Sociality in rodents: the New World fossorial hystricognaths as study models

Sociabilidad en roedores: los histricoñatos fosoriales del Nuevo Mundo como modelos de estudio

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ABSTRACT

Some rodents are social in that multiple adult individuals spend most of their lives in close association with other conspecific individuals, usually sharing a feeding area and a burrow system. The evolution of such sociality has been related to the distribution of food resources, the cost of burrowing, and the risk of predation. In this article I review these factors in the context of fossorial and semifossorial rodents and show that most of this theory has been formulated considering either North American ground-dwelling sciurids or African mole-rats. I review the behavioral ecology of some selected species of New World hystricognaths and suggest that future studies of species within this group of rodents will broaden our perspective of sociality in mammals and possibly other animal groups. Such studies will provide the independent tests that current hypotheses explaining the evolution of sociality need. I identify critical predictions of hypotheses and suggest complementary approaches to test them.

Key words: group-living, fossorial rodents, food distribution, risk of predation, cost of digging.

RESUMEN

Algunos roedores son sociales en el sentido de que varios individuos adultos viven asociados estrechamente con otros individuos de la misma especie, usualmente compartiendo un área común para alimentación y un sistema de madrigueras. La evolución de esta sociabilidad ha sido atribuida a factores tales como la distribución de recursos alimentarios, el costo de cavar, y el riesgo de depredación. En este artículo, reviso estos factores para el caso de roedores cavadores y muestro que una mayor parte de la teoría asociada ha sido formulada tomando en cuenta casi exclusivamente a roedores siúridos de Norte América o ratas topo de Africa. Reviso lo que se sabe de la ecología conductual de algunas especies seleccionadas de histricoñatos del Nuevo Mundo y sugiero que estudios futuros que utilicen estas (u otras) especies ampliarán sustancialmente nuestra perspectiva acerca de la sociabilidad en mamíferos y posiblemente otros grupos animales. Dichos estudios proporcionarán las pruebas independientes que requien las teorías actuales que intentan explicar la evolución de la sociabilidad. Señalo algunas predicciones claves de hipótesis alternativas y sugiero aproximaciones complementarias para someterlas a prueba.

Palabras clave: vida en grupo, roedores cavadores, distribución del alimento, riesgo de depredación, costo de cavar.

INTRODUCTION

Adults from different animal species, including invertebrates and vertebrates, may spend most of their lives in close association with other conspecific individuals (Wilson 1975, Lott 1991). Understanding the causes of such sociality (or group-living) is a major research goal of Sociobiology and Behavioral Ecology (Clode 1993, Krebs & Davies 1993, Danchin & Wagner 1997, Emlen 1997).

Sociality may result in fitness costs to group members, including increased transmission of parasites and diseases, increased aggression and competition for food, infanticide, or cuckoldry (Hoogland 1979a, 1985, Møller 1987, Davies et al.

1991, Møller & Birkhead 1993, Van Vuren 1996). Thus one should expect the existence of benefits acting to overcome these inherent disadvantages. Selective pressures favoring sociality include increased foraging efficiency, decreased risk of predation, increased energy savings through thermoregulation, or even increased access to mates (Alexander 1974, 1991, Madison 1984, Slobodchikoff 1984, Wrangham & Rubenstein 1986, Morton et al. 1990, Krebs & Davies 1993, Hoi & Hoi-Leitner 1997). However, group-living also may occur because solitary living is not a viable option to individuals due to ecological (Armitage 1981, Emlen 1982, 1994, Brown 1987, Waser 1988) or phylogenetic and life history constraints (Armitage 1981, Rodman 1988, Burda 1990, Van Rhijn 1990). In this case, individuals do not gain net benefits from living with conspecifics.

Among animals, many species of rodents (Rodentia) are social (Michener 1983, Solomon & Getz 1997) in that several adults interact frequently (usually amicably), and share feeding areas and a burrow system (Rayor 1988, Waterman 1995, Lacey et al. 1997). Theory called to explain sociality in rodents has been derived mainly from African mole-rats (Bathyergidae; Lovegrove & Wissel 1988, Burda 1990, Jarvis et al. 1994), and North American ground-dwelling squirrels (Sciuridae; Barash 1974, Armitage 1981, 1988, Hoogland 1981a, Slobodchikoff 1984, Arnold 1990a, 1990b, Blumstein 1996). Although such studies have been important in suggesting potential explanations to the causes of sociality in rodents, the validity of their hypotheses as general explanations of group-living in other groups of animals or even other rodent groups remains questionable. For instance, Bathyergidae includes species of both social and solitary-living individuals (Jarvis & Bennett 1991), which has been used to assess ecological factors favoring sociality (Lovegrove & Wissel 1988, Jarvis et al. 1994, Faulkes et al. 1997). A potential

caveat of using this approach is that hypotheses (see below) are developed and tested using information from the bathyergids themselves. Thus comparative analyses of these species do not provide a robust test of potential mechanisms (Lacey & Sherman 1997), and data on other subterranean groups are needed to provide such contrasts.

A similar critique can be posed against hypotheses formulated to explain sociality among North American sciurids. Species of ground squirrels, prairie dogs, and marmots have been ranked according to their tendency to live socially, and this information has been related to ecological and life history characteristics of these species (Barash 1974, Armitage 1981, Michener 1983, Blumstein & Armitage 1998). However, these empirical relationships have not been confirmed in rodents other than the North American sciurids used in this analysis. More recently, Slobodchikoff (1984) linked sociality to the distribution of food resources. Although his model was intended to be a more general explanation of group-living than previous hypotheses, experimental and comparative evidence supporting Slobodchikoff (1984)'s model comes mainly from a single species of prairie dog (Slobodchikoff 1984, Travis & Slobodchikoff 1993), and therefore, outgroup (nonsciurid) species are needed to test this hypothesis.

Herein, I argue that New World fossorial hystricognaths (Woods 1993) could be excellent subjects to provide independent tests of alternative hypotheses of sociality in rodents. Many species within this group are social, fossorial or semifossorial, and occupy both mesic and xeric environments (Kleiman 1974, Redford & Eisenberg 1992). In addition, since New World hystricognaths are taxonomically and geographically distinct to African mole-rats (Jarvis & Bennett 1990, Woods 1993), any behavioral and ecological similarity may reflect evolutionary convergence.

This article is not intended to consider every hypothesis that has ever been formulated as a possible explanation for group-living. Instead, I concentrate my attention on the potential influence of food distribution and its interplay with the energy cost of digging, as well as that of predation risk. I first review the empirical evidence that supports a role for these factors on the evolution of rodent sociality. After doing so, I use this framework to review potentially relevant aspects of the behavioral biology and natural history of some selected species of hystricognath rodents that might suggest a role for either the distribution of food resources or predation risk on the tendency of these species to live socially. When doing so, I further restrict my analysis to those species that are fossorial or semifossorial, which often live in groups. I identify specific predictions to the hypotheses, and suggest comparative and manipulative observations that could help testing these predictions. Throughout the text, I follow Wilson & Reeder (1993) for rodent taxonomy.

MAIN CURRENT EXPLANATIONS OF SOCIALITY IN RODENTS: EVIDENCE FROM BATHYERGIDAE AND SCIURIDAE

Distribution of food resources

Within Bathyergidae, the most comprehensive explanation of sociality corresponds to the aridity-food distribution hypothesis (Lovegrove & Wissel 1988, Lovegrove 1991, Jarvis et al. 1994). According to this model, group-living is necessary to cope with unpredictable and patchily distributed food resources in arid and semiarid environments. Damaraland (*Cryptomys damarensis*) and naked (*Heterocephalus glaber*) mole-rats are fossorial and social rodents that inhabit the hot, dry regions of eastern and southern Africa, respectively, and they both consume patchily distributed bulbs and

tubers, which can be reached only via extensive burrowing (Jarvis & Bennett 1990, 1993, Honeycutt 1992, Jarvis et al. 1998). Although both species occur in different types of soil, the substrates used by these two mole-rats can be efficiently excavated only when recently softened by rain (Jarvis et al. 1994, Jarvis et al. 1998). Thus, the patchy distribution of food, along with the excessive cost of burrowing to locate these food patches, and the brief periods of time during which tunnel excavation is possible (due the low abundance and unpredictability of rains) determine that solitary mole-rats would be unlikely to locate enough food to sustain themselves through long and unpredictable dry periods (Lovegrove & Wissel 1988, Jarvis et al. 1994, Lacey & Sherman 1997, Jarvis et al. 1998). As a consequence, individuals are forced to remain in their natal group, and group-living becomes a necessity to cope with the high cost of foraging (the aridity-food distribution hypothesis). Foraging cost includes the energy needed to dig tunnels and the risk of unproductive foraging. Some support to this hypothesis comes from the observation that both solitary and social Bathyergids occur in mesic habitats but only social species are abundant in xeric habitats (Jarvis et al. 1994, Faulkes et al. 1997). Thus solitary species are precluded from xeric and arid areas.

The aridity-food distribution hypothesis is more likely to apply to truly subterranean species in which foraging takes place underground through digging than to burrowing species in which individuals regularly feed aboveground. To such semifossorial species, digging is not essential to forage, which may facilitate solitary individuals to locate and obtain enough amounts of food. Nonetheless, the distribution of resources still may promote group living in animals that forage aboveground. One potential mechanism to this is that individuals in groups could be more efficient in defending food resources

than solitary individuals. According to Slobodchikoff (1984), more efficient defense of food will occur when food is abundant and patchily distributed, which will promote sociality. In contrast, when food is scarce and uniformly distributed, defense of food, or food territoriality, is precluded and solitary-living is favored (Slobodchikoff 1984). Observed variations in the social structure of the semifossorial and social Gunnison's prairie dogs (Cynomys gunnisoni) after manipulations of the abundance and distribution of their food offer empirical support to this hypothesis. Thus when the abundance and patchiness of food are increased (by adding seeds), the feeding territory of each group of prairie dogs contracts and the number of group members increases (Slobodchikoff 1984). When the abundance of food is decreased and its distribution made more uniform (by removal of plants), the size of feeding territories increases and the number of animals per group decreases (Slobodchikoff 1984). More recently, a comparison between two populations of Gunnison's prairie-dogs in habitats with different distributions of food resources has provided additional support to a functional association between food distribution and the size of prairie-dog groups (Travis & Slobodchikoff 1993). Further evidence supporting this hypothesis comes from comparisons between the social structure of white-tailed prairie dogs (C. leucurus) and that of the more social black-tailed prairie dogs (C. ludovicianus). Black-tails are found in places where quality of food patches is highly variable, whereas the less social white-tailed prairie dog seems to live in sites of fairly uniform, low-density food patches (Slobodchikoff 1984).

Risk of predation

Besides the abundance and distribution of food resources, predation risk also may influence sociality (Alexander 1974, 1991). Animals may live in groups

because by doing so they decrease the risk of being attacked by a predator compared with solitary animals. Among other mechanisms (Krebs & Davies 1993), decreased predation may occur because animals in groups detect predators sooner than solitary individuals, or because animals locate themselves such that other group members become more vulnerable to attacks (i.e. selfish-herd effects; Hamilton 1971). Among semifossorial rodents, decreased predation risk is a potential benefit of group-living black-tailed prairie dogs (Hoogland 1995). Prairie dogs in large groups detect potential predators more quickly than do prairie dogs in smaller groups (Hoogland 1981a). Selfish-herd effects also could influence the social structure of prairie dogs and other sciurids. In black-tailed prairie dogs and yellow-bellied marmots (Marmota flaviventris) individuals located in the periphery of a group devote more time to scan for predators than individuals in more central positions (Armitage 1962, Hoogland 1979b, 1981a). Presumably, the risk of predation is higher in peripheral as compared with central locations.

Any of the above provide mechanisms by which predation can have a direct influence on sociality. However, the influence of predation could be more indirect. Fossorial and semifossorial rodents construct subterranean burrows as a major strategy to avoid predators (Waser 1988, Jarvis & Bennett 1990, Jarvis et al. 1994). Therefore, constructing a burrow system could be essential for individuals to use open, more exposed, patches where the risk of predation from visually-oriented predators is probably high. If so, animals may live in groups and benefit from cooperation when building these subterranean refuges (Hoogland 1981a, 1981b, Jarvis & Bennett 1990, Powell & Fried 1992). Individuals in groups may spend less time and energy digging burrows than individuals living without conspecifics.

SOCIALITY IN OTHER RODENT GROUPS: HYSTRICOGNATHS AS STUDY MODELS

Distribution of food resources

Fossorial species

Among octodontids, *Spalacopus cyanus*, or cururo, has been signaled as potential "target" to provide important clues to the evolution of group-living (Lacey & Sherman 1997). Cururos are subterranean rodents endemic to Chile, where they occur in both arid and more mesic regions of coastal central Chile (Contreras et al. 1987, Redford & Eisenberg 1992). Although the behavioral ecology of cururos is poorly known, available information suggests a number of intriguing parallels with social African mole-rats. First, *S. cyanus* seems to be social. Groups may include from 6 to 15 animals (including several adults), belonging to three or more generations, and using a single burrow system (Reig 1970, Torres-Mura 1990). Second, the ecology of cururos resembles that of the social bathyergids. Cururos are found in arid and semi-arid environments where woody plants cover is less than 60% of ground surface (Contreras et al. 1987). In these areas, cururos feed on shoots of grasses and forbs when available, but mainly on storage organs of several geophytes to which cururos gain access by way of their burrows (Reig 1970, Castillo et al. 1978, Mann 1978, Torres-Mura 1990, Contreras & Gutiérrez 1991, Contreras et al. 1993). Geophytes are particularly consumed during the dry months (January and February) and in dry years (Cox et al. 1995). Although these food resources (geophytes) may be abundant and constant through time, they are patchily distributed (Contreras et al. 1993). Third, digging activity of cururos occurs mainly during the rainy season and when soil humidity is relatively high (Torres-Mura 1990; although see Contreras et al. 1993). Finally, precipitation is relatively infrequent and unpredictable within and among years in arid coastal central Chile (i.e. mid to northern distribution of *S. cyanus*), with the common occurrence of several years of drought (Armesto et al. 1993).

Although most ctenomyids (tuco-tucos) are solitary subterranean rodents (Nevo 1979, Reig et al. 1990), the recently described *Ctenomys sociabilis*, endemic to the western Limay Valley (Neuquén, Argentina), is social (Pearson & Christie 1985, Lacey et al. 1997). Groups of *C. sociabilis* may include as many as five adults sharing the same nest site and burrow system (Pearson & Christie 1985, Lacey et al. 1997). Thus, *C. sociabilis* offers a good opportunity to perform comparative studies with other solitary ctenomyids (e.g. *C. haigi*; Pearson & Christie 1985), and use this behavioral differences among closely related taxa to assess ecological correlates of group-living (see below). Besides *C. sociabilis*, some scattered reports of multiple adults sharing the same burrow system includes *C. peruanus* (Pearson 1959) and *C. azarae* (Contreras & Maceiras 1970). In fact, the possibility of intraspecific variation in the tendency to live in groups also has been reported in tuco-tucos (Reig et al. 1990).

Semifossorial species

The distribution of food resources also may influence the tendency to live in groups of semifossorial species that construct underground burrow systems but that usually feed aboveground. Thus when food is abundant but patchily distributed, individuals in groups could be more efficient in defending such food patches than solitary animals (Slobodchikoff 1984; Travis & Slobodchikoff 1993).

Among semifossorial species, voles and lemmings (Muridae; Arvicolinae) have been considered as potentially useful models to perform comparative studies with bathyergids (Solomon & Getz 1997). I propose octodontids as an attractive

possibility as well. In particular, the degu, *Octodon degus* (Octodontidae), seems an appropriate subject to test the food-defense hypothesis. Degus are medium sized (ca. 180 g, Jaksic & Yáñez 1979) rodents that inhabit areas of central Chile with a low cover of shrubs (Fulk 1975, Glanz 1977, Le Boulengé & Fuentes 1978, Jaksic et al. 1981). Degus are diurnal and social (Yáñez 1976, Le Boulengé & Fuentes 1978, Mann 1978, Iriarte et al. 1989). Individual groups include 2 to 5 females and 1 to 2 males that share the same burrow system (Fulk 1976, Yáñez 1976). Degus mainly consume young leaves of herbs and shrubs along with seeds (Bustos et al. 1977, Fuentes & Le Boulengé 1977, Meserve et al. 1983, 1984). Thus digging is not directly required for *degus* to obtain food. Seasonally, *degus* prefer young rather than mature leaves of herbs and shrubs, and parturition coincides with the time when young foliage is more abundant (winter and spring; Meserve et al. 1983, 1984). Since group members are aggressive (and probably territorial) against members of other such groups during this time of the year (Fulk 1976), sociality in degus may well be a strategy to defend patches of temporarily abundant young leaves. Although young leaves are temporarily patchy (i.e. they are mostly available during winter-spring but not during summer-fall), the assumption that they also are spatially clumped needs to be assessed.

Contrasting the social structure of degus to that of other species within *Octodon* could be informative in assessing the role of food distribution on the evolution of group-living. As so O. *degus*, coastal degus *(O. lunatus)* and Bridge's degus *(O. bridgesi)* are folivorous rodents (Ipinza et al. 1971, Meserve & Glanz 1978, Muñoz & Murúa 1987). However, *O. lunatus* and *O. bridgesi* prefer areas of higher shrub cover than degus to construct their nests (Glanz 1977, Tamayo & Frassinetti 1980, Muñoz & Murúa 1987). One might expect the distribution of leaves of shrubs and grasses to differ between areas of medium-to-low

and high shrub cover. If so, corresponding differences in the extent of sociality between degus and O. *lunatus* and O. *bridgesi* should be observed. Unfortunately, the social structure of O. *bridgesi* and O. *lunatus* is virtually unknown. Only Ipinza et al. (1971) have suggested that O. *bridgesi* might form family groups. Studies assessing the extent of sociality in these octodontids are strongly needed.

Risk of predation

The observations that degus give alarm calls in the presence of potential predators (Fulk 1976, Yáñez 1976) and that nearby noncallers respond accordingly to these calls (Vásquez 1997) suggest that group-living in degus may enhance survival through increased detection of (and warning from) predators. In fact, although degus foraging in groups decrease their per capita time spent vigilant compared to solitary-foraging degus, total vigilance when in groups increases with group size (Vásquez in 1997). Thus social degus seem to benefit from enhanced alertness to potential predators, which might have influenced their tendency to live socially.

In addition, the influence of predation risk on group-living by degus could be more indirect. Burrow systems dug by degus are extensive and elaborate, with several entrances, subterranean nests and tunnels (Fulk 1976, Yáñez 1976, Mann 1978). Degus are usually found in areas of relatively low shrub cover. In these places, burrows with multiple openings in open areas between shrubs seem to function as refuges to escape from potential predators (Yáñez 1976, Yáñez & Jaksic 1978). If so, extensive burrow systems could be necessary for degus to use open habitats where the risk of predation is presumably higher compared with denser habitats (Jaksic 1986, Meserve et al. 1984, Lagos et al. 1995). As a result, degus may be social to share the cost of constructing and maintaining these underground systems.

Comparing the social structure of degus to that of *O. lunatus* and *O. bridgesi* also could be rewarding to assess the role of predation risk on the evolution of group-living. In contrast to *O. degus*, the congeneric species *O. lunatus* and *O. bridgesi* are nocturnal and do not burrow as much as degus and they establish their nests in denser shrub areas than that where degus are found (Greer 1965, Ipinza et al. 1971, Glanz 1977, Mann 1978, Tamayo & Frassinetti 1980, Muñoz & Murúa 1987). Since nocturnal activity and the use of areas with more dense vegetation (i.e. with more cover) presumably provides a lower risk of predation from aerial raptors (the most common predators in areas of Chile inhabited by these octodontid species; Meserve et al. 1984, Jaksic 1986), *O. bridgesi* and *O. lunatus* are expected to be less social than *O. degus*.

Comparative studies between *O. degus* and more distantly related species of semifossorial rodents facing similar ecological problems also should be informative. The social structure of degus resemble that of North American prairie dogs (Sciuridae; Hoogland 1981a) in that degus are aggressive (and possibly territorial) against members of other groups during the breeding season (Fulk 1976). Further, social prairie dogs are usually found in open sites with low vegetational cover of shrubs, and predation seems to have played an important role in the evolution of sociality in these rodents (Hoogland 1981a, 1995). In fact, interspecific differences in the degree of sociality between black-tailed and white-tailed prairie dogs seem linked to differences in protective cover (Hoogland 1981a). White-tailed prairie dogs live in smaller, less densely populated groups than do black-tails, and unlike black tails, white-tail groups are located in places with more protective cover (Hoogland 1981a, 1995). Comparative studies within *Octodon* could provide an independent test of this hypothesis.

Although active at night (Branch 1993a), plains vizcachas (*Langostomus maximus;* Chinchillidae) may face ecological problems similar to those of degus. Plains vizcachas are social and live in open scrub areas (Weir 1974, Mares et al. 1989). In this habitat, group-living vizcachas are heavily preyed by mountain lions (Branch 1993a, Branch et al. 1996). As expected, vizcachas give at least two types of alarm calls which seem to signal different amounts of risk (Branch 1993a). When alarm calls are given in response to mountain lions (and dogs), neighboring vizcachas in fact run toward their principal burrows (Branch 1993a). In addition, foraging distances of vizcachas from their central burrows seem related to the risk of predation (Branch & Sosa 1994).

On the other hand, plains vizcachas also may excavate extensive burrow systems in open scrub areas (Weir 1974, Mares et al. 1989), which might be a response to escape from predators. Each group, normally composed of one or more males, several females and immatures, uses a burrow system communally (Branch 1993a, 1993b). Interestingly, all group members (independently of age and sex) participate equally in digging to maintain the communal burrow (Branch 1993a), which suggests that cooperation associated with digging of burrows is a benefit of group-living in these rodents.

Besides degus and plains vizcachas, predation may influence the social structure of small cavies (*Microcavia australis;* Caviidae). Small cavies are diurnal and social (Rood 1970, 1972); they are herbivorous, feeding above-ground, and they can excavate complex burrow systems (Contreras & Roig 1978). Within a group, animals seem to associate in smaller "family" groups whose members use the same burrow system (Contreras & Roig 1978). Although individuals do not use the burrows of other family groups, interactions between members of different family groups are rarely aggressive (Rood

1970, Contreras & Roig 1978). The fact that foraging above-ground occurs with a continuous mixing up of individuals from different groups (Contreras & Roig 1978) suggests that defending food resources is not a benefit of social cavies. In contrast, predation could be a more important factor. Small cavies give alarm calls in response to potential predators (Rood 1970, 1972), and burrow systems are typically built in association with shrubs with overhanging branches (Rood 1970, Tognelli et al. 1995). Since these shrubs usually are not consumed by cavies, protection from predators (rather than food) could be the cause of such selection of microhabitat (Tognelli et al. 1995).

The cavy, *Microcavia niata*, is an herbivorous rodent that lives in bog communities of the High Andean Plateau. In these areas, *M. niata* lives in groups of 4 to 17 individuals including multiple adults of both sexes which use the abandoned burrows of ctenomyids (Marquet et al. 1993). The fact that these social rodents use the abandoned burrows of other (truly fossorial) rodents, makes cooperation to burrow unlikely to be a benefit of group-living in this case. However, they can be useful models to test the influence of predation risk. *Microcavia niata* gives alarm calls elicited by potential human predators, and other group members react to these calls by running into their burrows (Marquet et al. 1993).

The wild guinea pig (*Cavia aperea;* Caviidae) also seem to obtain benefits from group foraging under predation risk. Individual guinea pigs spend less time vigilant when foraging in groups than when foraging singly, and such time savings are allocated to foraging (Cassini 1991).

Finally, truly fossorial rodents also are vulnerable to predation when they dispose excavated soil above ground (Jarvis & Bennett 1990, Jarvis et al. 1994). Cururos and tuco-tucos can be preyed upon by raptors (Pearson et al. 1968, Castillo et al. 1978, Mann 1978, Jaksic 1986), and they

have been noticed to give alarm calls in response to potential predators (Pearson 1959, Fulk 1976). These observations suggest that the potential role of predation on the tendency of cururos and tuco-tucos, as well as in other fossorial rodents to live socially needs to be assessed.

TESTING HYPOTHESES OF SOCIALITY

Both intraspecific and interspecific comparisons could be used to assess the aridity-food distribution hypothesis in New World hystricognaths. All else being equal, the aridity-food distribution hypothesis predicts that (1) the size of groups should increase with the patchiness of food resources, so more group members are needed to locate more widely dispersed food patches. Thus (2) the probability of locating patches of food resources should increase with the number of diggers. Whereas checking for intraspecific differences in the social structure of animals living in sites with different distributions of food resources will help assessing the first prediction, observations of the animals under more controlled conditions could be necessary to test the second expectation. Regarding interspecific comparisons, the patchiness of food resources in the habitat used by social species should be higher than the patchiness of food resources observed in the habitat of solitary-living species.

If animals live in groups to exclude conspecifics from patches of food, the size of communal territories should increase with the number of group members, and the intensity of group territoriality is expected to increase with the patchiness and abundance of food resources.

The hypothesis that sociality is a response to avoid predation will be supported by observations showing that the individual risk of predation decreases with an increase in the size of groups. Manipulations that decrease the risk of

predation (e.g. removing or excluding predators) should result in smaller numbers of individuals per group. Among species, the predation hypothesis will be supported by showing that the risk of predation is higher in habitats used by social species compared with those used by solitary-living species. If any of these effects are demonstrated, additional observations will be needed to assess the particular mechanisms by which individuals decrease their risk of predation when in groups as compared with solitary-living animals. Thus, if increased vigilance is important, the time required to detect (and then react to) a predator should decrease as group size increases. If protection occurs due to a selfish herd effect, individuals using more peripheral locations within a group should more likely be attacked (and killed) than animals in more central locations. If protection against predators is related to the quality of burrows, burrow systems of larger groups should offer more protection than burrows constructed by smaller groups.

Independently from whether burrow systems are needed to locate food or to construct refuges against predators, the influence of the energetic cost of digging on the tendency of individuals to live socially will be supported by showing that groups using patches whose soils are more difficult to dig (e.g. hard soils) are more numerous than groups living in less hard soils. Alternatively, the time that each individual allocates to digging activities (presumably a cost of digging) will be lower in more numerous groups compared with smaller groups. Comparing group size and digging activity of animals living under different soil conditions (e.g. hardness) will be necessary to test the above prediction. Alternatively, digging costs can be assessed in the laboratory to animals maintained on different types of soils and number of cagemates. In addition, soils of habitats preferred by solitary digging species are expected to convey a lower energy expenditure to diggers than soils of habitats used by their social counterparts.

Assessing the influence of any of the above factors may require the consideration of different spatial scales, and the appropriate scale of analysis will depend on the spatial pattern of variation of that particular factor. Thus, in the context of the aridity-food distribution hypothesis, food distribution and aridity might be expected to change little across the feeding area used by neighboring groups but greatly between nonneighboring groups pertaining to spatially separated populations. On the other hand, selfish-herd effects could be expected either at level of an entire colony –a group composed by all those individuals that share a burrow system (Waterman 1995, Lacey et al. 1997)– or during the formation of more occasional groups within the colony (e.g. when feeding). Thus predation risk might vary with the location of an animal's burrow within a colony, or according to the location of an individual within a feeding group.

CONCLUDING REMARKS

Despite some efforts to highlight the ecological factors influencing sociality in different groups of rodents (bathyergids: Lovegrove & Wissel 1988, Burda 1990, Jarvis et al. 1994; murids: Madison 1984, McGuire & Getz 1995, Berteaux et al. 1996; sciurids: Armitage 1981, 1988, Hoogland 1981a, Slobodchikoff 1984, Arnold 1990a, 1990b, Blumstein 1996), its causes still remain poorly understood. I suggest that future studies with New World hystricognaths will provide raw material to test hypotheses by means of comparisons with previously known groups, and improve our understanding of group-living in rodents.

Studies on the behavioral ecology of New World hystricognaths will provide insights into other closely related aspects of group-living. In particular, several species of New World hystricognaths are known to communally nurse their litters and to give

alarm calls to warn others from predators (Pearson 1948, Rood 1972, Macdonald 1981, Branch 1993a, Herrera & Macdonald 1993, Künkele & Hoeck 1995). Such behaviors suggest the occurrence of benefits that are not simply due to group size effects (sensu Jennions & Macdonald 1994), but of more elaborate ways of cooperation such as communal breeding and anti-predator signals (Dugatkin 1997). The evolution of cooperative breeding and alarm signals are particularly puzzling behaviors to explain as individuals exhibiting such comportments may incur in costs (Sherman 1985, Solomon & Getz 1997).

Moreover New World hystricognaths may provide models of cooperation among individuals of different species. Thus *O. degus* sometimes share their underground burrows (and possibly their nests) with the chinchilla rat, *Abrocoma bennetti* (Abrocomidae), and the behavioral interactions between these two rodents seem amicable (Fulk 1976, Mann 1978). Burrow-sharing among members of two different species of rodents also has been reported among small cavies and yellow-toothed cavies, *Galea musteloides* (Rood 1970, Contreras & Roig 1978).

Overall, this commentary is not only intended to promote future studies to test the influences of food distribution, digging costs, and predation risk on the evolution of sociality in rodents, but also to stimulate the realization of behavioral studies on South American hystricognaths. With a few exceptions, the behavioral ecology of most Neotropical rodents remains poorly known.

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