

## Dustbathing and intra-sexual communication of social degus, *Octodon degus* (Rodentia: Octodontidae)

### Baños de tierra y comunicación intra-sexual en el degu social, *Octodon degus* (Rodentia: Octodontidae)

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#### ABSTRACT

I observed the behavior of captive male and female *Octodon degus* to assess if dustbathing behavior plays a role in social communication among unfamiliar, same-sex conspecifics. Degus of a first group (control responders) were individually exposed during 10-min tests to an arena containing loose, clean soil. I compared the latency to first dustbathing as well as the overall frequency of dustbathing events recorded to control responders with the corresponding figures recorded to a second group of degus (experimental responders) after they were individually introduced into the same arena but with soil previously used for dustbathing by a same-sex conspecific (depositor). I also compared the location of dustbathing events by experimental responders with that of depositor individuals. Although male degus tended to exhibit shorter latencies to first dustbathing event when in clean soil, this variable was not significantly influenced by sex of responders or the type of soil (clean or used). In contrast, a significant interaction between both factors revealed that males dustbathe at a higher rate than females when on clean soil, but similarly so when in a substratum previously dustbathed by a same-sex conspecific. The place chosen by both male and female responders to conduct their dustbathing behavior was unrelated to the presence of previous marks left by a depositor degu. I conclude that dustbathing is involved in communication during male-male, but not during female-female, interactions in the degu. I suggest that such male-male interactions represent competition for mates.

**Key words:** sandbathing, scent communication, rodents.

#### RESUMEN

Observé el comportamiento de machos y hembras en cautiverio del roedor social *Octodon degus* para evaluar si la conducta de bañarse en tierra es parte de un mecanismo de comunicación social entre conespecíficos del mismo sexo, desconocidos entre sí. Un primer grupo de degus (respondientes controles) fueron introducidos individualmente durante ensayos de 10 min a un terrario con tierra suelta y limpia (no usada previamente por otros degus). Comparé el tiempo transcurrido desde el inicio de cada experimento hasta la observación del primer baño de tierra (latencia) así como el número total de baños de tierra realizados por cada respondiente control, con los valores equivalentes obtenidos de un segundo grupo de degus (respondientes experimentales), observados en la misma arena pero con tierra usada previamente por un conespecífico del mismo sexo (depositante). También comparé la ubicación espacial de los baños de tierra efectuados por respondientes experimentales con la posición de los baños de tierra realizados previamente por degus depositantes. Aunque los respondientes macho tendieron a mostrar una latencia más corta, esta variable no fue afectada significativamente ni por el sexo de los respondientes ni por el tipo de sustrato (limpio o usado). En cambio, una interacción significativa entre ambos factores mostró que los respondientes macho efectuaron un mayor número de baños de tierra que las hembras cuando ambos fueron expuestos a un sustrato limpio, pero que tales diferencias desaparecen cuando los individuos son expuestos a un sustrato usado previamente por otro individuo del mismo sexo. Los sitios de la arena seleccionados por respondientes macho y hembra para efectuar sus baños de tierra no estuvieron relacionados con la presencia de marcas dejadas por degus depositantes. Concluyo que los baños de tierra son usados por el degu como un mecanismo de comunicación olfativa durante interacciones entre machos, pero no entre hembras. Sugiero que tales interacciones entre machos representan competencia por apareamientos.

**Palabras clave:** revolcamiento, comunicación olfativa, roedores.

## INTRODUCTION

Communication occurs when signals given by one animal influence the behavior of another (Krebs & Davies 1993, Johnstone 1997). Nature of signals range widely, including visual (e.g., brightly colored body parts), auditory (e.g., calls, drumming), olfactory (e.g., pheromones), and tactile (e.g., grooming) signals (Feldhamer et al. 1999). Such signals may serve to attract a mate, to deter a competitor, or to warn conspecifics of an approaching predator (Krebs & Davies 1993, Johnstone 1997).

Most mammals produce chemical odors to signal sex, breeding status, rank of dominance, or territory ownership, and behaviors associated to deposition of these chemical signals often are highly specialized (Vaughan 1986, Feldhamer et al. 1999). Dustbathing (or sandbathing) could be one such specialized behavior. During dustbathing small mammals typically dig briefly into the ground with its fore claws and rubs its sides and ventrum in the dust (Eisenberg 1963, Eisenberg & Kleiman 1972, Randall 1993). Among rodents, dustbathing has been documented in several species of kangaroo rats (*Heteromyidae*), jerboas (*Dipodidae*), gerbils (*Muridae*), and squirrels (*Sciuridae*) (Steiner 1974, Wistrand 1974, Daly & Daly 1975, Betts 1976, Owings et al. 1977, Randall 1994).

An effect of dustbathing is to regulate the level of oil secretions in the pelage (Borchelt et al. 1976, Griswold et al. 1977, Randall 1981a). However, dustbathing also seems involved in social communication (Eisenberg 1963, 1981). Indeed, rodents seem to exchange information through chemical signals at these dustbathing loci to communicate species, sex and individual identity (Laine & Griswold 1976, Ågren et al. 1989, Randall 1981b, 1987, 1991). The source of the odor signals seems to be sebaceous glands associated with the hair or specialized scent glands (Eisenberg 1963, Randall 1987, 1993, 1994).

Despite not having been considered by recent reviews on the topic of social communication in rodents (e.g., Randall 1993, 1994), dustbathing has been reported in several families of New World hystricognaths, including *Abrocomidae* (chinchilla rats, Mann 1978), *Caviidae* (cavies and cuis, Rood 1970, 1972, Wilson & Kleiman 1974, Lacher 1981), *Chinchillidae* (*vizcachas*, Branch 1993), *Hydrochaeridae* (capybaras, Macdonald 1981), and *Octodontidae* (*vizcacha* rats and degus, Kleiman 1974, Wilson & Kleiman 1974). Among the octodontids, common degus, *Octodon degus* (Molina, 1782), do dustbathe. Although the function of dustbathing behavior in these rodents has not been examined, some fea-

tures of biology and ecology of degus suggest this behavior may play a role in social communication. First, common degus are diurnal, group-living rodents of semi-arid scrub areas of central Chile (Woods & Boraker 1975, Redford & Eisenberg 1992), and groups are suspected to defend a communal territory (Fulk 1976). Secondly, captive degus dustbathe at sites that are frequently urine marked (Wilson & Kleiman 1974). Thirdly, scent marking with urine, i.e., the use chemical signals, by degus is influenced by the presence of scent marks of same-sex conspecifics (Kleiman 1975). Finally, agonistic encounters among free-ranging animals may include dustbathing by one or both contenders (Fulk 1976, L.A. Ebensperger pers. obser., although see Davis 1975). The present study addresses the hypothesis that dustbathing is used by degus to deposit olfactory signals in a context of social communication (mainly competitive) among unfamiliar same-sex conspecifics. Degus are an interesting model to examine the above hypothesis, because most evidence linking dustbathing to social communication in rodents comes from solitary-living species, particularly heteromyids.

To accomplish the above objective, I observed the dustbathing behavior of male and female degus under laboratory conditions in response to dustbathing marks left recently by an unfamiliar, same-sex conspecific. If individual degus use dustbathing during competitive interactions with same-sex conspecifics, I predicted that degus would be inhibited from dustbathing when in an unfamiliar area containing marks of same-sex conspecifics.

## METHODS

*Animal subjects*

Experimental ("responder") subjects were laboratory reared degus born to pregnant females caught during 1998 at Lampa (33°17'S; 70°53'S), 30 km northwest of Santiago. Upon weaning, degus were kept in same sex-litter groups of 2-3 individuals inside 45 by 23 by 21 cm clear polycarbonate rat cages with a bedding of hardwood chips. Food (commercial rabbit pellet) and water were provided ad libitum. Animals were kept in a ventilated room in which ambient temperature was maintained at 21 ± 1°C (mean ± SD), and photoperiod was controlled at 12L:12D (with lights on at 07:00 h). Age differences among experimental degus were no greater than 7 d. Animals were 28 weeks old (i.e., fully adult) when observations began.

Adult degus to be used as “depositors” (3 male and 3 female) were live-trapped at Fundo Rinconada de Maipú, (33°29’S; 70°54’W), 30 km west of Santiago. They all were adult sized when caught. Depositors were caged individually and maintained under the same laboratory conditions described above, but in a room different from that housing the experimental degus. The origin and housing conditions during captivity of depositors ensured they were totally unfamiliar to responder degus. Kinship among depositor degus was unknown. Depositors were kept a minimum of three weeks in captivity before being used in the experiments.

#### *Design of experiments*

I used a rectangular shaped arena made of aluminum panels, with a base of 1.9 by 1.6 m, and a height of 1.5 m. The arena was placed into a climatically controlled room and illuminated with four 100 W “daylight” bulbs. Before each experiment, the bottom of the arena was covered with a homogeneous 10-20 mm layer of loose dirt. I obtained dirt from the field by digging and sieving (to eliminate rocks and stones larger than 10 mm diameter) the first 50 to 150 mm deepness. My soil collecting site was located at Rinconada on a place 30-50 m away from a degu “town” (i.e. where multiple degus and their burrows were commonly seen). Despite of the above, collected soil was neither part of a burrow system nor used by degus during their regular above ground activity. Once collected, soil was sprayed over a clean surface and allowed to sun dry indoors. After 2 to 3 days, dirt was stored into perforated plastic bags and kept in the laboratory at room temperature. Temperature of experimental room were set at  $20 \pm 1$  °C.

Responder degus were assigned to one of two groups such that sex and kinship was balanced. Degus on a first group (control responders) were observed while inside the arena when it contained “clean”, not to have been in contact with other degus, soil. A second group of degus (experimental responders) were observed inside the arena when it contained soil that has been dustbathed (“used”) by a same-sex depositor degu. Although body mass of male ( $229.1 \pm 23.2$  g) and female ( $205.7 \pm 15.4$  g) responders differed (two-way ANOVA:  $F_{(1,15)} = 5.75$ ,  $P = 0.03$ ), mass of male and female individuals assigned to a clean substratum ( $219.0 \pm 21.7$  g) did not differ from that of male and female individuals assigned to an used substratum ( $219.5 \pm 25.5$  g; two-way ANOVA:  $F_{(1,15)} = 0.06$ ,  $P = 0.81$ ).

I started testing control responders by placing a single degu into the arena containing clean soil. After degus began to explore the arena, animals were left undisturbed during 10 min when the experiment was terminated. I chose this time for two reasons. First, a relatively short time of exposure may better simulate natural conditions in which an animal finds a dustbathing site but it is not confined to remain close to it. Secondly, selected experimental time will make my results comparable with previous studies.

To test experimental responders, I first introduced a depositor degu into the arena containing clean soil. Upon 2 h, the depositor degu was removed and a responder degu was introduced immediately into the arena and left undisturbed for 10 min.

Upon completing each experiment, animals were returned to their original cage, and soil was discarded. Each tested degu was weighted 10 min before testing. Experiments were carried out between 09:30 and 13:00 hours, from late April through early July 1999. While all responding degus were used only once, depositors were used 1-2 times each, at a frequency of once every two weeks.

Behavior of all animals was videotaped with a Sony video camera recorder (model CCD-TR413PK), mounted on a tripod at a height of 2.5 m above floor level, and connected to a TV monitor in close circuit. To obtain a complete view of the arena interior, I fitted the camera with a Dietz semi-fisheye lens. I then used the videotapes to record the number and location of dustbathing events throughout the observation period. I also noted the time (latency) to first dustbathing rub. To assess the influence of location of dustbathing events by depositors on the location of dustbathing by responder degus, I mapped the location of dustbathing events on a paper grid representing the whole arena. Thus the arena was divided into 12, (3 by 4) similarly sized (0.48 by 0.53 m) quadrants such that two of them included the central area while the remaining eight quadrants included the periphery (sides and corners). I used this grid to record the number of dustbathing events by responders directed at none-to-moderately marked, and at highly marked arena quadrants. I used the mean number of dustbathing marks left by male (5 events per quadrant) and female (3 events per quadrant) depositors to differentiate these mutually exclusive categories.

#### *Statistical analysis*

I carried out statistical analysis with Statistica 5.1 for Windows (StatSoft Inc., Tulsa, Oklahoma),

and with StatView 4.5 for Windows (Abacus Concepts, Inc., Berkeley, California). Data are presented as mean  $\pm$  SD.

## RESULTS

### *General features of dustbathing behavior of degus*

Eleven male and 8 female degus served as responder subjects. Of these, all but one male degu were recorded to dustbathe into the arena. Dustbathing typically involved a degu rubbing its left and/or right sides against the substratum. Left and right sides were rubbed in an alternated fashion, or one side first. Besides side rubbing, two depositor and two responder male, and two depositor female degus were noted to occasionally rub their ventral pelage. Three of 11 male and 4 of 8 female responder degus were observed to scratch the soil immediately before rubbing their body against the substratum. Soil scratching was unrelated either to sex of responders (Fisher's exact test:  $P = 0.631$ ) or to the type (clean or used) of soil (Fisher's exact test:  $P > 0.999$ ). When ex-

posed to clean soil, both male (Goodness of fit chi-square test:  $\chi^2 = 235.4$ ,  $P < 0.0001$ ) and female ( $\chi^2 = 34.7$ ,  $P < 0.0001$ ) degus dustbathed more often than expected at corner but less frequent than expected at side-border and central quadrants of the arena. Such preferences also were evident among male ( $\chi^2 = 63.6$ ,  $P < 0.0001$ ) and female ( $\chi^2 = 43.7$ ,  $P < 0.0001$ ) degus exposed to used soil.

### *The influence of sex and conspecifics on dustbathing behavior*

A two-way analysis of variance revealed that sex of depositors and the type of soil significantly interacted to influence the dustbathing behavior of responders (interaction- $F_{(1,15)} = 4.82$ ,  $P = 0.044$ ). Thus, males dustbathed more than female degus when exposed to a clean, but dustbathed similarly when exposed to a substratum used previously by an unfamiliar same sex conspecific (Fig. 1). Although males tended to exhibit shorter latencies to first dustbathing event when in clean substratum (Fig. 2), neither sex of responders (sex- $F_{(1,14)}$

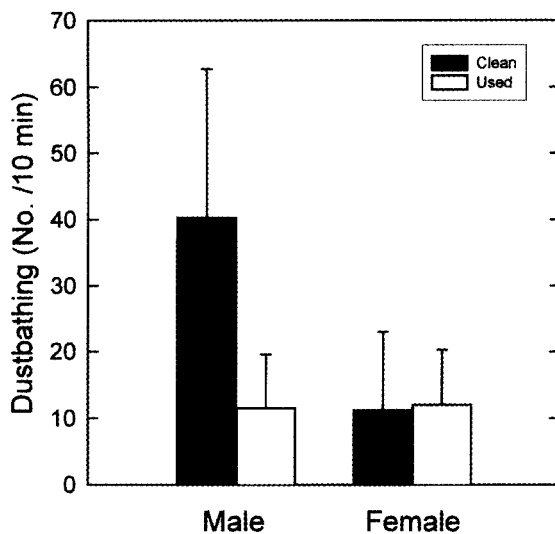


Fig. 1. Number of dustbathing events by individual male and female *Octodon degus* during 10-min trials when exposed to an arena with "clean" soil or to an arena with soil previously "used" (dustbathed) by a same-sex conspecific. Bars are mean  $\pm$  SD.

Número de eventos de baños de tierra por parte de individuos macho y hembra de *Octodon degus* durante experimentos de 10 min en una arena con tierra limpia ("clean"), o usada ("used") previamente por un conspecifico del mismo sexo para efectuar baños de tierra. Las barras indican valores promedio  $\pm$  DE.

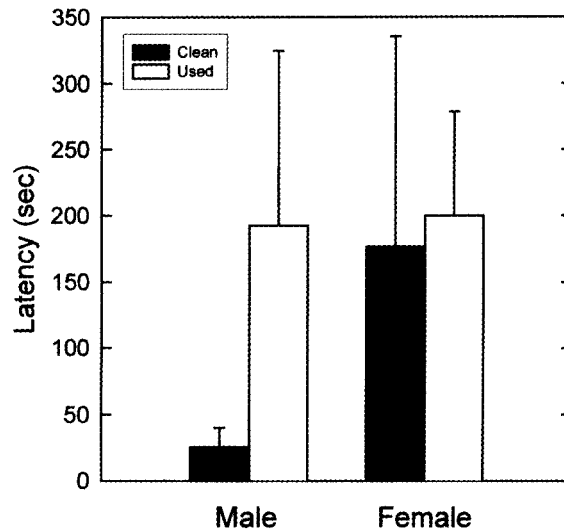


Fig. 2. Time (sec) to first dustbathing event recorded during 10-min trials to individual male and female *Octodon degus* when exposed to an arena with "clean" soil or to an arena with soil previously "used" (dustbathed) by a same-sex conspecific. Bars are mean  $\pm$  SD.

Tiempo (seg) transcurrido hasta el primer baño de tierra por parte de individuos macho y hembra de *Octodon degus* durante experimentos de 10 min en una arena con tierra limpia ("clean"), o usada previamente ("used") por un conspecifico del mismo sexo para efectuar baños de tierra. Las barras indican valores promedio  $\pm$  DE.

= 3.27,  $P = 0.092$ ), dustbathing marks left by conspecifics (dirt- $F_{(1,14)} = 2.28$ ,  $P = 0.153$ ), nor their interaction (interaction- $F_{(1,14)} = 1.87$ ,  $P = 0.193$ ) significantly influenced this variable. I detected no significant correlation between latency to first dustbathing event and body mass (partial  $R = 0.19$ ,  $t_{(14)} = 0.74$ ,  $P = 0.471$ ), or between the total number of dustbathing events and body mass (partial  $R = 0.10$ ,  $t_{(15)} = 0.38$ ,  $P = 0.707$ ) of responder degus after controlling for sex and type of dirt.

Overall, location of previous marks left by same-sex depositors did not influence the dustbathing behavior of male and female responders significantly. Responder males tended to dustbathe more often at highly marked (six or more dustbathing marks left by depositors) as compared with not marked to moderately marked (0 to 5 dustbathing marks) arena quadrants (Student t-test for dependent samples:  $t_{(4)} = 1.95$ ,  $P = 0.123$ ; Table 1). In contrast, female responders tended to dustbathe more often at not to moderately marked than at highly marked quadrants (Student t-test for dependent samples:  $t_{(3)} = 1.37$ ,  $P = 0.265$ ; Table 1).

#### DISCUSSION

##### *Dustbathing behavior and social communication in degus*

Male degus dustbathed at a significantly higher rate than female degus when exposed to clean soil, suggesting that dustbathing in degus is a sexually dimorphic behavior. More interestingly, results showed that male dustbathing is related to intra-sexual communication. Dustbathing activity by male degus is inhibited by previous marks left by other, unfamiliar males when dustbathing, which suggests that dustbathing is used by male degus to convey information to other, unfamiliar males. Interestingly however, location selected by male degus during dustbathing seemed uninfluenced by dustbathing activity carried out previously by an unfamiliar male. In contrast, the observation that dustbathing marks left by unfamiliar, same-sex conspecifics had no influence on the frequency and location of dustbathing by female degus suggests that this behavior is unrelated to intra-sexual communication among unfamiliar females.

Field observations suggest that common degus live in social groups, including two to five females and one to two males, which share a feeding range and an underground system of burrows (Woods & Boraker 1975, Fulk 1976, Yáñez 1976, Mann 1978). Most mating activity of degus takes

place during late fall to early winter, and dustbathing may in part be used by males to signal their presence to unfamiliar (competitor) males. In fact, the willingness of a male to tolerate the presence of another male decreases during breeding season (Solís & Rosenmann 1990).

The dustbathing response of male degus to previous dustbathing marks left by another male partially paralleled their urine-marking behavior suggesting that both behaviors may be coupled and play a similar role during intra-sexual interactions. Thus although male degus are attracted to spots with urine from same-sex conspecifics, they urine-mark less (Kleiman 1975, Fischer & Meunier 1985). In contrast, such coupling seems unlikely in the case of female degus, as they are simultaneously attracted and urine-mark more at spots with urine of other females (Kleiman 1975, Fischer & Meunier 1985).

Compared to other rodents such as gerbils (Daly & Daly 1975), kangaroo rats (Eisenberg 1963, Borchelt et al. 1976, Randall 1981b), ground squirrels (Steiner 1974, Betts 1976, Owings et al. 1977), and the more closely related cavies (Lacher

TABLE 1

Number of dustbathing events recorded to individual male and female *Octodon degus* during 10-min trials when exposed to an arena with soil previously used (dustbathed) by a same-sex conspecific. The number of dustbathing events directed at previously used quadrants with none to a few dustbathing marks (0-3 events for females; 0-5 events for males), and at quadrants with a high number of dustbathing (4 or more events for females; 6 or more events for males) marks are shown. Values are mean  $\pm$  SD

Número de eventos de baños de tierra por parte de individuos macho y hembra de *Octodon degus* durante experimentos de 10 min en una arena con tierra usada previamente por un conespecífico del mismo sexo para efectuar baños de tierra. Los datos corresponden al número de baños de tierra efectuados en cuadrantes sin o con pocos baños de tierra (0-3 para hembras; 0-5 para machos), y aquellos efectuados en cuadrantes con muchos baños de tierra (4 o más para hembras; 6 o más para machos). Los valores son promedios  $\pm$  DE

Quadrant	Females	Males
None-to-moderate dustbathed	8.8 $\pm$ 8.1 (n = 4)	3.4 $\pm$ 3.4 (n = 5)
Highly dustbathed	3.5 $\pm$ 1.7 (n = 4)	10.2 $\pm$ 8.1 (n = 5)

1981), degus only rarely rub their ventral pelage during dustbathing, which might be related to differences in the distribution of specialized skin glands.

*Dustbathing and social communication in rodents*

Evidence generally supports the hypothesis that dustbathing behavior is related to a context of intra- and inter-sexual communication in rodents. This seems to be the case of both male and female Merriam's kangaroo rats (*Dipodomys merriami*), bannertail kangaroo rats (*D. spectabilis*; Laine & Griswold 1976, although see Randall 1987), California ground squirrels (*Spermophilus beecheyi*; Owings et al. 1977), and male cavies (*Galea spixii*; Lacher 1981). Only the behavior of Great Basin kangaroo rats (*D. microps*) tend not to support a role for dustbathing in social communication as these rats are not particularly attracted to sites previously used by same-sex conspecifics (Randall 1981b).

My results add to previous observations on social gerbils (Ågren et al. 1989) in that the influence of dustbathing behavior to social communication in rodents is not restricted to solitary-living species such as most heteromyids (Jones 1993). Besides common degus, dustbathing also has been linked to social communication of other group-living hystricognaths, including the yellow-toothed cavies, *Galea spixii* (Lacher 1981) and *Galea musteloides* (Rood 1972), plains vizcachas (*Lagostomus maximus*, Branch 1993), and dwarf maras *Dolichotis salinicola* (Wilson & Kleiman 1974).

Lastly, dustbathing does not seem to be part of the behavioral repertoire of all rodents. Dustbathing is less developed in some tropical heteromyids (Eisenberg 1963), rare in wild cavies, *Cavia aperea* (Rood 1972), and absent in the rock cavy, *Kerodon rupestris* (Lacher 1981). Although habitat differences might explain some inter-specific variation in the use of dustbathing (Eisenberg & Kleiman 1972, Randall 1993, 1994), future comparative studies need to consider other potentially influencing variables, e.g., spacing, extent of sociality. In fact, such studies also might be used to examine other non-social functions of dustbathing behavior that have been hypothesized such as maintenance of pelage.

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LITERATURE CITED

- ÅGREN G, Q ZHOU & W ZHONG (1989) Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Animal Behaviour* 37: 11-27.
- BETTS BJ (1976) Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. *Animal Behaviour* 24: 652-680.
- BORCHELT PL, JG GRISWOLD & RS BRANCHEK (1976) An analysis of sandbathing and grooming in the kangaroo rat (*Dipodomys merriami*). *Animal Behaviour* 24: 347-353.
- BRANCH LC (1993) Social organization and mating system of the plains viscacha (*Lagostomus maximus*). *Journal of Zoology*, London 229: 473-491.
- DALY M & S DALY (1975) Socio-ecology of Saharan gerbils, especially *Meriones libycus*. *Mammalia* 39: 289-311.
- DAVIS TM (1975) Effects of familiarity on agonistic encounter behavior in male degus (*Octodon degus*). *Behavioral Biology* 14: 511-517.
- DEVENPORT JA (1989) Social influences on foraging in black-tailed prairie dogs. *Journal of Mammalogy* 70: 166-168.
- EISENBERG JF (1963) A comparative study of sandbathing behavior in heteromyid rodents. *Behaviour* 22: 16-23.
- EISENBERG JF (1981) The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. The University of Chicago Press, Chicago, Illinois. 610 pp.
- EISENBERG JF & DG KLEIMAN (1972) Olfactory communication in mammals. *Annual Review of Ecology and Systematics* 3: 1-32.

- FELDHAMER GA, LC DRICKAMER, SH VESSEY & JF MERRITT (1999) Mammalogy: adaptation, diversity, and ecology. McGraw-Hill, Boston, Massachusetts. 563 pp.
- FISCHER RB & GF MEUNIER (1985) Responses to conspecific's urine by the degu (*Octodon degus*). *Physiology & Behavior* 34: 999-1001.
- FULK GW (1976) Notes on the activity, reproduction, and social behavior of *Octodon degus*. *Journal of Mammalogy* 57: 495-505.
- GRISWOLD JG, PL BORCHELT, RS BRANCHEK & JA BENSKO (1977) Condition of the pelage regulates sandbathing and grooming behaviour in the kangaroo rat (*Dipodomys merriami*). *Animal Behaviour* 25: 602-608.
- HOLMES WG (1984) Predation risk and foraging behavior of the hoary marmot in Alaska. *Behavioral Ecology and Sociobiology* 15: 293-301.
- JOHNSTONE RA (1997) The evolution of animal signals. In: Krebs JR & NB Davies (eds) *Behavioural ecology: an evolutionary approach*: 155-178. Fourth edition, Blackwell Science, Oxford, United Kingdom.
- JONES WT (1993) The social systems of heteromyid rodents. In: Genoways HH & JH Brown (eds) *Biology of the Heteromyidae*: 575-595. The American Society of Mammalogists, Special Publication No. 10.
- KILDAW SD (1995) The effect of group size manipulations on the foraging behavior of black-tailed prairie dogs. *Behavioral Ecology* 6: 353-358.
- KLEIMAN DG (1974) Patterns of behaviour in hystricomorph rodents. *Symposia of the Zoological Society of London* 34: 171-209.
- KLEIMAN DG (1975) The effects of exposure to conspecific urine on urine-marking in male and female degus (*Octodon degus*). *Behavioral Biology* 14: 519-526.
- KREBS JR & NB DAVIES (1993) An introduction to behavioural ecology. Third edition, Blackwell Scientific Publications, Cambridge, Massachusetts. 420 pp.
- LACHER TE (1981) The comparative social behavior of *Kerodon rupestris* and *Galea spixii* and the evolution of behavior in the Caviidae. *Bulletin of Carnegie Museum of Natural History* 17: 1-71.
- LAINE H & JG GRISWOLD (1976) Sandbathing in kangaroo rats (*Dipodomys spectabilis*). *Journal of Mammalogy* 57: 408-410.
- LLANOS AC & JA CRESPO (1952) Ecología de la vizcacha ("*Lagostomus maximus maximus*" Blainv.) en el nordeste de la Provincia de Entre Ríos. *Revista de Investigaciones Agrícolas (Argentina)* 6: 289-378.
- MACDONALD DW (1981) Dwindling resources and the social behaviour of capybaras, (*Hydrochoerus hydrochaeris*). *Journal of Zoology, London* 194: 371-391.
- MANN G (1978) Los pequeños mamíferos de Chile: marsupiales, quirópteros, edentados y roedores. *Gallana Zoológica (Chile)* 40: 1-342.
- OWINGS DH, M BORCHELT & R VIRGINIA (1977) The behaviour of California ground squirrels. *Animal Behaviour* 25: 221-230.
- RANDALL JA (1981a) Comparison of sandbathing and grooming in two species of kangaroo rat. *Animal Behaviour* 29: 1213-1219.
- RANDALL JA (1981b) Olfactory communication at sandbathing loci by sympatric species of kangaroo rats. *Journal of Mammalogy* 62: 12-19.
- RANDALL JA (1987) Sandbathing as a territorial scent-mark in the bannertail kangaroo rat, *Dipodomys spectabilis*. *Animal Behaviour* 35: 426-434.
- RANDALL JA (1991) Sandbathing to establish familiarity in the Merriam's kangaroo rat, *Dipodomys merriami*. *Animal Behaviour* 41: 267-275.
- RANDALL JA (1993) Behavioural adaptations of desert rodents (Heteromyidae). *Animal Behaviour* 45: 263-287.
- RANDALL JA (1994) Convergences and divergences in communication and social organisation of desert rodents. *Australian Journal of Zoology* 42: 405-433.
- REDFORD KH & JF EISENBERG (1992) Mammals of the neotropics: the southern cone. The University of Chicago Press, Chicago, Illinois. 430 pp.
- ROOD JP (1970) Ecology and social behavior of the desert cavy (*Microcavia australis*). *The American Midland Naturalist* 83: 415-454.
- ROOD JP (1972) Ecological and behavioural comparisons of three genera of Argentine caviés. *Animal Behaviour Monographs* 5: 1-83.
- SOLIS R & M ROSENMANN (1990) Seasonal changes in intermale interactions and metabolism of *Octodon degus*. In: Gutiérrez O (ed) *Comparative psychobiology of aggression*: 51-64. Professors World Peace Academy, Santiago, Chile.
- STEINER AL (1974) Body-rubbing, marking, and other scent-related behavior in some ground squirrels (Scuridae), a descriptive study. *Canadian Journal of Zoology* 52: 889-906.
- THORSON JM, RA MORGAN, JS BROWN & JE NORMAN (1998) Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behavioral Ecology* 9: 151-157.
- VAUGHAN TA (1986) Mammalogy. Third edition, Saunders College Publishing, Fort Worth, Texas. 576 pp.
- WILSON SC & DG KLEIMAN (1974) Eliciting play: a comparative study. *American Zoologist* 14: 341-370.
- WISTRAND H (1974) Individual, social, and seasonal behavior of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). *Journal of Mammalogy* 55: 329-347.
- WOODS CA & DK, BORAKER (1975) *Octodon degus*. The American Society of Mammalogists, Mammalian Species 67: 1-5.
- YAÑEZ JL (1976) Ecoetología de *Octodon degus*. Tesis de Licenciatura en Ciencias, Universidad de Chile, Santiago. 67 pp.