

# On the evolution of group-living in the New World cursorial hystricognath rodents

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We used the comparative method to examine the evolutionary causes of group-living in the New World cursorial hystricognath rodents. To do so, we used the available literature to collect information on behavioral (group size, burrow digging), ecological (amount of plant cover in the habitat), and life history (body mass, time to sexual maturity) variables, along with phylogenetic relationships of these rodents. We analyzed these variables in the context of three major hypotheses. A first explanation poses that rodents live in groups to reduce the energy needed in the construction of their burrows. A second hypothesis suggests that grouped rodents increase their ability to detect and escape from predators. A third possibility states that group-living is adopted by rodents to provide extra parental care to their offspring. Our comparative analysis revealed that across species variation of group size is, to some extent, influenced by body size, and by the habit of burrow digging. Thus, large sized rodent species that actively dig their own burrows form larger group sizes than small sized species that do not dig burrows. In contrast, across species variation of group size was not influenced by differences in the amount of plant cover in the habitat (an indirect measure of predatory risk), or by differences in the time to first reproduction (a measure of parental care given). Therefore, group-living among the New World hystricognath rodents seems more linked to a strategy aimed to reduce their burrowing cost than to a strategy aimed to reduce their predatory risk, or to extend their parental investment. *Key words*: burrows, comparative analysis, parental care, predatory risk, rodent sociality. [*Behav Ecol* 12:227–236 (2001)]

Many animal species form groups, which range from temporary associations and aggregations to relatively stable units (Lee, 1994; Parrish et al., 1997). Fidelity to the group and genetic relatedness among individuals within such groups may vary widely, which influences the nature (e.g., cooperative, competitive) of social interactions among group members (Hoogland, 1995; Parrish et al., 1997). Because group-living may impose reproductive as well as survival costs to group members (Armitage, 1999; Davies et al., 1991; Hoogland, 1979, 1985; Møller, 1987; Møller and Birkhead, 1993; Van Vuren, 1996), evolutionary explanations to group-living have relied on either fitness advantages to individuals that might compensate these costs (Alexander, 1974, 1991; Krebs and Davies, 1993; Madison, 1984; Slobodchikoff, 1984; Wrangham and Rubenstein, 1986), or on constraints that might force individuals to form groups despite of the costs (Brown, 1987; Dunbar, 1996; Rodman, 1988; Van Rhijn, 1990; Waser, 1988).

For rodents, social groups have a variable number of adult individuals that share a feeding area, a den, and (often) a territory (Lacey et al., 1997; Rayor, 1988; Waterman, 1995). Although several non-mutually exclusive hypotheses have been suggested to explain the evolution of rodent group-living (see below), each model is often treated in isolation and in the context of specific taxonomic groups (e.g., Armitage, 1999; Jones, 1993). Herein, we use the available data to carry out a comparative analysis and assess the ability of several factors to explain group size variation across the New World hystricognath rodents (e.g., guinea pigs, chinchillas, capybaras). We specifically evaluate three alternative hypotheses posed to explain rodent group-living (see below). New World hystricognaths are particularly interesting as group-living in these rodents has not been examined in this context before (Eben-

sperger, 1998). Recent evidence based on fossils, number of parasite species shared, and analysis of molecular sequences supports an African monophyletic origin for these rodents (Gardner, 1991; Nedbal et al., 1994; Wyss et al., 1993). New World hystricognaths include species adapted to different modes of life; they are found in almost every type of habitat, and their social structure ranges from solitary-living to highly gregarious species (Eisenberg, 1989; Eisenberg and Redford, 1999; Nowak, 1999; Redford and Eisenberg, 1992).

## Hypotheses and predictions

The three hypotheses considered herein have been developed to understand the evolution of sociality in rodents that carry out most or all of their activities above ground, even though they may construct under ground burrows (i.e., being semi-fossorial; DeBlase and Martin, 1981).

Group-living has been linked to life in long-lasting, expandable nests (Alexander et al., 1991). Most rodents and other mammals need cavities and burrows as refuges to avoid predators, stressful weather conditions, or as sites for food hoarding and hibernation (King, 1984; Kinlaw, 1999; Reichman and Smith, 1987). Because constructing and maintaining burrows is energetically costly (Ebensperger and Bozinovic, 2000b; Lovegrove, 1989), animals may be forced to live in groups to share their use or minimize such energetic cost (Arnold, 1990; Jarvis and Bennett, 1990; Powell and Fried, 1992; West, 1977). Thus, and under the burrow-sharing hypothesis, active burrow-digging species are expected to form larger groups than non-diggers.

Second, individuals may live in groups to reduce their per capita predatory risk (Alexander, 1974; Alexander et al., 1991; Van Schaik, 1983). When grouped, individual rodents may increase their ability to detect and escape from predators, gain protection from predators because of simple dilution of per capita risk, locate themselves such that other group members become more vulnerable to attacks, or even repeal predators more efficiently (Bertram, 1978; Hamilton, 1971; Romey, 1997). Under the predatory risk hypothesis, species of more open, riskier habitats should exhibit larger group sizes than

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species of more vegetated, safer habitats (Dunbar, 1989; Kleiman, 1974; Lagory, 1986).

Finally, group-living among the North American sciurids (ground squirrels and marmots) is hypothesized to be the consequence of additional reproductive investment required beyond weaning age (Armitage, 1981, 1988, 1999). Sciurid social groups are often the result of offspring delaying dispersal (Armitage, 1999; Blumstein and Armitage, 1998; Michener, 1983). Dispersal is retarded in relatively large body-sized species, which require extended times to reach adult size and maturity, relative to time of active (growing) season of the habitat. A relatively long time to reach maturity in turn demands additional investment from the parents (Armitage, 1981, 1988, 1999; Barash, 1974, 1989). The extended parental investment hypothesis predicts that body size and age to first reproduction of social species should be larger than the corresponding figures of solitary-living or less social species.

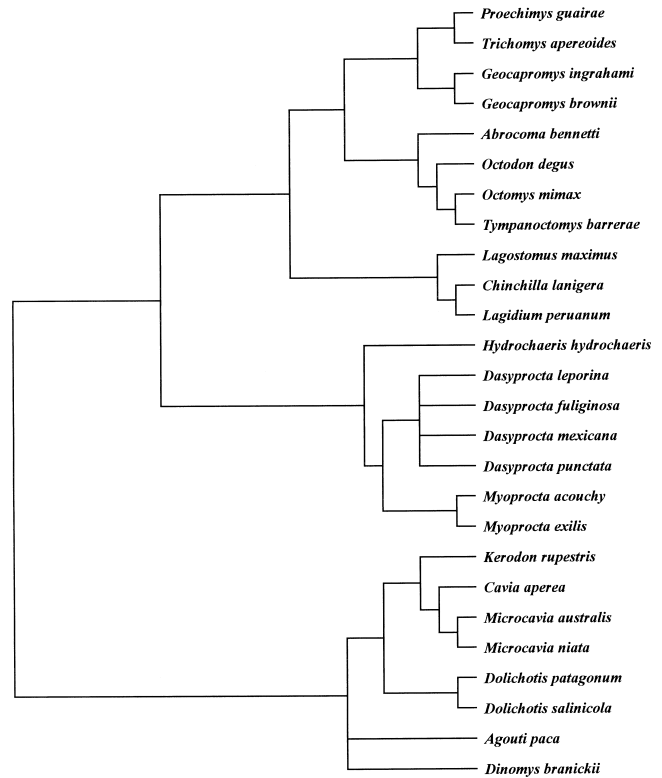
## METHODS

### The data

We used the available literature to collect basic information about behavior, life history, and ecology of New World hystricognath rodents (Appendix). We considered every cursorial species with available data on group size. We also collected information on body mass, time to first reproduction, and the amount of plant cover in the habitat as an indicator of predatory risk. We determined plant cover after ranking the habitat of each species, from totally open (i.e., consisting of mostly bare ground) to dense forest patches. Finally, we categorized species as being either active burrow diggers or not (Appendix).

In contrast to the burrow-sharing and the predatory risk hypotheses, the significance of group size to the extended parental investment hypothesis seems more limited as this hypothesis has been posed to explain social structure or complexity rather than group size (Armitage, 1981; Blumstein and Armitage, 1998). Social complexity involves the nature, number, and stability of individual interactions within groups (Blumstein and Armitage, 1998; Lee, 1994). Although such information is available for some rodent groups (Blumstein and Armitage, 1998), this is not so for most of New World hystricognaths. Despite this caveat, group size still may be used to examine the overall influence (or its absence) of life-history, as well as other (e.g., Faulkes et al., 1997; Hoogland, 1981) factors, on rodent group living. In fact, as the number of group members increases, there is an opportunity for more social interactions (Blumstein and Armitage, 1998).

There is no published hystricognath phylogeny that includes all cursorial species of interest. Therefore we combined partial phylogenies giving priority to studies based on molecular evidence. Nonetheless, we needed to use phylogenetic relations based on other sources of information (e.g., morphology), along with taxonomy to include additional species and resolve some soft polytomies. The use of different sources of information to infer phylogenies is not uncommon when performing comparative studies (Blumstein and Armitage, 1998; Dubois et al., 1998). Familial relationships (Figure 1) are largely based on molecular data (Nedbal et al., 1994). Relationships within Octodontidae and the placement of Abrocomidae were determined following the karyotypic analysis of Gallardo (1997). We used information on blood protein and taxonomy to determine the placement of Agoutidae and Dinomyidae (Woods, 1982). Relationships within Chinchillidae (Spotorno AE, unpublished data), and those between *Cavia* and *Microcavia* (Caviidae; Marín, 1999) were derived from molecular evidence, whereas the placement of *Ker-*



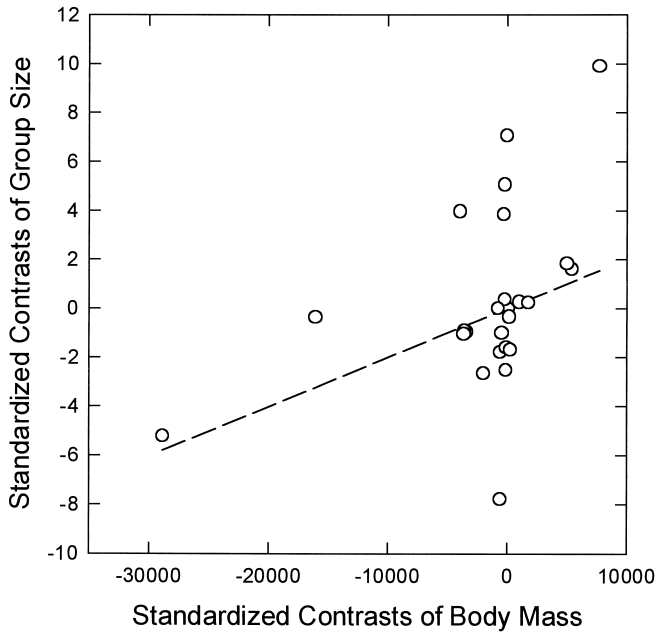
**Figure 1**

Topology for the 26 species of New World hystricognath rodents used in this study. Branch lengths are in arbitrary units.

*odon* and *Dolichotis* were based on morphological data (Quintana, 1996). Relations within Echimyidae and Dasyproctidae were derived solely from taxonomy (Woods, 1993). When analyzing the influence of time to first reproduction on group size, we needed to trim our phylogeny from 26 to 16 species as data on this life-history variable was not available for the remaining 10 species. We followed Woods (1993) for species names and overall taxonomy. Since branch lengths of our phylogenies were generally unknown, we considered three arbitrary algorithms, which differ in the model of evolution assumed (Harvey and Pagel, 1991). Under the first of these approaches, all branch lengths were left constant and equal to unity, which assumes that evolutionary change is punctuational, occurring only at speciation events (Blumstein and Armitage, 1998). In addition, we considered the Grafen's arbitrary method, which assumes a gradual Brownian motion model of evolution (Harvey and Pagel, 1991). Under Grafen's approach, the height of each node is assumed to be directly proportional to the number of species derived from it. The length of the branch linking any two nodes is thus the difference between their heights (Grafen, 1992). Last, we used the arbitrary method of Pagel (1992), which also assumes a gradual model of evolution. All three branch length algorithms were implemented with the use of the PDTREE module of the Phenotypic Diversity Analysis Program (Garland et al., 1993).

### Phylogenetically based statistical analyses

To control for possible phylogenetic non-independence of group size and of the independent variables analyzed, we used the independent contrasts method for continuous variables (Felsenstein, 1985; Martins and Hansen, 1996), and the autocorrelation method for categorical variables (Cheverud et



**Figure 2**

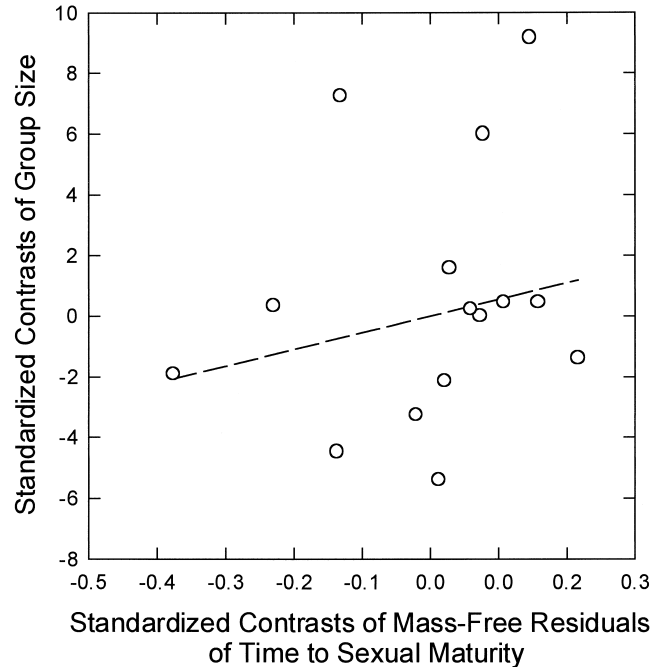
Relationship between the standardized contrasts of group size and the standardized contrasts of body mass. Dotted line represents the regression line after making all branch lengths of phylogeny equal to unity (i.e., the constant branch length method, cbm: partial  $r = .35$ ,  $r^2 = .04$ ,  $p = .044$ ). Regression parameters are given for two other branch length algorithms; Grafen's arbitrary method (gm: partial  $r = .38$ ,  $r^2 = .04$ ,  $p = .033$ ), and Pagel's arbitrary method (pm: partial  $r = .35$ ,  $r^2 = .04$ ,  $p = .044$ ). Contrasts were calculated using the topology of Figure 1.

al., 1985; Martins and Hansen, 1996). When using the first method, we regressed the standardized contrasts of group size against those of body mass, time to first reproduction, and plant cover of habitat. All regressions were forced through the origin (Garland et al., 1992). When examining the influence of time to first reproduction, a life history variable, we regressed the contrasts of this variable against the contrasts of body mass and used the residuals for subsequent analyses (Blumstein and Armitage, 1998; Martins and Garland, 1991).

Under the autocorrelation method, the phenotype of each species is represented as a sum of phylogenetic and non-phylogenetic components (Cheverud et al., 1985; Martins and Hansen, 1996). Thus, and when using the autocorrelation method, we took the non-phylogenetic component of group size and used two sample Student- $t$  tests to examine the influence of burrow digging on group size.

Independent contrasts were obtained using the Compare 4.2 program (Martins, 1999). Polytomies in our phylogenetic hypothesis were accounted for by bounding degrees of freedom (Purvis and Garland, 1993). Accordingly, degrees of freedom in tests were calculated as the total number of nodes in the phylogeny minus one (Garland and Díaz-Uriarte, 1999; Purvis and Garland, 1993). This correction was unnecessary in the case of tests using our trimmed phylogeny as it did not contain polytomies.

We also used the Compare 4.2 program to implement the autocorrelation method. As recommended by Martins (1996), we conducted our analysis both with and without the alpha parameter. The alpha parameter was introduced by Gittleman and Kot (1990) to improve the efficiency of the spatial autocorrelative model in removing phylogenetic correlation from the database. However, and according to recent computer simulation studies, the use of this correction factor may



**Figure 3**

Relationship between the standardized contrasts of group size and the standardized contrasts of the mass-free residuals of time to sexual maturity. Dotted line represents the regression line after making all branch lengths of phylogeny equal to unity (i.e., the constant branch length method, cbm: partial  $r = .21$ ,  $r^2 = .04$ ,  $p = .333$ ). Regression parameters are given for two other branch length algorithms; Grafen's arbitrary method (gm: partial  $r = .22$ ,  $r^2 = .05$ ,  $p = .205$ ), and Pagel's arbitrary method (pm: partial  $r = .21$ ,  $r^2 = .05$ ,  $p = .213$ ).

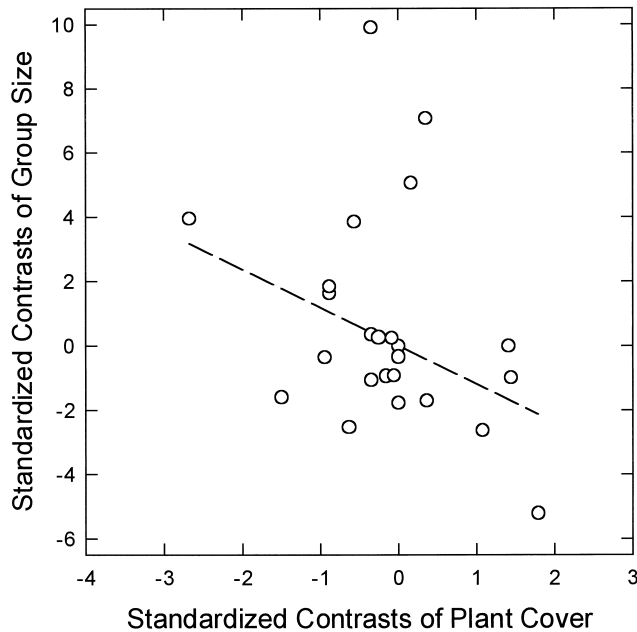
or may not improve the efficiency of the method (Martins, 1996). When used, the alpha parameter was estimated by the program using maximum likelihood. When not used, the alpha parameter was left fixed and equal to unity.

Regular statistical methods were implemented with the use of Statistica 5.1 for Windows (StatSoft Inc., Tulsa, Oklahoma, USA). We report results for one-tailed tests because of a-priori directional hypotheses (Zar, 1996). Data are presented as mean  $\pm$  SD.

## RESULTS

Data on group size were available for a total of 26 species of cursorial hystricognaths (Appendix). Overall, the three arbitrary algorithms used to estimate the length of branches of our topology rendered consistent results in terms of the sign of each regression after using the independent contrasts method. Our regression analysis revealed that body mass weakly but significantly influenced group size, where large body sized species exhibited larger group sizes than small sized species (Figure 2). In contrast, the tendency of group size to increase with time to first reproduction (Figure 3), and with the amount of plant cover in the habitat (Figure 4) were not statistically significant.

The raw across-species data showed that species that actively dig and maintain subterranean burrows tend to form larger groups than species that do not dig such burrows (Figure 5). Such a trend between burrow digging and group size was generally confirmed in a phylogenetic context. Thus and after using the autocorrelation method, the non-phylogenetic component of group size of species that dig burrows tended to be



**Figure 4**

Relationship between the standardized contrasts of group size and the standardized contrasts of plant cover in the habitat. Dotted line represents the regression line after making all branch lengths of phylogeny equal to unity (i.e., the constant branch length method, cbm: partial  $r = -.26$ ,  $r^2 = .04$ ,  $p = .110$ ). Regression parameters are given for two other branch length algorithms; Grafen's arbitrary method (gm: partial  $r = -.12$ ,  $r^2 = .04$ ,  $p = .283$ ), and Pagel's arbitrary method (pm: partial  $r = -.19$ ,  $r^2 = .04$ ,  $p = .180$ ). Contrasts were calculated using the topology of Figure 1.

greater than that of cursorial species that do not dig burrows (Table 1). This tendency was significant particularly when the program computed the alpha parameter using maximum likelihood (Table 1).

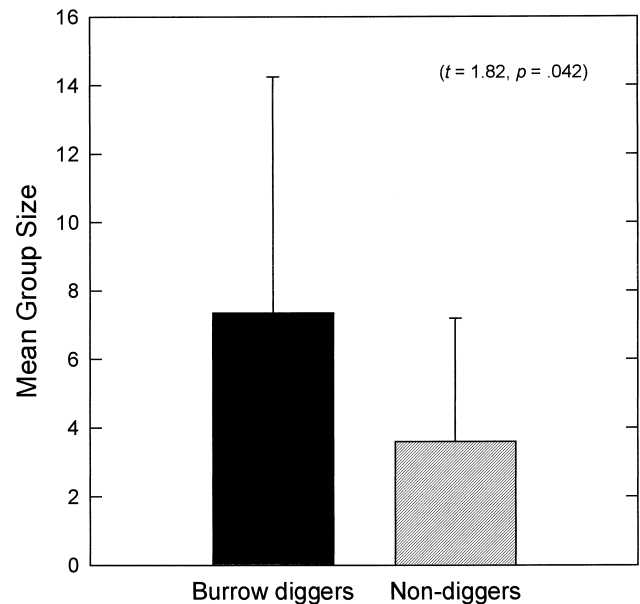
## DISCUSSION

### Group-living and burrows

The observation that group size of burrow digging species tended to be larger than that of non-digging species supports the burrow-sharing hypothesis. This finding suggests that the habit of burrow digging has been a major influence favoring the evolution of group-living of New World hystricognath rodents. Overall, the relationship between burrows and rodent social systems has received little attention, and current evidence supporting this hypothesis is largely circumstantial (King, 1984). For New World hystricognaths, the influence of burrow digging on group-living is supported by the observation that all group members of social plains vizcachas (*Lagotomus maximus*) participate equally in digging (Branch, 1993b), and that common degus (*Octodon degus*) in groups coordinate their digging and remove more soil per capita than solitary diggers (Ebensperger and Bozinovic, 2000a).

### Group-living and predatory risk

Our analysis also revealed that species of more open, riskier habitats do not form significantly larger group sizes than species of more vegetated, safer habitats, which contradicts expectations by the predatory risk hypothesis (Dunbar, 1989; Kleiman, 1974; Lagory, 1986). It can be argued that plant cover may not adequately measure overall predatory risk in the



**Figure 5**

Mean group size of species that dig ( $n = 10$ ) and of species that do not dig ( $n = 16$ ) underground burrows.

habitat. Plant cover not only may provide prey with hiding places, but obstruct and make predator detection more difficult to the prey (Schooley et al., 1996; Sharpe and Van Horne, 1998). Despite this, rodent behavior generally support an inverse relationship between the amount of plant cover and predatory risk. Guinea pigs (*Cavia aperea*), spiny rats (*Proechimys* sp.), and California ground squirrels (*Spermophilus beecheyi*) seek shrub cover upon the approach of potential (terrestrial or aerial) predators (Emmons, 1982; Hanson and Coss, 1977; Rood, 1972; Sherman, 1985). Individual wild guinea pigs and California ground squirrels spend more time alert when foraging far from shrub or tree cover (Cassini, 1991; Leger et al., 1983). Eastern chipmunks (*Tamias striatus*) and grey squirrels (*Sciurus carolinensis*) also spend more time pausing (a behavior that seems to improve anti-predator vigilance) when away from forest cover than when traveling back towards forest cover (McAdam and Kramer, 1998). Experimental evidence also support the predicted relationship between predatory risk and plant cover. Thus, red-backed voles (*Clethrionomys gapperi*) and northern pygmy gerbils (*Gerbillus*

**Table 1**

Non-phylogenetic component of group size (estimated through autocorrelation) of hystricognath rodents that dig ( $n = 10$ ), and that of species that do not dig subterranean burrows ( $n = 16$ )

Branch length algorithm	Alpha parameter	Burrow diggers (mean $\pm$ SD)	Non-burrow diggers (mean $\pm$ SD)	One-tailed $p$ -value
Constant length	fixed	.08 $\pm$ .26	-.05 $\pm$ .13	.045
	estimated	.08 $\pm$ .25	-.05 $\pm$ .13	.039
Grafen's method	fixed	.08 $\pm$ .25	-.05 $\pm$ .13	.053
	estimated	.09 $\pm$ .25	-.05 $\pm$ .13	.038
Pagel's method	fixed	.08 $\pm$ .26	-.05 $\pm$ .13	.049
	estimated	.08 $\pm$ .25	-.05 $\pm$ .13	.039

Comparisons are made for three branch length algorithms, and for two states of the alpha parameter (see Methods). Statistical contrasts were made with the use of one-tailed Student's  $t$  tests.

*pyramidum*) are less vulnerable to mammalian predators when in patches of greater density of cover than in patches of less cover (Kotler et al., 1991, 1992; Longland and Price, 1991; Wywalowski, 1987). Indeed, northern pygmy gerbils (*G. al-lenbyi* and *G. pyramidum*) limit their activity to safer shrub microhabitat when direct risk from aerial predators is increased, but they switch to using open, less protected patches when such predation risk decreases (Abramsky et al., 1996).

Our finding that predatory risk does not explain any variation in group size across cursorial hystricognath species does not negate that this factor may have influenced group-living of some particular species, as it occurs in other rodents (Hoogland, 1981; Kildaw, 1995). Thus, group-living capybaras (*Hydrochaeris hydrochaeris*) seem to rely on selfish herd effects (Hamilton, 1971), and group defense to decrease their predatory risk. In these rodents, individuals located at the periphery of a group devote more time to scan their surroundings than individuals at more central positions (Yáber and Herrera, 1994), and groups coordinate themselves to protect juveniles from the attack of feral dogs (Macdonald, 1981). Besides, overall group alertness has been shown to increase with group size in capybaras and degus (Vásquez, 1997; Yáber and Herrera, 1994), which may result in increased probabilities of detecting an approaching predator (e.g., Hoogland, 1981).

### Group-living and parental care

The observation that group size of large sized hystricognaths tended to be larger than that of small sized species gave initial support to the extended parental investment hypothesis. However, our finding of no significant association between group size and time to first reproduction contradicted the hypothesis. One can criticize this conclusion as the extended parental investment hypothesis has been posed in a context of social complexity rather than group size (Armitage, 1981, 1999; Blumstein and Armitage, 1998). However, additional considerations also point toward the unimportance of breeding constraints during the evolution of hystricognath group-living. The extended parental investment hypothesis is posed to explain the evolution of group-living among ground squirrels and marmots (Sciuridae), where social complexity has been shown to increase with body size and with time to first reproduction (Armitage, 1981, 1999; Blumstein and Armitage, 1998). Time to first reproduction in these rodents ranges from 1 year in the least social sciurids to 2–3 years in the most social species (Blumstein and Armitage, 1998). By contrast, most hystricognaths considered in this study are sexually ma-

ture before their first year of life (Appendix). Only the males of plains vizcachas and the large sized male and female capybaras attain sexual maturity within one to 1½ years old (Jackson, 1989; Mones and Ojasti, 1986; Weir, 1971). Such differences cannot be attributed to body size differences as mass of sciurids ranges from 100 g up to slightly more than 7 kg (Armitage and Blumstein, 2000), whereas size of hystricognaths used in this study goes from near 200 g to near 60 kg (Appendix). Finally, hystricognath rodents generally produce offspring that is more precocial than other similarly sized rodents, including sciurids (Eisenberg, 1981; Künkele and Trillmich, 1997). All of these considerations suggest that breeding constraints hypothesized to favor group-living in the sciurid rodents seems much less likely to apply in the case of New World hystricognaths.

### Group-living and body size

The observed relationship between body mass and group size could be a secondary effect of an association between body size and the size of brain's neocortex. The size of brain, including the neocortex, of mammals increases with body size (Gittleman, 1986; Harvey et al., 1980; Mace et al., 1981), and the neocortex in turn tends to be correlated with group size (Dunbar, 1995). The size of neocortex is suggested to limit the number of social relationships an individual can keep track of within its social group (Dunbar, 1992, 1995, 1996; Gittleman, 1986). Interestingly, a preliminary comparison using a few species of New World hystricognaths shows that the neocortex of the most social species is larger than that of the least social species (Bee de Speroni, 1995).

### Future prospects

Our study provides a starting point to begin unraveling the evolutionary causes of group-living in the New World hystricognaths. Nonetheless, future analyses should address some pending issues. First, our analysis is about group size but the ultimate goal should be about social complexity. Second, phylogenetic information about New World hystricognaths is still incomplete. Both the autocorrelation and the independent contrasts methods may lose power in detecting significant trends when phylogenies are not well resolved (e.g., when the number of species is < 40, or when soft polytomies are present; Díaz-Uriarte and Garland, 1998; Garland and Díaz-Uriarte, 1999; Martins, 1996; Martins and Hansen, 1996; Purvis et al., 1994). Indeed, absence of well resolved phylogenies may

## APPENDIX

### Life history, ecological, and behavioral traits of cursorial and semi-fossorial New World hystricognath rodents

Family (subfamily)/species name (common name)	Body mass (g)	Time to first breeding (years)	Typical habitat and its rank of plant cover	Burrow digging	Group size (number of adult group members)	Sources
Abrocomidae						
<i>Abrocoma bennetti</i> (common chinchilla rat)	220–307	?	shrublands (5)	yes	2–10	24, 38
Agoutidae						
<i>Agouti paca</i> (paca)	4300–10500	0.75 (♀) 1.00 (♂)	open and dense forests (6–7)	yes	1–2	11, 37
Capromyidae (Capromyinae)						
<i>Geocapromys brownii</i> (Jamaican hutia)	1000–2000	1.00 (♀)	exposed limestone and shrublands (2–5)	no	2–6	2, 11

## APPENDIX, continued

Family (subfamily)/species name (common name)	Body mass (g)	Time to first breeding (years)	Typical habitat and its rank of plant cover	Burrow digging	Group size (number of adult group members)	Sources
<i>Geocapromys ingrahami</i> (Bahaman hutia)	660–755	?	exposed limestone and shrublands (2–5)	no	1–3	2, 6, 16
Caviidae (Caviinae)						
<i>Cavia aperea</i> (wild cavy)	450–795	0.23 (♀)	grasslands, rocky areas (2)	no	5–10	38, 43, 44, 51
<i>Kerodon rupestris</i> (rock cavy)	900–1000	0.22 (♀) 0.32 (♂)	arid scrub and rock outcroppings (3)	generally no	4–5	21, 25, 28, 34
<i>Microcavia australis</i> (desert cavy)	248–326	0.23 (♀)	thorn bush (2–3)	yes	4–38	7, 20, 42, 43
<i>Microcavia niata</i> (mountain cavy)	190–380	?	altiplano boags (2)	yes	4–17	29
Caviidae (Dolichotinae)						
<i>Dolichotis patagonum</i> (mara)	9000–16000	0.66 (♀)	arid scrubs (2–3)	yes	2–30	13, 27, 44, 46, 49
<i>Dolichotis salinicola</i> (dwarf mara)	1000–2200	?	thorn scrub (3)	yes	≥2	19, 20, 25, 26, 34
Chinchillidae						
<i>Chinchilla lanigera</i> (Chilean chinchilla)	390–500	0.66 (♀♂)	desert scrub (2–3)	generally no	≥2	31, 32, 34, 38, 41, 52
<i>Lagidium peruanum</i> (Peruvian vizcacha)	1220–1360	0.58–1.00 (♀♂)	dry and open pampas (2)	no	2–24	36, 38
<i>Lagostomus maximus</i> (plains vizcacha)	3520–8840	0.59–0.69 (♀) 1.00–1.40 (♂)	open pampa and thorn scrub (2–3)	yes	1–17	4, 5, 17, 18, 22, 45
Dasyproctidae						
<i>Dasyprocta fuliginosa</i> (black agouti)	3500–6000	?	rainforest (7)	no	1–2	11
<i>Dasyprocta leporina</i> (red-rumped agouti)	3000–5900	0.50 (♀)	forests (6–7)	no	2	8, 11, 52
<i>Dasyprocta mexicana</i> (Mexican black agouti)	2000–4000	?	rainforest (7)	no	1–2	11, 39
<i>Dasyprocta punctata</i> (Central American agouti)	3000–5200	0.97 (♀)	rainforest (7)	no	1–2	9, 11, 14, 30, 47
<i>Myoprocta acouchy</i> (red acouchy)	1050–1450	0.68 (♀)	rainforest (7)	no	1	11, 19
<i>Myoprocta exilis</i> (green acouchy)	800–1200	?	rainforest (7)	no	1–2	8, 19, 34
Dinomyidae						
<i>Dinomys branickii</i> (pacarana)	10000–15000	?	rainforest (7)	no	1–5	11, 34, 53
Echimyidae (Eumysopinae)						
<i>Proechimys guairae</i> (spiny rat)	150–550	0.16 (♀) 0.25 (♂)	dense forests (7)	no	1	10, 11, 52
<i>Thrichomys apereoides</i> (punaré)	300–400	0.25 (♀)	rocky scrublands (5)	no	1	1, 28, 34, 40, 48
Hydrochaeridae						
<i>Hydrochaeris hydrochaeris</i> (capybara)	35000–65000	1.5 (♀♂)	savanna (4)	no	5–14	14, 15, 23, 33
Octodontidae						
<i>Octodon degus</i> (common degu)	170–260	0.50	open thorn bush savanna (3)	yes	3–7	12, 19, 20, 52
<i>Octomys mimax</i> (hairy-tailed rat)	121–144	?	desert scrub, rocky areas (2–3)	yes	1	24, 38, 50
<i>Tympanoctomys barrerae</i> (red vizcacha rat)	52–91	?	sand basins and dunes (1)	yes	1	3, 27, 35, 38

explain partially why we almost lack modern comparative analyses of rodent group-living and social systems (see Blumstein and Armitage, 1998 for an exception), which contrasts with the situation of mammals other than rodents (Brashares et al., 2000; Di Fiore and Rendall, 1994; Geffen et al., 1996). We hope our study will stimulate others to fill these gaps.

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Habitats are ranked according to the amount of plant cover, from no plant cover (1) to the highest amount of plant cover (7). Question marks indicate uncertainties in the data source. Sources: (1) Alho (1982), (2) Anderson et al. (1983), (3) Bozinovic and Contreras (1990), (4) Branch (1993b), (5) Branch (1993a), (6) Clough (1972), (7) Contreras and Roig (1978), (8) Dubost (1988), (9) Eisenberg (1989), (10) Emmons (1982), (11) Emmons and Feer (1997), (12) Fulk (1976), (13) Harris (1998), (14) Herrera and Macdonald (1987), (15) Herrera and Macdonald (1989), (16) Howe (1974), (17) Jackson (1989), (18) Jackson et al. (1996), (19) Kleiman (1970), (20) Kleiman (1974), (21) Lacher (1981), (22) Llanos and Crespo (1952), (23) Macdonald (1981), (24) Mann (1978), (25) Mares and Ojeda (1982), (26) Mares et al. (1981), (27) Mares et al. (1989b), (28) Mares et al. (1989a), (29) Marquet et al. (1993), (30) Meritt (1983), (31) Miller and Rottmann (1976), (32) Mohlis (1983), (33) Mones and Ojasti (1986), (34) Nowak (1999), (35) Ojeda et al. (1996), (36) Pearson (1948), (37) Pérez (1992), (38) Redford and Eisenberg (1992), (39) Reid (1997), (40) Roberts et al. (1988), (41) Rodríguez (1988), (42) Rood (1970), (43) Rood (1972), (44) Rood and Weir (1970), (45) Weir (1971), (46) Silva and Downing (1995), (47) Smythe (1978), (48) Streilein (1982), (49) Taber and Macdonald (1992), (50) Torres-Mura JC (personal communication), (51) Weir (1970), (52) Weir (1974), (53) White and Alberico (1992), (54) Yáñez (1976).

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