

A review of the evolutionary causes of rodent group-living

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I analyze and summarize the empirical evidence supporting alternative hypotheses posed to explain the evolution of rodent group-living. Eight hypotheses are considered: two rely on net fitness benefits to individuals, five rely on ecological and life-history constraints, and one uses elements of both. I expose the logic behind each hypothesis, identify its key predictions, examine how the available evidence on rodent socioecology supports or rejects its predictions, and identify some priorities for future research. I show that empirical support for most hypotheses is meager due to a lack of relevant studies. Also, empirical support for a particular hypothesis, when it exists, comes from studies of the same species used to formulate the original hypothesis. Two exceptions are the hypothesis that individual rodents live in groups to reduce their predation risk and the hypothesis that group-living was adopted by individuals to reduce their cost of thermoregulation. Finally, most hypotheses have been examined without regard to competing hypotheses and often in a restricted taxonomic context. This is clearly an unfortunate situation given that most competing hypotheses are not mutually exclusive. I suggest that in the future comparative approaches should be used. These studies should examine simultaneously the relevance of different benefits and constraints hypothesized to explain the evolution of rodent sociality.

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Introduction

Individuals from different species of invertebrates and vertebrates form groups with other conspecific individuals (Wilson 1975, Lott 1991). Such animal groups may form due to the action of physical forces and to the attraction of individuals to the same external stimulus (Parrish *et al.* 1997). In addition, animal groups may form and persist due to the mutual attraction of individual members, even though the extent of social interaction and cooperation among them may vary markedly across species (Parrish *et al.* 1997, Romey 1997). Thus animal groups may vary in size, ranging from temporary associations and aggregations to relatively stable units (Lott 1991, Lee 1994, Parrish *et al.* 1997). Fidelity to the group and genetic relatedness among individuals within such groups also may vary widely, which will in turn influence the nature of social interactions among group members (ie from cooperation to competition; Hoogland 1995, Parrish *et al.* 1997).

Understanding the functional aspects of group-living (or sociality) is one main research goal of sociobiology and behavioral ecology. To accomplish this, it is useful

to consider that several factors may prevent the formation of groups, imposing fitness costs to group members. Such costs may include increased transmission of parasites and diseases, increased aggression and competition for resources, infanticide, or cuckoldry (Hoogland 1979a, 1985, Armitage 1988, Caro 1989, Macdonald and Carr 1989, Davies *et al.* 1991, Müller and Birkhead 1993, Van Vuren 1996). Thus, one would predict the existence of benefits acting to overcome these inherent disadvantages, or constraints, that force individuals to live socially.

Among rodents (Rodentia), social systems range from solitary-living species to colonial (gregarious) and social species (Wilson 1975, Nowak 1999), in which several individuals interact frequently, share feeding areas, a territory, and often a den or a burrow system (Armitage and Johns 1982, FitzGerald and Madison 1983, Rayer 1988, Salvioni 1988, Ögren *et al.* 1989a, Waterman 1995, Lacey *et al.* 1997, Burda *et al.* 2000). Several hypotheses have been suggested to explain the origin and maintenance of rodent group-living. Whereas some rely more heavily on the existence of net fitness benefits to individuals, others emphasize the influence of constraints (see below). Since no comprehensive overview that considers all major hypotheses is available, the main objective of this article is to provide such a review. For each hypothesis, I identify its key predictions, examine how the available evidence on rodent socioecology supports or rejects these expectations, and identify some priorities for future research. I restrict my analysis to those more comprehensive hypotheses that might help explain variation of rodent sociality across species. Space given to each hypothesis reflects differences in the amount of information available to each. Although I hereafter consider each hypothesis in isolation, they should not be regarded as mutually exclusive. In fact, evidence from other animal groups (eg social hymenopterans and isopterans) shows that group-living evolved in response to a variety of contributing life-history, behavioral, and ecological factors and preconditions (Andersson 1984, Thorne 1997).

Throughout the text I refer to species (or populations) that are *more or less* social than others. A note of caution is needed, however, as there has been no agreement regarding the most appropriate way of measuring the extent of sociality (Wilson 1975). For some, group size is an adequate estimate of sociality (Bekoff *et al.* 1981, Hoogland 1981, Pulliam and Caraco 1984, Dunbar 1996, Faulkes *et al.* 1997, Beauchamp 1998, Jarvis *et al.* 1998). To others, an index of sociality must also include the nature, number, and stability (ie complexity) of interactions among group members (Crook *et al.* 1976, Dunbar 1989, Lee 1994, Blumstein and Armitage 1998, Pellis and Iwaniuk 1999, Yoerg 1999). Although it seems safe assuming that the number of social interactions will increase with the number of group members (Wilson 1975, Blumstein and Armitage 1998), it is not clear how the nature and stability of these interactions will vary with group size. For those studies dealing with differences in the extent of sociality between two or more species or populations, I present the evidence using the original measure of sociality employed by the authors.

Hypotheses of rodent sociality: benefit-based models

The resource-defense hypothesis

Group-living individuals may become more efficient at defending resources than solitary-living conspecifics (Wrangham 1980, Macdonald 1983). That is, the per capita amount of resources attained by an individual should increase with the extent of sociality (Table 1). In the case of rodents, resources may include breeding space, feeding areas, or burrows (King 1984, Slobodchikoff 1984, Armitage 1986, 1998). Under the resource-defense hypothesis, sociality should increase with the abundance and patchiness of resources (Table 1; Slobodchikoff 1984). In contrast, when resources are scarce and uniformly distributed, resource defense becomes energetically unfeasible and solitary-living is favored (Slobodchikoff 1984).

Support of the resource-defense hypothesis comes from changes recorded to group size and social structure of semifossorial Gunnison's prairie dogs *Cynomys gunnisoni* after manipulations of their food supply. Thus, when abundance and patchiness of food are increased (by adding seeds), the feeding territory of each prairie dog group 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 group territories increases and the number of animals per group decreases (Slobodchikoff 1984). In addition, relatively large-sized groups of prairie dogs prevail at areas where food resources are patchily distributed, whereas small-sized groups prevail at areas where food resources are uniformly distributed (Travis and Slobodchikoff 1993, Travis *et al.* 1995). Addition of patchily distributed food resources also increases intrasexual home range overlap (ie aggregation) among female grey-sided voles *Clethrionomys rufocanus* (Ims 1987) and female California voles *Microtus californicus* (Ostfeld 1986). In the case of male grey-sided voles, experimental clumping of sexually receptive females (a resource to male voles) induces aggregation (Ims 1988). Other supporting evidence includes an increase in the territory size defended by social Mongolian gerbils *Meriones unguiculatus* (Øgren *et al.* 1989a) and capybaras *Hydrochaeris hydrochaeris* (Herrera and Macdonald 1987, 1989; although see Jorgenson 1986) with the number of group members, which suggests that overall availability of resources increases with group size. However, that per capita access to critical resources of social gerbils and capybaras increases with the size of their territory needs to be demonstrated. Other aspects of gerbils' behavior provides further support to the importance of food resources. Thus, upon the experimental addition of grain for hoarding, more group members become active in the defense of the territory (Øgren *et al.* 1989b). Indeed, most group members take part in hoarding, and the grain is always brought to common caches (Øgren *et al.* 1989b). The resource-defense hypothesis also is supported by the habits of some species to aggregate at spatially clumped rock outcrops, which seems critical for their survival and successful breeding. Such is the case of bushy-tailed wood rats *Neotoma cinerea* (Moses and Millar 1992), and possibly rock cavies *Kerodon rupestris* (Lacher 1981)

Table 1. Predictions of hypotheses posed to explain rodent group-living, and the features of tests made to examine them. Only studies directly addressing a particular hypothesis are listed. Upper script letter *a* indicates studies not controlling for the influence of phylogeny, whereas upper script letter *b* indicates that comparisons could be regarded as across-species if each of the four chromosomal forms of the *Spalax ehrenbergi* complex involved are elevated to species category. 1 – Armitage (1981), 2 – Arnold (1990a), 3 – Bazin and MacArthur (1992), 4 – Bennett *et al.* (1991), 5 – Berteaux *et al.* (1996), 6 – Blumstein and Armitage (1998), 7 – Blumstein and Arnold (1998), 8 – Ebensperger and Bozinovic (2000b), 9 – Ebensperger and Cofré 2001, 10 – Faulkes *et al.* (1997), 11 – Ganem and Nevo (1996), 12 – Gębczyński (1969), 13 – Getz and McGuire (1997), 14 – Hoogland (1979a), 15 – Hoogland (1979b), 16 – Hoogland (1981), 17 – Jones (1993), 18 – Kildaw (1995), 19 – Koprowski (1996), 20 – Layne and Raymond (1994), 21 – Madison *et al.* (1984), 22 – Manning *et al.* (1995), 23 – Moinard *et al.* (1992), 24 – Morton (1978), 25 – Nevo *et al.* (1992), 26 – Slobodchikoff (1984), 27 – Spinks *et al.* (1998), 28 – Tertilt (1972), 29 – Travis and Slobodchikoff (1993), 30 – Travis *et al.* (1995), 31 – Yáber and Herrera (1994).

Hypothesis	Prediction	Nature of test			Authority
		Type of comparison	Estimate of sociality used	Type of evidence	
1	2	3	4	5	6
Benefit-based models					
Resource-defense	Sociality increases with patchiness of critical resources Per capita resources attained by group members increase with sociality	within-species none	group size	supportive	26, 29, 30
Predatory risk	Sociality increases with riskiness of habitat	across-species	group size	negative	9
(‘many eyes’)	Predator detection ability increases with sociality	within-species	group size	supportive	16
(‘selfish-herd’)	Predatory risk varies with location within groups	within-species	group size	supportive	15, 16, 18, 31
(‘dilution’)	Predatory risk decreases with sociality after alertness and spatial location are controlled for	none			
(‘group defense’)	Chance of defeating a predator increases with sociality	within-species	group size	supportive	22
Social thermoregulation	Sociality more frequent in species of colder habitats Sociality increases during cold seasons Thermoregulation cost decreases with sociality	none within-species within-species	group size group size group size	supportive negative supportive negative	19, 20, 21, 24 13 2, 3, 12, 23, 28 5, 7
Constraint-based models					
Aridity food distribution	Sociality increases with aridity of habitat Sociality increases with patchiness of food resources	across-species across-species	group size group size	supportive supportive	10 ^(a) 10 ^(a)

hypothesis, the precise mechanism postulated by this hypothesis is not. Thus lagoons (ie single rich feeding patches) are not actively defended from other mara groups as predicted by the model (Taber and Macdonald 1992).

Seasonal changes in the size of capybara groups also seem not to support the resource-defense hypothesis. Capybaras depend upon water to sustain their food plants, to thermoregulate, and to seek refuge against predators (Macdonald 1981, Herrera and Macdonald 1989). Capybara groups actively defend water pools or their shoreline against other such groups throughout the wet season, when lagoons are more abundant and evenly distributed (Herrera and Macdonald 1987, 1989). However, when pools become scarce and patchy, group territoriality relaxes and the size of capybara groups seems to increase (Herrera and Macdonald 1987).

Further disagreement with the resource defense hypothesis comes from the spacing behavior of field voles *Microtus agrestis*. Both males and females of this species tend to live solitarily (Erlinge *et al.* 1990), and manipulations increasing the abundance and patchiness of sexually active females either decrease or have no influence on the aggregation by the males (Nelson 1995). Other evidence conflicting with the resource defense hypothesis includes the observation that group size of golden marmots *Marmota caudata* is unrelated to availability of food resources (Blumstein and Foggin 1997), and that wild guinea pigs *Cavia aperea* forage in groups even though food resources (grasses and forbs) appear to be evenly distributed (Rood 1972).

Carefully planned manipulative studies to examine the resource-defense hypothesis are needed. In addition, emphasis should be given to using comparative approaches to examine the extent of group-living across species. To accomplish this, however, it seems critical to identify the appropriate correlates of resource patchiness.

The predatory risk hypothesis

Individuals may live in groups to reduce their risk of predation (Alexander 1974, Treisman 1975, Van Schaik 1983, Alexander *et al.* 1991). Reduction of predation risk may occur by different mechanisms, including: (a) enhanced ability to detect predators (the 'many eyes effect'), (b) individuals locating themselves such that other group members become more vulnerable to attacks (the 'selfish herd effect'), (c) grouped individuals repelling predators more efficiently than solitary-living animals (ie group defense), (d) or simple dilution of per capita risk (Hamilton 1971, Pulliam 1973, Bertram 1978, Pulliam and Caraco 1984, Romey 1997). Accordingly, predictions by the predatory risk hypothesis will vary according to the particular mechanism postulated. If the many eyes effect plays a role, animals in larger groups are expected to detect predators sooner than individuals of smaller groups (Table 1). If the selfish herd effects predominate, per capita risk should vary with the location of individuals within groups (eg higher predatory risk at the edges of a group), and individuals are expected to compete for attaining those less risky locations (Table 1). Under the simple dilution effect, per capita risk is expected to

decrease with increasing number of group members (ie independently of an individual's location and of changes in the overall alertness of group members; Table 1). Lastly, under the group defense mechanism, an individual's success in repelling a predator should increase with the number of defendants nearby (Table 1). In addition, the predatory risk hypothesis predicts that sociality should prevail among species in riskier habitats (Table 1). Riskiness of habitat might be expected to increase with the abundance of local predators, and with decreasing amount of plant cover (Kleiman 1974, Dunbar 1989).

Studies on rodent behavior generally support that per capita risk of predation decreases with increasing group size. Thus, grouped bank voles *Clethrionomys glareolus* and yellow-necked mice *Apodemus flavicollis* seem to be attacked less often by weasels than solitary individuals, and individual voles and mice are killed less often when in groups (Jędrzejewski *et al.* 1992). Solitary voles (*Microtus epiroticus*) are killed faster by kestrels than grouped voles, although no such effect seems to occur in the field vole (Hakkarainen *et al.* 1992). The many-eyes effect is supported by the observation that large-sized groups of black-tailed prairie dogs *Cynomys ludovicianus* and white-tailed prairie dogs *Cynomys leucurus* detect predators sooner than prairie dogs of smaller groups (Hoogland 1981). Similarly, red-tailed squirrels *Sciurus granatensis* respond more quickly to human predators when foraging in groups than when foraging solitarily (Heaney and Thorington 1978). The behavior of prairie dogs also suggests a role for dilution. Prairie dogs forage farther from the nearest burrow entrance (ie a refuge to escape from predators) when density of above-ground individuals increases (Devenport 1989). The occurrence of selfish herd effects seem to be supported by the behavior of black-tailed prairie dogs, yellow-bellied marmots *Marmota flaviventris* and capybaras. In these rodents, individuals located at the periphery of a group devote more time to vigilance than individuals at more central positions (Armitage 1962, Svendsen 1974, Hoogland 1979b, 1981, Yáber and Herrera 1994). In fact, prairie dogs forage nearer the center of their foraging group when group size is experimentally reduced (Kildaw 1995). Whether the risk of predation is higher in peripheral, as compared with central, locations remains to be demonstrated.

Preliminary evidence also supports the possibility that rodents use active group defense to decrease their per capita risk. Groups of capybaras coordinate themselves to protect juveniles from the attack of feral dogs (Macdonald 1981). Belding's ground squirrels *Spermophilus beldingi* chase weasels inside their colony (Turner 1973, Robinson 1980), and mobbing of reptilian predators has been detected in black-tailed prairie dogs (Loughry 1987), California ground squirrels *Spermophilus beecheyi* (Owings and Coss 1977, Owings *et al.* 1977), and Cape ground squirrels *Xerus inauris* (Waterman 1997). Active group defense also seems a strategy to deter conspecific intruders. Female house mice *Mus musculus* and Belding's ground squirrels that share their nest or territory with conspecifics (usually relatives) suffer less infanticide than individuals that do not do so (Sherman 1980, Manning *et al.* 1995).

Several aspects of rodent behavior and ecology support an inverse relationship between the amount of plant cover and predatory risk. Thus, wild guinea pigs aggregate more at places with decreasing height of vegetation (Cassini and Galante 1992), and white-tailed prairie dogs, which live in smaller, less densely populated groups than do black-tailed ones, are located in places with more protective cover (Hoogland 1981, 1995). Guinea pigs, spiny rats *Proechimys* sp., and California ground squirrels seek shrub cover upon the approach of potential (terrestrial or aerial) predators (Rood 1972, Emmons 1982, Sherman 1985, Hanson and Coss 1997). When exposed to potential predators, North American porcupines *Erethizon dorsatum* foraging in open habitats move to plant cover more frequently than porcupines foraging in more vegetated habitats (Sweitzer and Berger 1992). White-footed mice *Peromyscus leucopus*, California ground squirrels, grey squirrels *Sciurus carolinensis*, and guinea pigs spend less time foraging in patches with less plant cover (Lima *et al.* 1985, Newman *et al.* 1988, Barnum *et al.* 1992), and spend more time alert when foraging far from shrub or tree cover (Leger *et al.* 1983, Cassini 1991). Eastern chipmunks *Tamias striatus* and grey squirrels 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). The predicted relationship between predatory risk and plant cover also is supported by experimental evidence. Thus, red-backed voles *Clethrionomys gapperi* and Egyptian sand gerbils *Gerbillus pyramidum* are less vulnerable to mammalian predators when in patches of greater density of cover than in patches of less cover (Wywiałowski 1987, Kotler *et al.* 1991, 1992, Longland and Price 1991). More interestingly, black-tailed prairie dogs avoid foraging at locations with short vegetation when group size is experimentally reduced (Kildaw 1995).

In spite of the above, some uncontrolled variables may potentially obscure the relationship between predatory risk and the amount of plant cover. First, vegetation may not only provide prey with hiding places but also visually obstruct and make predator detection more difficult to the prey (Armitage 1982, Metcalfe 1984, Lima 1987, 1990, Lima *et al.* 1987, Elgar 1989, Goldsmith 1990, Cassini and Galante 1992, Lazarus and Symonds 1992, Schooley *et al.* 1996, Funston *et al.* 1998, Sharpe and Van Horne 1998). Secondly, safety due to plant cover may vary with the type of predator (Treisman 1975). Thus plant cover may decrease prey vulnerability to aerial predators but it may increase prey vulnerability to mammalian and reptilian predators (Cassini and Galante 1992, Kotler *et al.* 1992, Pierce *et al.* 1992). Many social rodents use acoustic (eg alarm calls) as well as visual (eg tail flagging) signals to convey information on predatory risk to nearby conspecifics. Since plant cover may either favor or obstruct transmission of sounds (ie auditory signals) depending upon their height above ground and on the frequency of sounds emitted by the signaler (Morton 1975, Marten and Marler 1977, Hunter and Krebs 1979, Römer and Lewald 1992), vegetation might constrain the extent of rodent grouping through decreasing the efficiency of acoustic (and visual) signal transmission (Hoogland 1981). Indeed, reaction of common voles *Microtus arvalis* to the escape

behavior of nearby voles decreases with distance among group members if transmission of acoustic signals is experimentally impaired (Gerkema and Verhulst 1990).

At a mechanistic level, the above evidence supports that group-living decreases predatory risk of individual rodents. However, the overall role played by predators during the evolution of sociality across species remains debatable. Upon controlling for the influence of phylogeny, a comparative analysis of group-living across the New World hystricognaths did not support the predatory risk hypothesis (Ebensperger and Cofré 2001). Species that form relatively large social groups do not use particularly open, riskier habitats as might be expected under the predatory risk hypothesis (Table 1; Ebensperger and Cofré 2001). Whether such a discrepancy between comparative across species and within species approaches is unique to the New World hystricognaths will be resolved by comparative examination of group-living across other taxonomic groups such as murid and sciurid rodents.

The social thermoregulation hypothesis

The social thermoregulation hypothesis poses that individuals of endotherm species may form groups to reduce the energy needed to keep a constant body temperature (Madison 1984, West and Dublin 1984, Koprowski 1998). Such a reduced energy expenditure results from animals tightly huddling and thereby reducing their surface area to volume ratio compared with solitary animals (Canals *et al.* 1989, 1997). According to the social thermoregulation hypothesis, sociality, and communal nesting in particular, should prevail in species of relatively cold habitats, and at times when cold conditions predominate (Table 1). Besides, per capita energy expenditure should decrease with increasing number of den members (Table 1).

A first line of evidence supporting the social thermoregulation hypothesis includes the observation that energy expenditure by individual rodents decreases when they are allowed to huddle with conspecifics. Such an effect has often been recorded in the laboratory for individuals of several rodent families, including Bathyergidae (*Heterocephalus glaber* – Withers and Jarvis 1980), Muridae (*Abrothrix andinus*, *Abrothrix lanosus* – Canals *et al.* 1997; *Apodemus agrarius* – Tertilt 1972; *Apodemus flavicollis* – Fedyk 1971; *Clethrionomys glareolus* – Górecki 1968, Gębczyński 1969, Gębczyńska and Gębczyński 1971; *Eligmodontia typus* – Canals *et al.* 1997; *Meriones unguiculatus* – Contreras 1984; *Mus musculus* – Prychodko 1958, Stanier 1975, Martin *et al.* 1980, Contreras 1984; *Microtus townsendii* – Andrews *et al.* 1987; *Ochrotomys nuttali* – Springer *et al.* 1981; *Ondatra zibethicus* – Bazin and MacArthur 1992; *Peromyscus leucopus* – Glaser and Lustick 1975, Vogt and Lynch 1982; *Peromyscus maniculatus* – Andrews and Belknap 1986; *Phyllotis darwini* – Canals *et al.* 1989, 1997; and *Reithrodontomys megalotis* – Pearson 1960), Myocastoridae (*Myocastor coypus* – Moinard *et al.* 1992), Octodontidae (*Octodon degus* – Canals *et al.* 1989), and Sciuridae (*Ammospermophilus leucurus* – Karasov 1983; *Glaucomys volans* – Stapp *et al.* 1991).

Other evidence supporting the social thermoregulation hypothesis includes the observation that grouping and burrow sharing increases during winter (cold) as

compared with other times of year. This is the case of round-tailed ground squirrels *Spermophilus tereticaudus* (Dunford 1977), southern flying squirrels *Glaucomys volans* (Stapp *et al.* 1991, Layne and Raymond 1994), grey squirrels (Koprowski 1996), house mice (Morton 1978), meadow voles *Microtus pennsylvanicus* (Madison *et al.* 1984), red-backed voles *Clethrionomys rutilus* (West 1977), white-footed mice (Nicholson 1941), and wood mice *Apodemus sylvaticus* (Wolton 1985). Besides, body weight loss decreases, and survivorship increases with the number of nestmates in deer mice, white-footed mice, and free-ranging alpine marmots *Marmota marmota* (Sealander 1952, Andrews and Belknap 1986, Arnold 1990a).

The above evidence contrasts with observations showing that the formation of groups in prairie voles *Microtus ochrogaster* (Getz *et al.* 1993, Getz and McGuire 1997, but see Getz and Hofmann 1986, Getz *et al.* 1987) seems unrelated to seasonal changes in ambient temperature, and that survivorship of juvenile golden marmots during hibernation is unrelated to adult group size (Blumstein and Arnold 1998). More importantly, energy expenditures by meadow voles kept within outdoor enclosures (ie exposed to natural conditions of weather) do not differ from energy expenditures of voles kept in solitude (Berteaux *et al.* 1996). Clearly, further observations are needed to confirm that energy savings observed for species under laboratory conditions are indeed attained in the wild. Comparative studies need to assess if variation of rodent sociality across-species is related to weather conditions.

Hypotheses of rodent sociality: constraint-based models

The aridity food-distribution hypothesis

The aridity food-distribution hypothesis has been posed to explain variation in sociality across subterranean (fossorial) species of bathyergid (Bathyergidae) rodents. Fossorial bathyergids (mole-rats) carry out most of their activities below ground, including foraging on subterranean parts of plants (Jarvis and Bennett 1991, Lovegrove 1991, Jarvis *et al.* 1994). According to the aridity food-distribution hypothesis, foraging is costly. Foraging costs include the energy needed to dig tunnels and the risk of unproductive foraging (Lovegrove 1991, Jarvis *et al.* 1994). That risk is calculated from the probability distribution of the distances that would have to be burrowed before a suitable food item is found (Lovegrove and Knight-Eloff 1988). Risk of unproductive foraging is expected to increase with aridity of habitat as food resources become more patchy and rainfall more unpredictable (ie the period during which digging becomes possible, or less energetically costly; Jarvis and Bennett 1991, Lovegrove 1991, Jarvis *et al.* 1994, Jarvis *et al.* 1998). Thus, when food distribution is spatially clumped, rainfall is highly unpredictable, and the energetic cost of digging is high, solitary species would be unlikely to locate enough food to sustain themselves (Lovegrove and Wissel 1988, Jarvis *et al.* 1994, 1998, Lacey and Sherman 1997). The aridity food-distribution hypothesis predicts that sociality should be more common in species of more arid habitats, in species of

habitats with a more patchy distribution of food resources, and in species of habitats with hard soil conditions (Table 1). Also, individuals foraging in larger groups should locate food patches with a higher probability than individuals of smaller groups (Table 1).

The aridity food-distribution hypothesis is supported by observations showing that aridity may limit dispersal, colony formation, and foraging efficiency of mole-rats. Thus, immigration and emigration by common mole-rat *Cryptomys hottentotus hottentotus* colonies of xeric, arid sites are lower than those of common mole-rat colonies of mesic sites (Spinks *et al.* 2000). In addition, small colonies of Damaraland mole-rats *Cryptomys damarensis* are more likely to fail than large colonies, suggesting they are unable to dig tunnels long enough to sustain themselves during the draught season (Jarvis *et al.* 1998). Computer simulations suggest that spatially clumped food resources along with hard soil conditions (due to sporadic rainfall) interact to reduce foraging efficiency, but that increased group size coupled to cooperative foraging reduces the risk of unproductive foraging (Spinks and Plagányi 1999). In fact, naked mole-rats *Heterocephalus glaber* recruit other group members to food sources recently discovered by successful foragers (Judd and Sherman 1996), and common mole-rats store part of their food at central common caches for later consumption (Spinks *et al.* 1999). More direct support of the aridity food-distribution hypothesis comes from the observation that social but not solitary bathyergids tend to occur in xeric habitats (Jarvis *et al.* 1994, Faulkes *et al.* 1997), and that group size of mole-rat species increases with unpredictability of rainfall and with the size and patchiness of their food supply (Lovegrove and Knight-Eloff 1988, Faulkes *et al.* 1997). Nonetheless, the aridity food-distribution hypothesis is not supported by the observation that social mole-rats also occur in mesic areas of Africa (Wallace and Bennett 1998, Burda *et al.* 2000).

Future studies are needed to assess the mechanistic details of this hypothesis, according to which individuals in larger groups should locate food patches with a greater probability than individuals in smaller groups. Comparative studies need to consider fossorial rodents other than African bathyergids. One group of fossorial rodents for which we have relatively good data on its socio-spatial systems and habitat features is the North American geomyids (gophers). Other less well known but highly diverse rodents in terms of their social behavior and habitat features are the South American ctenomyids (tuco-tucos).

The life-history constraint hypothesis

Burda (1990) posed the life-history constraint hypothesis as an alternative to the aridity food-distribution hypothesis. According to Burda's model, sociality of bathyergid mole-rats is the result of selective pressures acting to reduce body size. A small body size in species with altricial young results in slow rates of development and breeding females being unable to store and mobilize enough body fat reserves. The combination of these two factors would result in solitary-living females unable to successfully rear their offspring (Burda 1990, Burda and

Kawalika 1993). Under the life-history constraint hypothesis, sociality should prevail in rodents that are small sized, with a reduced ability to store fat reserves, and with a low rate of postnatal growth (Table 1).

Some preliminary evidence supports the life-history constraint hypothesis. The two eusocial mole-rats, Damaraland mole-rats and naked mole-rats, are among the smallest Bathyergidae and Hystricognathi, and consequently, they have the longest developmental times of all rodents (Burda 1990, O'Riain and Jarvis 1998). In addition, a study using a larger number of bathyergid species confirmed that the pups of solitary genera grow and mature more rapidly than those of social genera (Bennett *et al.* 1991). Nonetheless, other evidence contradicts the life-history hypothesis. Autopsies of freshly captured reproductive females of solitary-living *Georychus* and of four species of social *Cryptomys* revealed fat deposits (Bennett *et al.* 1994). Overall, comparative studies controlling for phylogenetic relationships are strongly needed to re-examine predictions of this hypothesis. Again, the relatively high variation of body size found in the highly diverse South American ctenomyids (tuco-tucos) and in the North American geomyids could be used to test Burda's hypothesis.

The water-energy stress hypothesis

A critical pre-condition for group-living to evolve is social tolerance between individuals (Nevo 1995, Ganem 1998). It has been argued that such social tolerance may result from selection to decrease aggression of rodents of arid environments (Nevo *et al.* 1992, Ganem and Nevo 1996). This selection could result from an inverse relationship between aggression and water economy, and from a direct relationship between aggression and the level of glucocorticoids, which lead to energy mobilization and loss (Christian 1970, Ganem and Nevo 1996). Although these relationships between hormones and behavior were not considered in a context of explaining rodent sociality (Ganem 1998), a potential implication of them is that sociality could be the by-product of selection acting to increase water and energy conservation through decreasing aggressive behavior. If so, the water energy-stress hypothesis predicts that sociality should prevail in species of more arid habitats (where water and food availability are particularly limited, Table 1). In addition, less aggression is expected in the more social species as compared with the less social and solitary-living species (Table 1).

The biology, ecology, and behavior of subterranean blind mole-rats *Spalax ehrenbergi* (Spalacidae) support a link between aggression and glucocorticoid levels. These rats are found from cool and humid to warm and dry regions of the middle east area (Yahav *et al.* 1989). Aggression (ie social intolerance), as measured experimentally during staged dyadic encounters, is lower in the mole-rats of more arid regions as compared with those of mesic regions (Nevo *et al.* 1992, Ganem and Nevo 1996). Intensity of aggression by mole-rats during social encounters is correlated with increased levels of plasma corticosterone (a glucocorticoid; Ganem and Nevo 1996). Such enhancement of corticosterone is greater in mole-rats of

mesic areas than in mole-rats of arid regions (Ganem and Nevo 1996). A link between aggression and the level of glucocorticoids also seems to hold in the social guinea pig (Sachser and Lick 1991, Sachser 1998).

Evidence from other subterranean species does not support the water energy-stress hypothesis. Common mole-rats of arid regions show less social tolerance than mole-rats from mesic regions when confronted with conspecifics in dyadic encounters (Spinks *et al.* 1998). In addition, the expectation of decreased aggression in the more social species seems not to hold. Thus, the per capita rate of aggressive interactions within white- and black-tailed prairie dog, yellow-bellied marmot, and Olympic marmot groups generally increases with group or colony size (Barash 1973a, Armitage 1975, 1977, Hoogland 1979a, 1995).

At a mechanistic level, experimental evidence is needed to confirm that water and energy deprivation decreases overall aggressiveness. Future studies need to consider that less aggression may result from unconsidered benefits of sociality instead of selection acting directly to increase water and energy economy, and that some predictions by the water energy-stress hypothesis are shared by the aridity food-distribution hypothesis (Table 1). North American sciurids and heteromyids could be appropriate models to test predictions by the water energy-stress hypothesis.

The parental investment hypothesis

Among North American ground squirrels and marmots (Sciuridae), group-living is hypothesized to have evolved as a means of continuing reproductive investment beyond weaning (Armitage 1981, 1988). Sciurid social groups are often the result of offspring delaying dispersal (Michener 1983, Blumstein and Armitage 1998, Armitage 1999). Dispersal is more likely retarded in large sized species, which require extended times to reach adult size and sexual maturity, relative to the time at which food is available in the habitat. Longer times to reach sexual maturity in turn demands additional investment from the parents (Barash 1973a, 1974, 1989, Armitage 1981, 1988, 1999). According to the parental investment hypothesis, individuals of social species should exhibit a larger body size than individuals of solitary-living or less social species (Table 1). Secondly, time to reach sexual maturity is expected to be extended, and dispersal delayed in the large sized and more social species (Table 1). Finally, time at which food resources are easily available should be shorter in the habitat of more social species (Table 1).

The evidence supporting the parental investment hypothesis comes from comparisons of North American sciurids (Armitage 1981, Barash 1989, Blumstein and Armitage 1998), which is not surprising given that this group of rodents was the basis for the original argument (Barash 1974, Armitage 1981; Table 1). Thus, social complexity (ie sociality) of North American sciurids is positively correlated with body size, age to sexual maturity, and dispersal, but negatively correlated with the length of the growing season (Barash 1973a, 1974, 1989, Armitage 1981). Moreover, most of these relationships hold after controlling for the influence of phylogeny (Blumstein and Armitage 1998). For sciurids of temperate habitats, the

length of the growing season seems determined by the duration of snow cover (Svendsen 1974, Van Vuren and Armitage 1991). The biology of North American tree squirrels also seems supportive of the parental investment hypothesis. Tree squirrels are relatively small sciurids that do not delay reproduction beyond the first year, and as predicted, they tend to be solitary-living rodents (Heaney 1984, Koprowski 1998). The parental investment hypothesis also is supported by within species comparisons. Social interactions among yellow-bellied marmots of areas with relatively short growing seasons are less agonistic and more friendly (ie socially tolerant) than those among marmots of areas with longer growing seasons (Barash 1973b, 1989). Similarly, Gunnison's prairie dogs reach sexual maturity more rapidly, and disperse at a younger age at sites with more extended growing seasons than prairie dogs of habitats with shorter growing seasons (Rayor 1985). Lastly, the rate of amicable interactions within groups (a measure of sociality) of Columbian ground squirrels *Spermophilus columbianus* decreases with the length of the plant (food) growing season (Ritchie and Belovsky 1990).

In contrast to the above, however, within species variation in the social structure of North American woodchucks *Marmota monax* is not particularly supportive of the parental investment hypothesis. Sociality of woodchucks varies despite no differences in the length of active growing season (Meier 1992). Similarly, evidence from sciurids other than those from North America is debatable. That alpine marmots (group size ranges from 2–11 adults; Arnold 1990a) and golden marmots (group size ranges from two-seven adults; Blumstein and Arnold 1998) do not disperse before sexual maturity at the age of 2 (Arnold 1990b) and 3 years (Blumstein and Arnold 1998), respectively, is in accordance with the parental investment hypothesis. However, and contrary to predictions of this hypothesis, dispersal by alpine marmots is more frequent among offspring that have suffered higher mass loss during the previous winter, suggesting that weaker individuals are forced to leave (Arnold 1990b). Similarly, the parental investment hypothesis is not supported by the biology of Cape ground squirrels. Despite being social (group size ranges from one-four adults), these African sciurids reach adult size, reproductive maturity, and dispersal age at less than 1 year, and they are active throughout the entire year (Waterman 1995). Comparative studies including non-North American sciurids are strongly needed to assess the general relevance of the parental investment hypothesis to the origin and maintenance of sciurid sociality. Moreover, these studies should address simultaneously the importance that thermo-regulatory benefits (see below) may have in explaining group-living among ground-squirrels and marmots (Arnold 1990a, b, Meier 1992, Blumstein and Arnold 1998).

Regarding non-sciurid rodents, Jones (1993) made a preliminary examination (ie without controlling for phylogenetic relationships) of life-history variation across North American heteromyid species (pocket mice, kangaroo mice and rats). Social systems of heteromyids range from solitary (most species) to incipiently social forms (Jones 1993). Contrary to expectations by the parental investment hypothesis, sexual maturity is not particularly delayed in larger heteromyids as it

occurs in the sciurids (Jones 1993). Similarly, analysis of group-living across the New World hystricognath rodents did not support the parental investment hypothesis either (Ebensperger and Cofré 2001). Variation of group size across species seems unrelated to differences in the time to first reproduction (a measure of parental care given).

Hypotheses of rodent sociality: mixed models

The burrow-sharing hypothesis

Group-living also has been linked to life in long-lasting, expansible nests or microhabitats safe from predation (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, Reichman and Smith 1987, Kinlaw 1999). If naturally occurring refuges are limited, or if constructing a burrow is costly (Reichman and Smith 1987), animals may be forced to live in groups to share burrow use or minimize the cost of burrow construction (West 1977, Arnold 1990b, Jarvis and Bennett 1990, Powell and Fried 1992, Jackson 1999). Under the burrow-sharing hypothesis, sociality should prevail in species that regularly dig to construct and maintain a burrow system. Secondly, the per capita cost of burrowing should decrease with increasing sociality (Table 1). Thirdly, sociality is expected to increase whenever naturally occurring refuges are limited (Table 1).

The relationship between burrows and rodent social systems has received little attention (King 1984). This is puzzling given the evidence showing that burrowing may convey a relatively high energetic cost to individual diggers (Lovegrove 1989, Ebensperger and Bozinovic 2000a). The hillock mouse *Mus spicilegus* builds earthen mounds in autumn, which are then used communally by more than two parents to deposit and provision their immature offspring with grain (Muntyanu 1990, Garza *et al.* 1997). These mounds are large, take several days to build, and are provisioned with 3 to 5 kg of grain, and thus they are energetically costly (Muntyanu 1990). The observation of multiple individuals participating in mound building (Garza *et al.* 1997) suggests that hillock mice might live in groups to share the cost of constructing a burrow. Other social rodents in which group members communally dig their burrows include the semifossorial plains vizcachas *Lagostomus maximus* (Chinchillidae, Branch 1993).

Social structure of prairie voles ranges from solitary to communally nesting individuals (Getz *et al.* 1993, Getz and McGuire 1997), and they dig simple and complex underground burrow systems (Davis and Kalisz 1992). Burrows of communal groups are larger and more complex than burrows of male-female pairs (Mankin and Getz 1994). It remains to be assessed whether greater size and complexity of burrows provide direct benefits to their occupants. At first, the observation that common degus *Octodon degus* (Octodontidae) in groups do not

reduce their burrowing time compared with solitary diggers does not support the burrow-sharing hypothesis (Ebensperger and Bozinovic 2000b). However, the observation that degus in groups coordinate their digging and remove more soil per capita than solitary diggers suggests that social burrowing may reduce the cost of burrow construction in the long term (Ebensperger and Bozinovic 2000b). Similar arguments may apply to naked mole-rats (Lovegrove 1989), which also are capable of coordinating their digging behavior during burrowing (Jarvis and Sale 1971). Further support to a link between the habit of burrow digging and group-living comes from recent comparative analyses. Thus, species of New World hystricognath rodents that actively dig their own burrows form larger group sizes than small sized species that do not dig burrows (Ebensperger and Cofré 2001).

Evidence generally supports that resource availability influences philopatry of rodents (Garrett and Franklin 1988, Jones *et al.* 1988, Keane 1990, Boutin *et al.* 1993, Ribble 1992, Lambin 1994, Lurz *et al.* 1997, Gundersen and Andreassen 1998, Byrom and Krebs 1999, Solomon *et al.* 1999). However, evidence for a more specific connection between availability of burrows and philopatry (and sociality) is much more limited. Banner-tailed kangaroo rats *Dipodomys spectabilis* den individually in single mounds formed by a labyrinth of tunnels, which provide refuge against predators, extreme weather conditions, and sites for seed hoarding (Schroder 1979, Waser 1988). Although these rats live solitarily and defend these mounds from conspecifics throughout most of the year (Schroder 1979), mound sharing between mothers and weaned offspring is common. As might be expected, when unoccupied mounds are common, juveniles disperse earlier than usual (Waser 1988). Indeed, kangaroo rats disperse less under high population density than at low population density despite no changes in the number of mounds (Jones *et al.* 1988), which suggests that low availability of burrow systems induces philopatry and mound sharing. In addition, the formation of social groups by the close kin of female bushy-tailed wood rats has been related to a need for sharing highly clumped rock outcrops (ie den sites), which seems critical for over-winter survival and successful breeding of these rats (Moses and Millar 1992). In contrast, the behavior of water voles *Arvicola terrestris* seems not supportive of the burrow-sharing hypothesis. In grasslands, water voles rely heavily on the use of burrows to escape from predators (Jeppsson 1990), and even though these burrows seem limited and energetically costly to dig, water voles do not aggregate or share their use (Jeppsson 1990). Other evidence not supportive of the burrow-sharing hypothesis includes the observation that most subterranean rodents tend to be solitary and territorial rather than social (Nevo 1995, Lacey and Sherman 1997, Burda *et al.* 2000). Note, however, that formal comparative analyses including both fossorial and semi-fossorial species are not yet available.

Both the cost of burrow digging and the availability of burrows could potentially be manipulated in future studies. Besides experimental manipulation of habitat features, observed variations in the extent burrowing across species may provide data for comparative analyses. Forthcoming contributions aimed at examining the

burrow-sharing hypothesis also should consider the aridity food-distribution, and possibly the water energy-stress hypotheses as they share some predictions (Table 1).

Conclusions and future prospects

Both benefits and constraints seem to have played some role during the evolution of rodent social structure as it seems to be case of mammalian insectivores (Rychlik 1998), pinnipeds (Cassini 1999), primates (Janson and Goldsmith 1995, Di Fiore and Rendall 1994), and birds (Arnold and Owens 1999, Beauchamp 1999). However, discerning the relative importance of particular benefits and constraints across different rodent groups remains unclear. I suggest this is so because of many reasons. Firstly, empirical support to each competing hypothesis is generally meager. That is clearly the case of the resource-defense and the life-history constraint hypotheses, which have been rarely considered in studies other than those by their original authorities (Table 1). Secondly, such support, when it exists, often comes from a few studies using the same set of species whose differences in sociality need to be explained. This is particularly true in the case of the parental investment and the aridity food-distribution hypotheses (Table 1). The nature of such evidence provides, at best, a weak test of hypotheses. At a mechanistic level, the predatory risk hypothesis seems better supported than other models. In particular, evidence supporting the many eyes version of this hypothesis tends to be common and involves species in different taxonomic groups (Table 1). Another relatively well supported hypothesis is the social thermoregulation hypothesis (Table 1).

Thirdly, most hypotheses posed to explain rodent sociality have been treated in isolation or in a context of specific rodent species or groups. Such an oversimplification is unjustified for at least two reasons. First, most hypotheses considered in this review are clearly not mutually exclusive. For instance, rodents that forage in groups to reduce their predatory risk also may use huddling to reduce their energetic cost of thermoregulation when in their burrows. Second, hypotheses (eg the aridity-food distribution hypothesis) may share some predictions with competing arguments (eg the water energy-stress hypothesis, Table 1).

Although future studies examining the evolutionary origin and maintenance of rodent sociality must consider different explanations simultaneously, one should recognize that some hypotheses might be more pertinent to some groups of rodents than to others. For instance, researchers interested in the social behavior of fossorial rodents might need to focus their attention on the aridity food-distribution, the water-energy stress, or the life-history constraint hypotheses (among others) as valid alternatives. The predatory risk, and the resource-defense hypotheses might be more pertinent to semifossorial rodents.

Fourthly, the future examination of alternative hypotheses can be achieved either through the study of species used previously to generate the original

hypotheses, or through considering other, previously unexamined species and groups. The second alternative will provide stronger (more independent) tests of hypotheses (Lacey and Sherman 1997). Previously unconsidered rodents that may provide appropriate data for future comparisons include the Old World murids, the Palearctic and Ethiopian sciurids (Barash 1989, Nowak 1999), and the Neotropical “caviomorph” rodents (Ebensperger 1998). In particular, neotropical hystricognaths include species adapted to different modes of life; they are found in almost every type of habitat, and their social behavior ranges from solitary-living to highly gregarious (Eisenberg 1989, Nowak 1999, Redford and Eisenberg 1992). These features provide an excellent opportunity for comparative and manipulative studies (Ebensperger 1998, Ebensperger and Cofré 2001).

One other critical question that remains is distinguishing causes from consequences of rodent group-living (Burda *et al.* 2000). For example, once a group is formed to cope with a lack of available den sites or burrows, advantages to burrow mates may arise as a consequence of grouping, including a decreased cost of thermoregulation while resting in their shared burrows, or a higher ability to detect predators when foraging nearby. Once evolved then, group-living becomes part of the environment, which in turn may originate new selective pressures that influence an individual’s behavior (Cahan *et al.* 1999, Pellis and Iwaniuk 1999). Classical cost and benefit analysis may help establish if group-living is currently being maintained by natural selection (Krebs and Davies 1993, Alcock 1998). However, establishing that group-living renders net benefits (eg enhanced ability to detect predators) to group members through observational and experimental approaches does not demonstrate that such benefit was the origin of grouping. Some current benefits could be exaptations rather than true adaptations (Gould and Vrba 1982). One potential way to unravel the evolutionary origins of group-living is through the use of directional comparisons where the states of group-living (ie the trait of interest), along with the environmental features of contemporary forms, are contrasted with those previously reconstructed ancestral states (Harvey and Pagel 1991, Martins and Hansen 1996). Accuracy of directional analyses depends on having a well resolved phylogeny of the group of interest, as well as on an accurate reconstruction of ancestral character states. Absence of well resolved phylogenies may explain partially why we only recently began using modern comparative methods to examine rodent group-living and social systems (Table 1; see Blumstein and Armitage 1998, Ebensperger and Cofré 2001), which contrasts with the situation of other vertebrate groups such as birds (Dubois *et al.* 1998, Rolland *et al.* 1998, Arnold and Owens 1999, Beauchamp 1999) and mammals other than rodents (Gittleman 1989, Wrangham *et al.* 1993, Di Fiore and Rendall 1994, Janson and Goldsmith 1995, Geffen *et al.* 1996).

There is an increasing amount of evidence showing that the social systems of vertebrates exhibit phenotypic plasticity and variation across populations (Lott 1984, 1991). Thus, the spatial structure and grouping of many rodents vary with season, habitat conditions, and local density of conspecifics (Jannett 1978, Busher

et al. 1983, Getz and Hofmann 1986, Sachser 1986, Herrera and Macdonald 1987, Madison and McShea 1987, Armitage 1988, Ferron and Quellet 1989, Zwicker 1989, Jeppsson 1990, Wolff and Cicirello 1990, Ylönen 1990, Meier 1992, Taber and Macdonald 1992, Wauters and Dhondt 1992, Perrin *et al.* 1993, Agrell 1995, Salvioni and Lidicker 1995, Travis *et al.* 1995, Getz and McGuire 1997, Jackson 1999). Such variation may hinder future comparative analyses as most comparative techniques assume intraspecific variation in the trait of interest to be negligible (Martins and Hansen 1996). However, plasticity and variation across populations of social systems could be the subject of future comparative analyses in their own right (Ostfeld and Klosterman 1990, Lott 1991).

Finally, appropriate and widely accepted measures of sociality, and of any other behavioral trait, are critical to increase the value of comparative studies (Maher and Lott 1995, Keller and Perrin 1995, Burda *et al.* 2000). Most studies addressing some aspect of rodent sociality have considered group size as a measure of sociality (Table 1). Indeed, group size is a feature of social organization, which can be used to compare the complexity of different social systems (Wilson 1975, Pulliam and Caraco 1984). Moreover, data on group size are available for many rodents and mammals in general (Nowak 1999). However, how group size relates to other attributes of sociality such as the number, nature, and stability of social interactions, is unclear. The resolution of this matter may lie partially in the way individual fitness changes with group size (Avilés 1999).

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