Sociality in New World hystricognath rodents is linked to predators and burrow digging

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The importance of predation and burrow digging in explaining the evolution of sociality is generally unclear. We focused on New World hystricognath rodents to evaluate three key predictions of the predation hypothesis. First, large-bodied surface-dwelling species will be more vulnerable because they are more detectable; thus sociality should be associated with body size. Second, surface-dwelling, diurnal species will be more vulnerable to predators than nocturnal species; thus sociality should be associated with the evolution of diurnality. Third, species living in open habitats will be more vulnerable; thus sociality should evolve in species living in open habitats. Regarding the importance of burrows, we tested if species that dig burrows can benefit from communal labor; thus, sociality should be associated with burrow digging. All traits had significant phylogenetic signal, thus comparative analyses should explicitly address this. In a comparative analysis on independent contrasts we found that sociality was correlated with body size (larger species were more social), diurnality (diurnal species were more social), and burrowing (burrowing species were more social), but we found no effect of overhead plant cover of habitat on sociality in hystricognath rodents. Somewhat different results were found when we analyzed the raw data. Taken together, our results provide support for a link between predation risk, burrow digging, and sociality in this group. Key words: burrow digging, diurnality, group living, New World rodents, plant cover, predation risk. [Behav Ecol 17:410–418 (2006)]

Many animal species form groups, which range from temporary associations and aggregations to relatively stable social units (Blumstein, 2002; Lee, 1994; Parrish et al., 1997). Because group living, or sociality, may impose reproductive as well as survival costs to group members (Hoogland, 1979; 1985; Van Vuren, 1996), evolutionary explanations to group living have relied on fitness advantages to individuals that might compensate these costs (Alexander, 1974; Bertram, 1978; Krebs and Davies, 1993). Alternatively, however, individuals might be ecologically constrained to remain in groups despite some associated costs (Brown, 1987; Waser, 1988).

Several nonmutually exclusive hypotheses about the benefits of sociality have been suggested. These include a decreased risk of predation, decreased costs of thermoregulation, lower costs of den or burrow construction, or an improved access to critical resources (Ebensperger, 2001; Krause and Ruxton, 2002). Regarding predation, individuals may reduce their per capita predation risk either through increasing collective vigilance and predator detection, diluting the risk, or through collective defense (Alexander, 1974; Pulliam, 1973; Van Schaik, 1985). Abundant evidence from within-species studies on vertebrates and invertebrates generally supports the hypothesis that individuals in larger groups increase collective vigilance and predator detection (e.g., Ebensperger and Wallem, 2002; Hoogland, 1981; Kenward, 1978; Uetz et al., 2002), dilute their per capita risk (e.g., Krause and Godin, 1995; Watt and Chapman, 1998; Watt et al., 1997), or improve chances of collective defense (e.g., Duffy et al., 2002). Together, this evidence suggests that decreasing predation risk is one major factor that maintains group living in some species.

Although intraspecific studies on contemporary organisms support a role for predators influencing the maintenance of sociality, conditions favoring the evolution of a trait need not be the same as those involved in its subsequent maintenance (Reeve and Sherman, 1993; Shelley and Blumstein, 2005). While both initial conditions favoring the evolution of a trait and those involved in its subsequent maintenance can be studied by means of the comparative method (Harvey and Pagel, 1991; Martins and Hansen, 1996), the effect of predation risk on sociality remains inconclusive. For instance, there is some support of the predation-risk hypothesis in some avian clades; the frequency of colonial nesting is more common among species that nest in more open, exposed to predation locations (Rolland et al., 1998). However, the analysis of two other metrics of sociality provides equivocal results. Thus, and contrary to expectations, communal roosting is more common in larger species of predatory birds, which supposedly face little predation risk because of their size and weaponry (Beauchamp, 1999, 2002). Similarly, avian flock feeding is not more common in open, relatively exposed habitats (Beauchamp, 2002). More recently, avian flocking was seen to disappear as predicted on some islands devoid of predators but persisted on several others (Beauchamp, 2004).

There is a suggestion that insularity rather than predation risk may be responsible for the loss of such antipredator behavior following isolation on islands (Blumstein and Daniel, 2005).

Comparative evidence from mammals also provides some conflicting results. In support of the predation-risk hypothesis, large-bodied antelope species that use open habitats tend to be group living, whereas small-sized species that seek cover to hide from predators are either solitary or pair living (Brashares et al., 2000; Caro et al., 2004). Similarly, group size of delphinid species is positively associated with habitat openness (Gygax, 2002). In contrast, more social primates do not suffer less predation as compared with their less social counterparts once the activity period is taken into account (Hill and Dunbar, 1998; but see Hill and Lee, 1998).

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Sociality has also been linked to living in long-lasting, expandable nests or microhabitats safe from predation (Alexander et al., 1991). Thus, burrow digging has been linked to sociality in organisms such as rodents (Jarvis et al., 1994; Lacey and Ebensperger, in press; Powell and Fried, 1992). Cavities and burrows may provide several benefits to individuals, including a refuge to avoid unfavorable climatic conditions and a predator-free refuge (Kinlaw, 1999; Reichman and Smith, 1987). This seems particularly the case for species that need to be aboveground when active (Blumstein and Pelletier, 2005; Jackson, 2000; Karels and Boonstra, 1999; Kramer and Bonenfant, 1997). Therefore, individuals would benefit through sharing the costs of burrow construction and use. Alternatively, the set of safe burrows is limited and thus forms an ecological constraint that selects for group living. Either way, we predicted that burrow digging must be associated with sociality but mostly for species in open habitats where burrows would be most beneficial.

Rodents are a particularly good model system to examine correlates of predation risk on the evolution of sociality. Rodents are frequently prey of a large array of avian, mammalian, and reptilian predators (e.g., Jaksic, 1986; Jaksic et al., 1981), and available evidence from intraspecific studies generally supports the hypothesis that for some species group living is currently maintained through benefits derived from increased collective vigilance and predator detection (Ebensperger, 2001). In contrast, the role of predation risk in explaining rodent sociality across species has received less attention. Thus, sociality in the subterranean bathyergids (mole-rats) has been linked to ecological constraints on dispersal (Faulkes et al., 1997), whereas sociality among sciurids (marmots, squirrels) has been related to life-history constraints on dispersal (Armitage, 1999) and thermoregulatory benefits during hibernation (Arnold, 1993). The potential role of predation risk in the origin of sociality in these rodents remains unexplored.

Previous analyses of New World hystrixgnath rodents (guinea pigs, cavies, vizcachas) revealed no evidence for group living to be linked to a need for further parental investment, a potential life-history constraint (Ebensperger and Cofré, 2001). These analyses, on a smaller data set, also found that while group living was more prevalent among large-sized, supposedly more conspicuous, species, more social species did not use more open habitats (Ebensperger and Cofré, 2001). Intriguingly, species that actively dig their own burrows were also more social, which supported a link between burrows and group living. Here, we use an expanded data set on Neotropical hystrixgnath rodents, with a better-resolved phylogenetic hypothesis, to reexamine correlates of sociality in a rigorous phylogenetic context. Specifically, we examined interspecific associations between group size (an index of sociality) and three indices of predation risk. The influence of predation risk might be assessed through predation rate estimates. However, such estimates are difficult to obtain and are available for a very limited number of Neotropical hystrixgnath (Kraus and Rödel, 2004). And, perhaps more importantly, a history of successful adaptations to this risk might lead to low contemporaneous levels of predation despite its historic importance. Thus, we used three other correlates of predation risk: (1) the amount of overhead shrub or tree cover in the habitat, a measure of habitat openness; (2) body size; and (3) activity period. In the case of burrow digging, we examined how group living varies across burrow-digging and nondigging species.

We expected that rodents in the open would live in larger groups. Overhead shrub or tree cover is widely used in comparative studies as a proxy to predation risk when more direct estimates of predation risk are not available (Brashares et al., 2000; Caro et al., 2004; Rolland et al., 1998; for an exception see Hill and Dunbar, 1998). We chose this index because rodents, other mammals, and birds generally perceive overhead shrub or tree cover as protective (Ebensperger, 2001; Ebensperger and Hurtado, 2005). For instance, experimental studies have revealed that predation by birds on small mammals is higher in open patches compared with bushy habitats (Dickman et al., 1991; Kotler et al., 1988, 1991; Longland and Price, 1991). Note, however, that overhead cover may have no effect against ground-dwelling predators such as snakes (Pierce et al., 1992), and some species (e.g., larger-bodied kangaroos) might actually find cover obstructive (Blumstein and Daniel, 2002).

We expected larger sized rodents to live in larger groups. Because rodents are typically much smaller than their predators (e.g., Jaksic et al., 1981), rodent size is more likely to increase conspicuousness and overall susceptibility to predation, rather than to provide an effective defense against predation (i.e., Beauchamp, 1999). Large-bodied rodent species would have a more difficult time hiding in vegetation and would require larger home ranges (i.e., greater exposure; Norrdahl and Korpimäki, 1998) than small-bodied species (Wolff and Guthrie, 1985). Studies documenting how predation rate varies with size within and across small subsets of species (typically 2–4) provide conflicting results: while some report large-sized species to suffer increased predation (Castro and Jaskic, 1995; Halle, 1988; Kotler et al., 1988; Longland and Jenkens, 1987), others studies reveal either no influence of size (Norrdahl and Korpimäki, 1998; Sundell et al., 2003), higher predation on small-sized species (Dickman et al., 1991; Longland and Jenkins, 1987; Trejo and Guthmann, 2003), or that this effect changes seasonally (Halle, 1988). However, a clearer pattern emerges from studies comparing larger sets of prey species. Thus, avian and mammalian predators of different continents are reported to select larger rodent prey, irrespective of their abundance, most likely to satisfy their energy requirements (Bozinovic and Medel, 1988; Jaksic, 1989). Additionally, rodents from islands typically increase their body size when compared to their mainland counterparts (Lomolino, 1985), most likely in response to decreased predation (Adler and Levins, 1994; Smith, 1992).

We expected that in surface-dwelling hystrixgnath rodents, diurnal species would be more social. Activity time is expected to influence predatory risk in three ways. First, diurnality might increase prey vulnerability to most visually oriented predators because it will improve prey detection. Illumination typically increases the ability of crepuscular and nocturnal bird predators to capture their rodent prey (Kotler et al., 1988, 1991; Topping et al., 1999), suggesting that nocturnality is an antipredator strategy to rodents. By the same token, nocturnality might be expected to increase predation risk of social species: because for predators that hunt using auditory cues, multiple individuals will increase noise, that is, solitary living will be favored. Third, diurnality is expected to assist in predator detection and monitoring. Sentinel behavior and collective visual scanning would be less efficient to avoid nocturnal predators (Beauchamp, 2002; Terborgh and Janson, 1986). Thus, and in contrast to a recently reported pattern finding no link in a much more diverse group of 209 species of rodents (Shelley and Blumstein, 2005), we predicted that for surface-dwelling hystrixgnath rodents, diurnal species would be found in larger groups than nocturnal species.

We expected that animals that dig burrows would be more social through its effect on reducing costs of burrow construction. Burrow digging has been linked to sociality in voles and mole-rats (Jarvis et al., 1994; Powell and Fried, 1992). Cavities and burrows may provide several benefits to most rodents (Kinlaw, 1999; Reichman and Smith, 1987). Therefore, individuals would benefit through sharing the costs of burrow construction and use. In particular, cooperative burrow digging or
maintenance could be an adaptation for species that dwell on the surface for which burrows represent critical refuges from extreme thermal conditions and predators. Alternatively, the set of burrows is limited and thus forms a constraint that selects for group living. Either way, we predicted that burrow digging should be associated with sociality.

We evaluated our hypotheses comparatively by fitting regression models to raw data and phylogenetically independent contrast values.

MATERIALS AND METHODS

The data set

We collected basic information about behavior and ecology of New World hystriognath rodents (Appendix), a well-supported monophyletic clade (Huchon and Douzery, 2001). We considered every surface-dwelling species with available data on group size, a measure of sociality (e.g., Faulkes et al., 1997). A total of 32 species fitted this requirement, which comprised 32% of all surface-dwelling species of hystriognaths (Woods, 1993), and included representatives of all 10 extant families containing surface-dwelling species. We excluded fully subterranean (Ctenomyidae), arboreal (Erethizontidae), and fully aquatic (Myocastoridae, Myocastor coypus) forms as they (1) represented species with different modes of life, and (2) very little is known about their behavior and ecology. Our metric of group size included the number of adults reported as sharing a den or burrow system (most cases) or a territory (one case: Hydrochaeris hydrochaeris). Despite that our definition of group size emphasizes the sharing of dens or burrows, and social species included in our analysis also tend to be social foragers, that is, they are social when active above-ground (Appendix). Of these, we collected information on body mass, the amount of overhead shrub or tree cover in the typical habitat, activity period, and burrow-digging habits. We determined overhead plant cover after ranking the habitat of each species, from totally open (consisting of mostly bare ground, rank = 1) to dense forest patches (rank = 7). Activity was categorized either as mostly diurnal or mostly nocturnal. Finally, we categorized species as being either active burrow diggers or not (Appendix). Examinations of digging patterns were scant for surface-dwelling hystriognaths but the few available demonstrate that social species do communally dig burrows (Branch, 1993a; Ebensperger and Bozinovic, 2000).

Phylogenetic information

We used the McKenna and Bell (1997) phylogeny to establish major relationships among the 32 species for which we obtained complete information. From there, we resolved polytomies within genera by using recent molecular information from species-level phylogenetic hypotheses (Shelly and Blumstein, 2005). The placement of Trimynys was based on Leite and Patton (2002), and the positions of Galea were based on Rowe and Honeycutt (2002).

Phylogenetically based statistical analyses

Before conducting a comparative analysis, it is desirable to determine whether or not there is a phylogenetic "signal" present for the traits of interest; without it, it may not be necessary to use formal phylogenetic analyses (Garland et al., 2005; Irschick et al., 1997; Losos, 1999). A recent study found that more than 90% of comparative analyses that had more than 20 species illustrated some degree of nonrandom phylogenetic signal (Blomberg et al., 2003). Nonetheless, we determined whether traits were phylogenetically independent using the program Phylogenetic Independence 2.0 (Reeve and Abouheif, 2003) and selecting the 1000 simulations option. This program implements the test for serial independence (Abouheif, 1999) that tests for the nonrandomness in the set of trait values. We found that all six traits were significantly autocorrelated and thus not phylogenetically independent (all p values ≤ .001). We evaluated our hypotheses giving priority to the results of independent contrasts (Felsenstein, 1985, 2003). However, because the serial independence test (and other such approaches) has limitations (see Blomberg et al., 2003), we also provide results from raw analysis. To calculate independent contrasts we defined sociality as the log10 of the midpoint of the range of observed group sizes. Our continuous independent variables were the log10 of the midpoint of the range of observed body masses and the midpoint of the range of habitat tree cover. Midpoints are appropriate measures of central tendency, given a wide range of values within a species. We transformed group size and body mass to eliminate outliers and to meet assumptions of linear models. For some species, we only had a single value; these are noted in the Appendix with a ‘?’ and this single value was used as the best estimate of that species’ trait value. Following others (e.g., Purvis et al., 2000; Stuart-Fox and Ord, 2004), we calculated contrasts for dichotomous variables, in our case whether the species was diurnal or nocturnal and whether the species burrowed or not. Because our phylogeny did not have consistently good estimates of branch lengths, we assumed several models of evolution: a speciation model (where branch lengths were made equal and set to 1.0), the arbitrary transformation of Grafen (1989), a Nee transformation (cited in Purvis, 1995; where the distance from the tips to the focal node was calculated by log10 transforming the number of tips descending from that node), and a Pagel (1992) transformation (where nodal depth was made equal to the left and right descendent taxa, plus 1). We implemented these transformations in the PDAP 1.07 module (Midford et al., 2005) for Mesquite 1.06 (Maddison WP and Maddison DR, 2005). As required by the method, we forced all regressions through the origin. Given these various phylogenies, we then calculated independent contrasts in Compare 4.5 (Martins, 2003).

Given a set of raw variables and sets of independent contrasts, we analyzed them separately. First, we fitted a linear model on the raw data. For this, we included an intercept. Second, we fitted the same model with each of the different sets of standardized independent contrasts. As required by the method, there was no intercept and the regression was forced through the origin. Results from these different analyses on independent contrasts were identical, and we thus report only the results from the speciation model. In all cases, we interpret p values < .05 as significant, and we report R2 values and partial η2 as a measure of effect size. All models were fitted in SPSS-11 for the Macintosh.

RESULTS

Raw data analyses

Overall, 69.6% of the variation in sociality was explained by a model fitted to species values (p < .001; Table 1). Larger species were more social, species living in more open habitats were more social, species that dug burrows were more social, and diurnality had no effect on sociality. We interpret these raw values with caution because all traits were significantly autocorrelated and thus not phylogenetically independent (all p values ≤ .001).

Phylogenetically based analysis

Overall, 64.5% of the variation in sociality was explained by group size (p < .001; Table 1; Figure 1). Larger species were
more social, habitat had no effect on sociality, burrow-digging species were more social, and diurnal species were more social.

**DISCUSSION**

Rodents are frequent prey of a large array of avian, mammalian, and reptilian predators. Our analysis revealed that important correlates of predation risk influenced group size across species in a way consistent with the hypothesis that variation in predation risk contributed to the evolution of sociality in surface-dwelling hystricognath rodents. Regardless of analysis, body size had a large effect on group living: larger species are more social. Burrowing had a small effect on sociality that, interestingly, was significant only in the analysis of phylogenetically independent contrasts. The effects of diurnality and habitat openness varied substantially based on the analytical method used. Because all traits were significantly phylogenetically nonindependent contrasts, the effects of diurnality and habitat openness varied substantially based on the analytical method used. Because all traits were significantly phylogenetically nonindependent contrasts, we feel more confident interpreting the results from the analyses calculated with independent contrasts. Thus, we interpret our findings as meaning that large-sized, diurnal hystricognaths are more social, most likely in response to their higher conspicuousness to predators. On the other hand, our study complemented previous analyses (Ebensperger and Cofré, 2001) in that more social species were also active burrow diggers, a finding supporting a link between sociality and burrow digging.

There are several explanations for our findings. First, avian and mammalian predators are reported to select larger rodent prey, and large-bodied rodent species would have a more difficult time hiding in vegetation and would require moving over larger areas (i.e., suffering greater exposure) than small-bodied species (Bozinovic and Medel, 1988; Norrdahl and Korpinäki, 1998; Wolff and Guthrie, 1985). Second,illumination typically increases the ability of crepuscular and nocturnal bird predators to capture their rodent prey (Kotler et al., 1988, 1991; Topping et al., 1999). Thus, diurnal species are likely more conspicuous to predators. Nocturnality, in turn, may select against sociality because social foragers will attract the attention of predators using auditory cues. Simultaneously, by being social, diurnal species could engage in corporate vigilance and increase the rate at which they detect predators. Sentinel behavior and collective visual scanning would be less efficient to avoid nocturnal predators (Beauchamp, 2002; Terborgh and Janson, 1986).

Cavities and burrows may provide rodents with multiple benefits, including protection against extreme climatic conditions, places to hide and contain offspring, and general protection against predation, among others (Kinlaw, 1999; Reichman and Smith, 1987). Therefore, either selection to decrease the costs of burrow construction and use (Branch, 1993a; Ebensperger and Bozinovic, 2000) or a limitation in the number of available burrows is expected to favor rodent group living.

Is there a link between predation risk and burrow digging? Clearly, yes. One major function of burrows is to provide a refuge against most mammalian and avian predators, particularly for those species that spend much of their active time

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**Table 1**

<table>
<thead>
<tr>
<th></th>
<th>Raw data</th>
<th>Contrasts</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>$\eta^2$</td>
<td>$b$</td>
</tr>
<tr>
<td>Model</td>
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<td>&lt;.001</td>
</tr>
<tr>
<td>Intercept</td>
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</tr>
<tr>
<td>Mass</td>
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<td>0.292</td>
</tr>
<tr>
<td>Habitat tree cover</td>
<td>0.144</td>
<td>0.102</td>
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</tbody>
</table>

Raw data results contain an intercept, whereas the model of independent contrasts did not contain one (see text for details).
aboveground (Blumstein and Pelletier, 2005; Holmes, 1984; Jackson, 2000; Karels and Boonstra, 1999; Kildaw, 1995; Kramer and Bonenfant, 1997; MacHutchon and Harestad, 1990). Thus predation risk will select for social living indirectly as individuals of these species would benefit through sharing the costs of burrow construction and use, as suggested for degus or plains vizcachas (Branch, 1993a; Ebensperger and Bozinovic, 2000). Even if the set of safe burrows is limited, such a constraint should select for group living. Collectively then, a need to cooperate during burrows and/or burrow sharing may proximately cause social living to (i.e., it will reduce costs of digging) but ultimately may reflect predation.

Unexpectedly, our analysis based on phylogenetically independent contrasts found no relationship between the amount of shrub or tree cover in the habitat and group size, suggesting that species living in open habitats were no more likely to evolve sociality as compared with species living in more vegetated areas (Figure 2). This finding is at odds with available evidence that demonstrates that predation by birds on small mammals is higher in open patches compared with bushy habitats (Dickman et al., 1991; Kotler et al., 1988, 1991; Longland and Price, 1991). Our finding also is in conflict with more indirect evidence supporting that shrubs provided protection against predation in some social New World hystricognaths such as cavies (Cavia apera; Asher et al., 2004; Cassini, 1991) or degus (Ebensperger and Wallem, 2002; Lagos et al., 1995; Vásquez et al., 2002). More intriguingly, major events of hystricognath radiation in the New World overlapped a period of climatic changes that included the establishment of seasonally drier and more open habitats (Flynn and Wyss, 1998; Vucetich et al., 1999). Discrepancies may be explained, to some extent, if predators of hystricognaths are mostly terrestrial carnivores (which may use bushes to hide from their prey) rather than raptors. Available evidence suggests this might be so in the case of cavies (Kraus and Rödel, 2004), plains vizcachas (Lagostomus maximus; Branch, 1995), and capybaras (H. hydrochaeris; Macdonald, 1981) but not so in degus (Jaksic et al., 1981).

Despite the above caveat, our study adds to a body of existing evidence linking predation risk and sociality across mammals. For instance, large-sized artiodactyls that use more open habitats are typically social, whereas small-sized species that seek cover to hide from predators are either solitary or live in pairs (Brashares et al., 2000; Caro et al., 2004). Heightened predation risk from using open habitats also may explain high degrees of sociality in mongooses (Veron et al., 2004). Among cercopithecoid primates, species and populations within species of habitats with a high frequency of predation tend to live in larger sized groups (Hill and Lee, 1998; but see Hill and Dunbar, 1998).

In the context of rodent sociality, our findings depart from previous comparative analyses of other rodent groups that linked group living to ecological and life-history constraints on dispersal (Armitage, 1999; Faulkes et al., 1997) and therefore are consistent with the hypothesis that no single factor is responsible for driving the evolution of sociality (i.e., Ebensperger, 2001). Future comparative analysis of different rodent groups will benefit from contrasting the role of predators with that of other constraints simultaneously. For instance, feeding habits may predispose some organisms to adopt social life (Beauchamp, 2002; 2004). Most New World hystricognaths are generalist herbivores, but species differences do occur (e.g., Mares and Ojeda, 1982), and body size, the factor explaining most (53–55%) of the variation in hystricognath group size, can influence feeding habits (Brown, 1995). Feeding habits, in turn, may impinge on foraging behavior, including social foraging strategies.

Figure 2
The relationships between (a) standardized independent contrasts of log<sub>10</sub> body mass and standardized contrasts of log<sub>10</sub> group size, (b) standardized contrasts of burrowing and log<sub>10</sub> group size, (c) standardized contrasts of diurnality and log<sub>10</sub> group size, and (d) standardized contrasts of habitat openness (large numbers are more closed) and log<sub>10</sub> group size.
### APPENDIX

#### Morphological, ecological, and behavioral traits of cursorial and semifossorial New World hystricognath rodents

<table>
<thead>
<tr>
<th>Species</th>
<th>Range (midpoint) of body size (g)</th>
<th>Habitat and rank of tree cover</th>
<th>Burrow digger</th>
<th>Activity period</th>
<th>Group* size (adults per group) (midpoint)</th>
<th>Sources</th>
</tr>
</thead>
</table>

Habitats are ranked according to the amount of tree cover, from no cover (1) to the highest amount of cover (7). Question marks indicate uncertainties in the data source. Asterisks are used to indicate group-living species with reports of social foraging. Values enclosed in [ ] are values used in analyses.
REFERENCES


