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Ambient temperature limits above-ground activity of the subterranean rodent Spalacopus cyanus

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Abstract

We studied daily activity patterns of the subterranean rodent *Spalacopus cyanus*, in the field during summer and winter, and under laboratory conditions at two different temperatures, 15° C and 30° C. This rodent exhibited nocturnal activity in the laboratory, but diurnal above-ground activity in the field. We suggest that this discrepancy between field and laboratory results is a consequence of differential space-use inside burrows during the day, and that low external ambient temperatures appear to constrain activity of *S. cyanus* outside their burrows during the night in summer and winter. In contrast, we hypothesize that high summer temperatures constrain above-ground activity at midday. © 2003 Elsevier Science Ltd. All rights reserved.

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1. Introduction

A subterranean mode of life has often been related with constant environments and reduced predation risk, at the expense of high energetic costs of burrowing

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(Nevo, 1979, 1999). Because daily activity of non-fossorial species is related with, and sometimes restricted by, external factors such as photoperiod, temperature and humidity, and it is also linked with foraging periods, Nevo et al. (1982) postulated that random activity patterns and the absence of circadian rhythms should be a generalized trait among small subterranean mammals. Although some studies support this hypothesis (*Heliophobius argenteocinereus*, Jarvis, 1973; *Cryptomys hottentotus*, Hickman, 1980), other studies have reported well-defined patterns of activity in subterranean species (*Tachyoryctes splendens*, Jarvis, 1973; *Thomomys bottae*, Reiter et al., 1994; *Georychus capensis*, Lovegrove and Muir, 1996; *Heterocephalus glaber*, Buffenstein, 2000, pp. 62–110). Daily activity arrhythmicity is not, therefore, necessarily consistent with a subterranean mode of life.

Ambiguous results regarding activity patterns and fossoriality have been obtained even within a species, as subspecies of *Nannospalax ehrenbergi* have been reported to either show daily rhythms (Rado et al., 1991, pp. 581–589) or being absolutely arrhythmic (Ben Shlomo et al., 1995). Moreover, in some cases rhythmicity was described as a general condition for a whole colony (e.g. *C. damarensis*, Lovegrove et al., 1993), whereas in others it was an attribute of only some individuals within a colony (*Ctenomys talarum*, Luna et al., 2000). These studies were, however, performed in the laboratory, where endogenous circadian rhythmicity appears to explain the activity patterns observed. In the field, Benedix (1994) reported defined patterns of activity in free-ranging pocket gophers *Geomys bursarius* through telemetry observations, in both spatial and temporal scales. Because the genus *Geomys* was previously described as non-rhythmic based on laboratory observations (*G. bursarius*, Vaughan and Hansen, 1961; *G. pinetis*, Ross, 1980), Benedix (1994) postulated that patterns of activity of *G. bursarius* were environmentally induced.

Activity patterns often reflect endogenous rhythmicity, coupled with environmental cues and/or constraints. However, few studies have attempted to discriminate these two effects, because circadian rhythms observed in the laboratory may not reflect activity patterns in field. This issue has been raised for the coruro (*Spalacopus cyanus*), an octodontid rodent inhabiting semi-arid environments of central Chile. *S. cyanus* is a highly social species that live in extensive galleries underground, forming groups up to 26 individuals (Begall et al., 1999). Although above-ground activity of coruros is relatively scarce and apparently not associated with foraging behavior (Torres-Mura and Contreras, 1998), there is evidence suggesting that *S. cyanus* do forage above-ground in some cases (Begall and Gallardo, 2000). However, large amounts of bulbs hoarded in food chambers within their galleries, as well as qualitative observations of their activity pattern above-ground, suggest that foraging occurs primarily underground (Begall and Gallardo, 2000).

In this context, the study of activity patterns of the coruro is particularly appealing for several different factors: *S. cyanus* is a highly adapted burrowing rodent closely related with other surface-dwelling octodontids (Gallardo and Kirsch, 2001), within each some species are diurnal (*Octodon degus*, Kenagy et al., 2002; Bacigalupe et al., 2003) and others mostly nocturnal (*O. bridgesi*, Verzi and Alcover, 1990; *O. lunatus*, Muñoz-Pedreros and Yánez, 2000). Thus, coruros are a potentially good model to assess the effects of a subterranean mode of life on daily rhythmicity as well as in activity patterns, being reinforced by the fact that above-ground activity in this species is extremely rare. In addition, literature regarding daily rhythmicity in *S. cyanus* is controversial as well. Coruros have been classified as diurnal, based on field observations. Laboratory measurements, in contrast, suggest that this species lacks circadian rhythmicity in oxygen consumption (Contreras, 1986, pp. 231–250), although it does show nocturnal locomotor activity (Begall et al., 2002).

We hypothesize that environmental factors, particularly ambient temperature, may account for these contradictory results. If temperature indeed affects aboveground activity of *S. cyanus*, animals should change their behavior seasonally, especially because temperatures in central Chile show large variations in both daily and seasonal scales. On the other hand, random activity would be expected if temperature is not affecting locomotor activity. Consequently, the primary goal of this study is to analyze daily activity patterns of *S. cyanus*, using both field and laboratory approaches, and their relationship with environmental variables that could be affecting such patterns.

2. Materials and methods

2.1. Field observations

Field observations took place at the locality of Juan Soldado ($29^{\circ}50'S$; $72^{\circ}46'W$), 10 km from La Serena. Observations were carried out for five consecutive days during summer (February) and winter (August), respectively, from 0800 to 1800 h. To determine above-ground daily activity of *S. cyanus*, three observation sites were disposed at approximately 30 m from the active colonies. Surface activity was quantified considering observations of: (i) soil deposition and/or (ii) direct observation of individuals outside their burrows, although coruros were not individually marked. Each sighting was considered an event of activity. Underground activity was determined in the laboratory (see below), but not in the field. Concomitant with activity observations, environmental temperatures were recorded hourly in an adjacent active colony, using a Yellow Spring Instrument telethermometer (model 44TC) shielded from solar radiation. To determine the potential ambient temperatures that animals may face, records were carried out: (i) 60 cm above-ground (T_a), (ii) on the surface (T_s), and (iii) between 1 and 1.5 m under the ground (T_g).

2.2. Laboratory trials

Four adult males and one female (mb= 88.5 ± 18.3 g) were caught with padded leg-hold traps at Ventanas (34°45′S; 71°29′W) during September–October 1999. A juvenile individual was also captured, though it was immediately released. This locality, at approximately 20 m a.s.l., is characterized mainly by sandy dunes, similar to Juan Soldado. Animals were transferred to the laboratory within 2 days of capture and were housed individually in acrylic cages ($60 \times 30 \times 70$ cm³) filled with

about 30 cm of humid dirt, and were fed carrots, apples and tomatoes *ad lib*. Temperature and photoperiod were held at $30.0 \pm 2.0^{\circ}$ C and 12L:12D, respectively.

Animals were acclimated to laboratory conditions 1 month before experiments began. To determine locomotor activity of *S. Cyanus* we used the methodology described in Antinuchi et al. (1999), consisting of a system of galleries built with PVC tubes with several micro switches implanted into the base of the tubes and connected to a computer. Depressing these switches closed an electrical circuit, and the time and location of the incident was automatically recorded. Two separate galleries with a similar design to the one in Antinuchi et al. (1999) were built, allowing simultaneous records of two individuals in each trial. We provided nest material at one side of each gallery, while apples and carrots were placed at the opposite side. The nest side had two switches that were activated whenever individual entered, while the food side had only one. Two parallel corridors, each one with one micro switch, connected both rooms. Therefore, animals had to pass over at least four micro switches on their way from the nest to the food supply.

Photoperiod was maintained with 12L:12D, and food was always provided *ad lib*. Galleries had holes of approximately 1 mm^2 at each 20 cm, allowing air circulation and the detection of external photoperiod. Animals were placed in the experimental system 1 day before the experiments, allowing them to get used with the experimental conditions. Measurements lasted 24 h. Two individuals randomly chosen were measured simultaneously in the parallel corridor circuits each time, and these were weighed before and after each measurement. Each individual was tested twice, at 15°C and at 30°C. Temperature at each trial was randomly assigned, and measurements were separated by at least 2 weeks. These values of temperature are in accordance with temperature values described in the field by Begall and Gallardo (2000), that reported temperatures inside burrows between 14.2°C and 31.2°C.

2.3. Data analysis and statistics

Because animals could activate a single switch several times within a short period, data were filtered with a software designed ad hoc. Basically, filtration of data was performed in the following manner: repeated pulses from a single switch were not considered, unless there was 1-min difference between two pulses, or another switch was activated during this period. Therefore, activity was mainly recorded as animals displaced from one switch to another, or if they activated the same switch repeatedly over a relatively long time lag.

Statistical analyses were performed using Statistica (1997). Two factors were considered in the comparisons: photoperiod and ambient temperature. To determine the presence of circadian rhythm, as well as differences between diurnal and nocturnal activity within treatments, we employed a Wilcoxon matched-pairs test. Activity was considered as the total number of times that an individual activated the switches within each period (12 h), and daily and nocturnal activity per individual were compared. Daily activity and its relationship with ambient temperature were analysed with a Wilcoxon matched-pairs test, comparing values obtained per individual at the same hour under different temperatures. Comparisons were made

with total daily activity, and diurnal and nocturnal activity, separately. All results are shown as mean \pm S.E.

3. Results

3.1. Field observations

There were seasonal differences in above-ground activity of *S. cyanus*. During summer coruros showed a bimodal activity pattern, with a conspicuous peak from 0800 to 1100 h, and a smaller one from 1600 to 1800 h (Fig. 1a). The low activity



Fig. 1. Surface activity and environmental temperatures 0.6 m above-ground (T_a) , at the surface (T_s) , and 1.5 m under ground (T_g) , at different times of the day during summer and winter. Periods of darkness are represented with black zones, periods of light with white zones. The dashed line represents the lower limit of the thermoneutral zone of *S. cyanus*, according to Contreras (1986). Data are shown as mean \pm S.E.

values observed between 1100 and 1600 h were coincident with the maximum values of T_a , T_s and T_g . Surface temperature (T_s) was particularly high, surpassing 32°C during this period, while the maximum value attained inside the burrows, T_g , was 20.4°C (Fig. 1a).

On the other hand, winter activity did not show the bimodal pattern observed during summer, and a single activity peak from 1000 to 1600 h was detected (Fig. 1b). During this season T_a , T_s and T_g were remarkably similar, contrary to the pattern observed during summer, exceeding 20°C from 1100 to 1400 h, with a maximum value of temperature of 21.6°C at the surface.

3.2. Activity in the laboratory

In the laboratory we observed a defined daily rhythm of activity in *S. cyanus* similar for both temperatures of measurement (Fig. 2). Animals were significantly more active during the night, from 2000 to 0800 h, at both 15°C and 30°C (Z = 3.36, p < 0.001 and Z = 4.12, p < 0.001, respectively; Fig. 3).

Regarding the effects of ambient temperature on overall activity levels, we observed significant differences between measurements at 15°C and 30°C. Animals were more active when submitted to 15°C (Z = 2.66, p = 0.008; Fig. 4). These differences were also reflected in diurnal and nocturnal activity, when analysed separately (Z = 4.09, p < 0.001 and Z = 2.02, p = 0.044, respectively; Fig. 4).

4. Discussion

Our laboratory and field approaches showed contrasting results regarding activity patterns of *S. cyanus*. In the field these animals displayed diurnal above-ground activity. In fact, no animals were trapped at night in this study or in previous ones (Reig, 1970; Contreras, pers. comm.). Such a pattern suggests restricted nocturnal activity in *S. cyanus*. Nevertheless, in laboratory all individuals showed higher activity during dark periods. Thus, under semi-natural conditions nocturnal activity appears to be conspicuously higher, with activity patterns similar at both temperatures, but coruros do remain active to some degree during the day (Fig. 2). These results are in agreement with the latest report of activity patterns of *S. cyanus* under laboratory conditions (Begall et al., 2002).

Previous papers have shown differences in daily activity patterns of some fossorial species depending on the approach used to study them (e.g. Kenagy, 1976; Benedix, 1994). In addition to the diurnal/nocturnal controversy on the activity of *S. cyanus*, Contreras (1986) described non-rhythmicity on metabolic rates of *S. cyanus*, which seems to be characteristic of a fossorial mode of life (see Kenagy and Vleck, 1982). Contreras' laboratory approach and our own were, however, carried out under a controlled thermal environment, which does not necessarily reflect real conditions in the field. Nevertheless, such a pattern (or the absence of it) reinforces our prediction that changes in behavior, rather than in physiology, are likely to cope with environmental thermal variation and, therefore, thermoregulatory costs.



Fig. 2. Daily locomotor activity of *S. cyanus* in the laboratory, measured at 30° C and 15° C. Dark periods are represented by black zones, light periods by white zones. Data are shown as mean ±S.E. Overall activity changed significantly with both temperature and photoperiod (see text).

Our laboratory experiments showed that, when ambient temperature is controlled, animals display nocturnal locomotor activity in their artificial galleries. The generality of this pattern (see Fig. 3) suggests that this behavior is shared among all individuals of *S. cyanus*, and not a merely attribute of some animals within a population, as described for *C. talarum* (Luna *et al.*, 2000). Two factors, however, must be taken into account: (i) our sample might be reflecting males activity patterns, as only one female was measured in the laboratory, and (ii) we did not determine if such a nocturnal pattern inside their galleries would also reflect above-ground



Fig. 3. Diurnal activity plotted against nocturnal activity per individual at 15° C (closed circles) and 30° C (open circles). Dotted line (slope = 1) represents equal proportions of diurnal and nocturnal activity.



Fig. 4. Mean diurnal and nocturnal activity of S. cyanus at different temperatures. Data are shown as mean \pm S.E.

activity. It has been described that, under laboratory conditions, *S. cyanus* spent almost 90% of their time underground when able to burrow, and above-ground activity was always during periods of dark (Begall et al., 2002). However, food was provided only on the soil surface and temperature was maintained constant through the light–dark cycle ($T_a = 25^{\circ}$ C), possibly overestimating above-ground activity when compared with natural conditions. In the field, above-ground activity of *S. cyanus*

occurs diurnally, with marked differences between summer and winter (Fig. 1), and the bimodal pattern observed during summer is in agreement with preliminary data on underground activity through radiotelemetry (Lacey, Ebensperger and Wieczorek, unpublished data). Diurnal above-ground activity probably increases predation risk to coruros, which being black colored, are more conspicuous during day light (see Jaksic et al., 1981). Thus, factors other than predation are should be affecting *S. cyanus* activity rhythms in the field, and generating the apparently incongruent results previously described.

Seasonal changes in daily activity have also been reported in Ammospermophilus leucurus, a semi-fossorial sciurid species, as well as in O. degus, a closely related species of S. cyanus (Chappell and Bartholomew, 1981; Kenagy et al., 2002). This switch from a bimodal to an unimodal pattern has been related with environmental thermal constraints on activity patterns, and that was shown to be the case for both of the species previously mentioned (Chappell and Bartholomew, 1981; Bacigalupe et al., 2002). Our results strongly suggest that the differences observed between field and laboratory activity of coruros could be indeed the consequence of differential use of burrows depending on environmental temperature. In fact, previous studies on S. cyanus energetics have shown that this species is very sensitive to thermal stress. Thermal acclimated individuals exhibited low metabolic plasticity as well as low tolerance to lower temperatures (Nespolo et al., 2001). Also, S. cyanus is not able to maintain body temperature when ambient temperature surpasses 32°C (Contreras, 1986). In the field, low activity during the day at summer occurs when $T_{\rm s}$ attains its higher values ($T_{\rm s} < 32^{\circ}$ C, Fig. 1a), suggesting that this variable may be constraining above-ground activity. On the other hand, the activity peak observed in winter occurs simultaneously with the higher values of ambient temperature, even though these never exceed 22° C (being approximately 5°C below the lower limit of thermoneutral zone of S. cyanus; Contreras, 1986). Thus, above-ground activity of coruros during winter has additional energetic costs in order to maintain body temperature. Activity outside burrows appears to be, therefore, thermally constrained, and animals are active outside their galleries at times where ambient temperatures are less stressful.

As Nevo (1999) stated, the activity of subterranean herbivore and insectivore rodents appears to be linked with feeding periods. Literature regarding foraging behavior of *S. cyanus* suggests that this species usually feeds underground, and only rarely venturing outside their burrows (Torres-Mura and Contreras, 1998; but see Begall and Gallardo, 2000). Nocturnal activity in the laboratory is certainly linked with these foraging periods, and the greater locomotor activity observed at 15°C could be the result of animals facing higher thermoregulatory costs in this treatment (Fig. 4). As most of the activity of subterranean mammals takes place underground and involves maintaining and expanding their burrow system (Vleck, 1979, 1981; Nevo, 1985), we postulate that *S. cyanus* spend the night foraging (and therefore digging). On the other hand, surface deposition of soil accumulated during burrowing, characteristic of other subterranean species (see Benedix, 1994), may occur only when ambient temperatures allow for it. The maintenance of some locomotor activity in the laboratory during the day could be explained at least in

part due to this second behavior, extremely important in the field but not possible under our laboratory conditions.

Another factor that may affect activity within this species that was not taken into account in the laboratory, is sociality. Kenagy (1976) postulated that social isolation was one of the factors explaining differences between activity patterns of *Dipodomys* merriani in captivity and field. This could be the case for S. cyanus as well. Begall and colleagues showed that coruros tested in individual records showed mostly nocturnal activity, while this pattern was not so conspicuous in group records, where individuals were active also during the day (Begall et al., 2002). These authors also suggest a strong social interaction effect on rhythmicity of S. cyanus. Moreover, coruro colonies may have as many as 26 individuals, and territorial behavior has been described in this species (Torres-Mura, 1990; Torres-Mura and Contreras, 1998). In this context, because individuals within the observed colony were never marked, diurnal surface activity reported in this study could result from the observation of several distinct individuals active above-ground at different hours of the day. For instance, Benedix (1994) observed a bimodal pattern of activity in G. bursarius, though it was emphasized that the same individuals were never active throughout the entire periods. Sex differences in temporal and spatial activity may also be affecting our conclusion of a general activity pattern in S. cyanus. Although sex-related differential activity might be explaining why more males were captured in this study, our previous experience in another population suggests that that is not the case, as several females were captured (one individual being pregnant; Rezende and Bacigalupe, pers. obs.). Future works using telemetry or marking individuals may provide the solution for this question.

In summary, it is quite clear that field or laboratory studies per se may lead researchers to different conclusions; therefore, extrapolations should be carried out cautiously. In this context, *S. cyanus* provides another example of ambiguous results regarding daily activity patterns on subterranean species. So far, our results emphasize that, despite the maintenance of a relatively constant thermal environment inside burrows when compared with above-ground fluctuations, ambient temperature does affect activity patterns of subterranean species in both temporal and spatial scales. On the other hand, because activity patterns appear to be diverse among subterranean species, it is important to add more information regarding daily activity on other subterranean rodents.

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References

- Antinuchi, C.D., Luna, F., Busch, C., 1999. Automatic data recording of circadian rhythms. Journal of Biological Education 33, 220–222.
- Bacigalupe, L.D., Rezende, E.L., Kenagy, G.J., Bozinovic, F., 2002. Variability in activity and space use by *degus*: influences of shade cover and food availability. Journal of Mammalogy 84, in press.
- Begall, S., Gallardo, M.H., 2000. Spalacopus cyanus (Octodontidae, Rodentia): an extremist tunnel constructing and food storing among subterranean mammals. Journal of Zoology (London) 250, 53–60.
- Begall, S., Burda, H., Gallardo, M.H., 1999. Reproduction, postnatal development and growth of social coruros, *Spalacopus cyanus* (Octodontidae, Rodentia) from Chile. Journal of Mammalogy 80, 210–217.
- Begall, S., Daan, S., Burda, H., Overkamp, G.J.F., 2002. Activity patterns in a subterranean social rodent, Spalacopus cyanus (Octodontidae). Journal of Mammalogy 83, 153–158.
- Benedix, J.H., 1994. A predictable pattern of daily activity by the pocket gopher *Geomys bursarius*. Animal Behaviour 48, 501–509.
- Ben Shlomo, R., Ritte, U., Nevo, E., 1995. Activity pattern and rhythm in the subterranean mole rat superspecies Spalax ehrenbergi. Behavioral Genetics 25, 239–245.
- Buffenstein, R., 2000. Ecophysiological responses of subterranean rodents to underground habitats. In: Lacey, E.A., Patton, J.L., Cameron, G.N. (Eds.), Life Underground: The Biology of Subterranean Rodents. The University of Chicago Press, London, 449pp.
- Chappell, M.A., Bartholomew, G.A., 1981. Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus*, in winter and summer. Physiological Zoology 54, 215–223.
- Contreras, L.C., 1986. Bioenergetics and distribution of fossorial *Spalacopus cyanus* (Rodentia): thermal stress, or cost of burrowing? Physiological Zoology 59, 20–28.
- Gallardo, M.H., Kirsch, J.W.A., 2001. Molecular relationships among Octodontiadae (Mammalia: Rodentia: Caviomorpha). Journal of Mammalian Evolution 8, 73–89.
- Hickman, C.G., 1980. Locomotory activity of captive *Cryptomys hottentotus* (Mammalia: Bathytergidae), a fossorial rodent. Journal of Zoology (London) 192, 225–235.
- Jaksic, F.M., Greene, H.G., Yañez, J.L., 1981. The guild structure of a community of predatory vertebrates in central Chile. Oecologia 49, 21–28.
- Jarvis, J.U.M., 1973. Activity patterns in the mole-rats *Tachyoryctes splendens* and *Heliophbius* argenteocinereus. Zoologica Africana 8, 101–119.
- Kenagy, G.J., 1976. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia 24, 105–140.
- Kenagy, G.J., Vleck, D., 1982. Daily temporal organization of metabolism in small mammals: adaptation and diversity. In: Aschoff, J., Daan, S., Groos, G. (Eds.), Vertebrate Circadian Rhythms. Springer, Berlin, pp. 322–338.
- Kenagy, G.J., Vásquez, R.A., Nespolo, R.F., Bozinovic, F., 2002. A time-energy analysis of daytime surface activity in degus, *Octodon degus*. Revista Chilena de Historia Natural 75, 149–156.
- Lovegrove, B.G., Muir, A., 1996. Circadian body temperature rhythms of the solitary Cape mole rat, *Georychus capensis* (Bathyergidae). Physiology and Behavior 60, 991–998.
- Lovegrove, B.G., Heldmaier, G., Ruf, T., 1993. Circadian rhythms in colonies of "blind" molerats, *Cryptomys damarensis* (Bathyergidae). South African Journal of Zoology 28, 46–55.
- Luna, F., Antinuchi, C.D., Busch, C., 2000. Ritmos de actividad locomotora y uso de las cuevas en condiciones seminaturales en *Ctenomys talarum* (Rodentia, Octodontidae). Revista Chilena de Historia Natural 73, 39–46.
- Muñoz-Pedreros, A., Yánez, J.L., 2000. Mamíferos de Chile. Ediciones CEA, Valdivia, Chile.
- Nespolo, R.F., Bacigalupe, L.D., Rezende, E.L., Bozinovic, F., 2001. When non shivering thermogenesis equals maximum metabolic rate: thermal acclimation and phenotypic plasticity of fossorial *Spalacopus cyanus* (Rodentia). Physiological and Biochemical Zoology 74, 325–332.
- Nevo, E., 1979. Adaptive convergence and divergence of subterranean mammals. Annual Review of Ecology and Systematics 10, 269–308.
- Nevo, E., 1985. Mammalian evolution underground. The ecological-genetic-phenetic interfaces. Acta Theriologica 3, 9–31.

- Nevo, E., 1999. Mosaic Evolution of Subterranean Mammals: Regression, Progression and Global Convergence. Oxford University Press, New York, 512pp.
- Nevo, E., Guttman, R., Haber, M., Erez, E., 1982. Activity patterns of evolving mole rats. Journal of Mammalogy 63, 453–463.
- Rado, R., Gev, H., Goldman, B.D., Terkel, J., 1991. Light and circadian activity in the blind mole-rat. In: Ricklis, E. (Ed.), Photobiology. Plenum Press, New York, 1100pp.
- Reig, O.A., 1970. Ecological notes on the fossorial octodont rodent *Spalacopus cyanus* (Molina). Journal of Mammalogy 51, 592–601.
- Reiter, R.J., Reiter, M.N., Hattori, A., Yaga, K., Barlow, D.C., Walden, L., 1994. The pineal melatonin rhythm and its regulation by light in a subterranean rodent, the valley pocket gopher (*Thomomys bottae*). Journal of Pineal Research 16, 145–153.
- Ross, J.P., 1980. Seasonal variation on thermoregulation in the Florida pocket gopher, *Geomys pinetis*. Comparative and Biochemical Physiology A 66, 119–125.
- Statistica, 1997. Statistical Release 5 (Quick Reference) for the Windows 95 Operating System, 3rd Edition. Statsoft, Inc. Tulsa, OK.
- Torres-Mura, J.C., 1990. Uso del espacio en el roedor fosorial *Spalacopus cyanus* (Octodontidae). M.S. Thesis, Universidad de Chile, Santiago, Chile.
- Torres-Mura, J.C., Contreras, L.C., 1998. Spalacopus cyanus. Mammalian Species 594, 1-5.
- Vaughan, T.A., Hansen, R.M., 1961. Activity rhythm of the plains pocket gopher. Journal of Mammalogy 42, 541–543.
- Verzi, D.H., Alcover, A., 1990. Octodon bridgesi Waterhouse, 1844 (Rodentia, Octodontidae) in the Argentinian living mammalian fauna. Mammalia 54, 61–67.
- Vleck, D., 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52, 122–136.
- Vleck, D., 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. Oecologia 49, 391–396.