Priotto and Polop 1997; Vieira and Baumgarten 1995). However, the Akodontini, including O. nasutus (present study), Bolomys lasiurus (Vieira and Baumgarten 1995), and A. montensis (Graipel et al. 2003), generally have diurnal or crepuscular habits with biphasic activity, or they exhibit 24-h activity with peaks varying through the year (e.g., A. azarae; Priotto and Polop 1997).

Published studies indicate distinct daily activity patterns for Oxymycterus species. Kravetz (1972) reported nocturnal and crepuscular activity periods both in the field and in the laboratory for Oxymycterus rufus platensis. Borchert and Hansen (1983) reported that Oxymycterus roberti was active mainly at night, but increased its diurnal activity as vegetative cover recovered from wildfires. Our results indicated that O. nasutus also had a circadian pattern, but most of its activity occurred soon after sunrise (between 0600 and 0800 h), with a less intense peak before sunset (between 1600 and 2000 h).

Biological rhythms may be understood only against the background of changes in the environment (Halle 2000a). Ambient light is a major influence on small-mammal activity patterns. For example, several nocturnal species reduce their activity during bright moonlight periods (Julien-Laferrière 1997; Kaufman and Kaufman 1982; O’Farrell 1974; Price et al. 1984; but see Vieira and Baumgarten 1995), which likely is related to predator avoidance (Julien-Laferrière 1997). Our results showed a very different pattern for O. nasutus, because most activity by this rodent was diurnal and even nocturnal activity was positively associated with ambient light.

In our study area the most frequent predators are diurnal raptors, owls, and predators with both nocturnal and diurnal activity, such as foxes (Cerdocyon thous and Pseudalopex gymnocercus) and several snake species. The dense grass cover of habitat of O. nasutus, in addition to providing milder microhabitat temperatures, probably also gives some protection against predators. The positive relationship between their nocturnal activity and light suggests that elevated light levels may facilitate foraging activities or the ability to escape from predators.

Rodents may alter their foraging behavior, social interaction, or activity period in response to seasonal climate changes, particularly in temperature (Stokes et al. 2001). We showed that O. nasutus changes its activity seasonally, mainly adjusting its activity according to the timing of sunset and sunrise. Additionally, during summer this species completely ceased activity in the hottest hours of the day (between 1000 and 1400 h). Both light and temperature influenced the activity of nocturnal small mammals in an Atlantic Forest area in southeastern Brazil (Bittencourt et al. 1999). In our study, polynomial regression indicated that temperature also

![FIG. 4.—Relationship between probability of capture of Oxymycterus nasutus (proportion of 1-h intervals with captures) and ambient temperature (in °C classes). Symbols represent mean successful intervals at each class of temperature.](https://academic.oup.com/jmammal/article-abstract/87/4/733/963671)
influenced activity patterns of *O. nasutus*. Whittaker and Feldhamer (2005) also detected a polynomial relationship (albeit not statistically significant, \( P = 0.09 \)) between ambient temperature and number of captures for the southern short-tailed shrew (*Blarinella carolinensis*). Because *O. nasutus* forages primarily on invertebrates, and temperature likely influences the activity of soil invertebrates (Merritt and Vessey 2000), foraging behavior by *O. nasutus* may be influenced by such changes.

Most authors report few or no differences between sexes (Drickamer 1987; Halle 2000b; Vieira and Baumgarten 1995) or among age classes (Rust 1978; but see Bäumler 1975) for small mammals. Similarly, we did not detect any sex- or age-related differences in daily activity. Synchronous patterns of daily activity, as seemed to be the case in our study, are in accordance with a strategy to reduce individual predation risk during diurnal activity (see Halle 2000a). However, we were not able to perform comparisons of age classes for all seasons or otherwise analyze activity of juveniles, and therefore we cannot disregard potential age-related differences.

Our study revealed detailed patterns of daily activity of *O. nasutus*. This sigmodontine rodent has a diurnal biphasic pattern with some nocturnal activity, influenced by ambient light. The timing of peaks in diurnal activity was relatively constant among seasons relative to sunrise and sunset events. We found no differences in activity times between sexes or ages (subadults \( \times \) adults). Temperature also influenced activity, with a reduction during the hottest midday hours, especially in summer, and more captures occurring between 3°C and 6°C, and a sharp reduction above 21°C. Although diurnal activity of other *Oxymycterus* species has been reported elsewhere, this is the 1st study to rigorously quantify a basically diurnal activity pattern of a neotropical rodent in the field.

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**LITERATURE CITED**


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