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Source: *Journal of Mammalogy*, 92(1):12-20. 2011.

Published By: American Society of Mammalogists

DOI: 10.1644/09-MAMM-S-420.1

URL: <http://www.bioone.org/doi/full/10.1644/09-MAMM-S-420.1>

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Capybara social structure and dispersal patterns: variations on a theme

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Capybaras, (*Hydrochoerus hydrochaeris*) are large, herbivorous New World hystricomorphs, common in the seasonally flooded savannas of tropical and subtropical South America. In this paper we review the social structure and dynamics of capybaras across much of their geographic range. Wherever they have been studied capybaras live in groups. Capybara groups are stable social units composed of adult males and females (sex ratio biased toward females) with their young. A linear dominance hierarchy characterizes interactions among males, and the dominant male obtains most matings. Group sizes range from 6 to 16 adult members and vary with habitat characteristics and population density. At higher densities group sizes and the proportion of floaters (apparently unaffiliated animals; mostly males) increase. In 1 low-density location dispersal appears to occur in groups of both sexes, whereas in another location, where density is higher, males disperse and females are philopatric. We also discuss more conceptual issues (mostly proximate and ultimate mechanisms) that relate to intraspecific variation in social behavior in general, and capybaras in particular.

Key words: capybaras, dispersal, *Hydrochoerus hydrochaeris*, intraspecific variation, social structure

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DOI: 10.1644/09-MAMM-S-420.1

Intraspecific variation in social behavior has been a recurrent theme in vertebrate behavioral ecology for decades (Lott 1979). Such variation is important because selection for genetic variants in behavior, or for phenotypic plasticity in behavioral expression, can have significant consequences for social evolution: adaptability can be crucial in the face of changing ecological circumstances. In birds, for example, the presence of helpers at the nest is related to population density, availability of nest sites, and predation, as shown in the classic study of Seychelles warblers (*Acrocephalus sechellensis*) by Komdeur et al. (1995). In a mammalian herbivore, the pronghorn (*Antilocapra americana*), males were more territorial when resources (forbs) were more abundant and of higher quality (Maher 2000).

Among rodents in particular, intraspecific variation in social behavior is probably widespread but little studied. Tang-Martínez (2003) identified intraspecific variation as 1 of the most neglected but fundamental issues in the study of rodent sociality. In some cases this variation is transient phenotypic plasticity that depends on temporary ecological or demo-

graphic conditions (Randall et al. 2005; Verdolin 2009). In others the variation may have a genetic basis as a result of long-term selection in different types of habitats (Cushing et al. 2001; Roberts et al. 1998a). However, at present, the evidence does not indicate unambiguously sources of variation in most species.

Most examples of intraspecific variation that have been described in rodents come from temperate species. The best known example is the highly social prairie vole (*Microtus ochrogaster*), a species in which significant variation in social behavior has been reported for 3 populations in 3 different states in the United States (Tang-Martínez 2003). Specifically, these populations appear to vary in a large number of social and demographic variables. These variables include levels of affiliation, aggression, alloparenting, paternal care, group size, degree of monogamy and sexual dimorphism, home-range



size, and likelihood of philopatry rather than dispersal over longer distances (Cushing et al. 2001; Lonstein and DeVries 1999; Lucia et al. 2008; Roberts et al. 1998a, 1998b). The reasons for all of these differences are not well understood, but resource and habitat characteristics, including climate and resource abundance, might be important (Cushing et al. 2001; Roberts et al. 1998b).

Among sciurids, variation in social behavior has been reported in the yellow-bellied marmot (*Marmota flaviventris*—Armitage 1977) and among several populations of woodchucks (*Marmota monax*—Ferron and Oullet 1989; Meier 1992; Swihart 1992). In the latter species the degree of philopatry is greatest when resource abundance is high (Maher 2004, 2006). Population density, resource abundance, latitude, and climate all appear to affect intraspecific variation in social organization and behavior in the red squirrel (*Tamiasciurus hudsonicus*—Heaney 1984; Layne 1954; Smith 1968). In a highly social sciurid, Gunnison's prairie dog (*Cynomys gunnisoni*), the distribution of food resources (i.e., patchy versus uniform) affects the mating system (Travis et al. 1995).

Differences in population density, in turn almost certainly affected by resource availability, often have been associated with intraspecific variation in social structure in rodents. For instance, Lucia et al. (2008) have shown experimentally that prairie voles are more philopatric and form larger groups at higher densities. Dispersal patterns and social structure in the great gerbil (*Rhombomys opimus*) also depend on density (Randall et al. 2005).

In this paper we examine intraspecific variation in the social behavior and organization of capybaras (*Hydrochoerus hydrochaeris*; Rodentia: Hystricomorpha). As large, conspicuous animals living primarily in open habitat and with an economic value (Ojasti 1991), capybaras have been studied extensively, including their behavior and social structure. Ever since the pioneering work of Ojasti (1973), who provided several insights (subsequently corroborated) into the social structure of capybaras, a number of studies on the behavioral ecology of the capybara have been conducted, mostly in the Llanos of Venezuela (Azcárate 1980; Congdon 2007; Herrera and Macdonald 1987; Macdonald 1981; Salas 1999) but also in the Brazilian Pantanal (Alho and Rondon 1987; Schaller and Crawshaw 1981) and the Colombian Llanos (Perea and Ruiz 1977). Work in progress in the Esteros del Iberá in Argentina is providing additional data to complement the range of studies on the ecology and social behavior of capybaras (M. J. Corriale, pers. obs.). Although capybaras also are found along rivers in forested habitat, they have not been studied there.

Capybaras are the largest extant rodents, and as New World hystricomorphs (caviomorphs) they exhibit a number of interesting features such as large body size (about 50 kg as adults) and extremely precocious young: newborn capybaras can feed on grasses a few days or even hours after birth (Ojasti 1973). Capybaras always are found near water, which they use as a refuge from predators, for thermoregulation, and for

feeding, because many of the grasses they feed on are semiaquatic (Ojasti 1973). In this paper we review several features of the social structure of capybaras, including patterns of philopatry and dispersal, across both space and time and relate them to prevailing ecological conditions and population density. Much of the review is based on 3 studies (Congdon 2007; Herrera and Macdonald 1987, 1989; Salas 1999) carried out at sites a short distance (<50 km) from each other and in the same general ecosystem, seasonally flooded savannas. Moderate differences in resource distribution and abundance between sites and studies are associated with marked differences in density, intragroup sex ratio, and dispersal patterns.

Any attempt to summarize variation in capybara social behavior and organization is a challenge because the plasticity of their behavior makes generalization difficult. Nonetheless, the existing studies now make it possible for us to try to integrate the available information. We 1st describe and compare several aspects of capybara social structure, then discuss conceptual issues relevant to intraspecific variation in general, and end with final remarks and suggestions for further studies.

CAPYBARA SOCIAL DYNAMICS

Wherever capybaras have been studied they are social and live in groups. Capybara groups are composed of both males and females with a bias toward females (see below), and the groups are closed and relatively stable social units. Identified individuals seen together long enough to be classified as belonging to a group remain so for months or even years at a time (Herrera and Macdonald 1987; Perea and Ruiz 1977; Salas 1999; Schaller and Crawshaw 1981; E. R. Congdon, Drexel University, pers. obs.). Individuals seen in >1 territory that appeared not to be stable members of any single social unit are called floaters.

A striking, and up to now invariable, feature of the capybara social system is the strictly linear dominance hierarchy among males, resulting from stereotyped agonistic interactions (E. R. Congdon, pers. obs.; Herrera and Macdonald 1993; Salas 1999). The dominant male tends to be bigger and have a larger snout scent gland, called the morrillo (Herrera and Macdonald 1993). The best predictor of social status among males was age, suggesting the existence of a queuing system (Kokko and Johnstone 1999; Salas 1999). After experimental or accidental removal of the dominant male, the top-ranking subordinate takes the dominant position (Herrera and Macdonald 1993; Salas 1999).

The mating system within capybara groups is clearly polygynous, although the degree of monopolization of reproductive success by the dominant male has not been completely ascertained. Individually, dominant males, on average, obtain more matings than subordinate males, but as a group, subordinates obtain more matings than dominants (Herrera and Macdonald 1993). In the study by Salas (1999) dominant males exhibited clearer advantage over subordinates

TABLE 1.—Demography of capybaras (*Hydrochoerus hydrochaeris*), showing locality, ecological density (density in the section of the ecosystem where animals are found), average group size (number of adult members in stable social units), socionomic sex ratio (sex ratio in social groups; M = male, F = female), and home-range size of groups.

Locality	Ecological density (individuals/km ²)	Group size (\pm SD)	Socionomic sex ratio (M:F)	Group home-range size (ha)	Source
Pantanal, Brazil	9.5	10.6 \pm 3.8	1:2.9	12	Alho and Rondon (1987)
Pantanal, Brazil	12.5	5.9 \pm 5.8	1:2.5	12–200	Schaller and Crawshaw (1981) ^a
Llanos, Venezuela	~150	9.6 \pm 3.8	1:1.7	10	Herrera and Macdonald (1987)
Llanos, Venezuela	172.9	11.25	1:1.2	—	E. R. Congdon, Drexel University, pers. obs.
Llanos, Venezuela	200–400	16 (IQR ^b = 9.5)	1:2.0	14	Salas (1999)
Esteros del Iberá, Argentina	Probably high	15.2 \pm 3.4	1:2.8	—	M. J. Corriale, Universidad de Buenos Aires, pers. obs.
Llanos, Colombia	—	—	—	10–56	Perea and Ruiz (1977)

^a Calculated from 10 stable groups studied in detail by Schaller and Crawshaw (1981). Home-range size is reported as ranging from 12 to 200 ha, but because it uses a different definition than in this study, the smaller value is used here for comparison.

^b IQR = interquartile range.

in mating success so that, even as a group, subordinates did not do as well as dominants. Additionally, dominant males frequently interrupt courtships initiated by subordinate males (Herrera and Macdonald 1993; Salas 1999). Indirect evidence also suggests that the dominant male may be able to monopolize females in his group. If he could not do so, sperm competition could arise; however, this does not seem to be the case, because typical characteristics of species subjected to sperm competition have not been observed in this species. Testes of capybaras are not large for their body size (Herrera 1992b; López et al. 2008), and they appear to be dedicated more to testosterone production than to sperm production. Testosterone-producing tissue (composed of Leydig cells) occupies a greater proportion of testis volume than spermatid tubules (Costa and Paula 2006; Moreira et al. 1997). Additionally, a number of factors appear to limit the chances of successful breeding by subordinate males, even if they mate. These factors include spontaneous ovulation (López-Barbella 1987); a short period of receptivity of females (only 8 h—S. López-Barbella, Universidad Central de Venezuela, pers. comm.), which would allow guarding by the dominant male; a lengthy courtship (\leq 30 min, usually about 10 min) giving the dominant male a chance to interrupt (Bedoya 2008; Ojasti 1973); need for several mountings to ensure fertilization (López-Barbella 1987); and patterns of apparently passive female choice (Bedoya 2008; Salas 1999).

Although comparisons across studies are always difficult, in general, group size of capybaras appears to increase with population density. Particularly relevant are 3 studies (Congdon 2007; Herrera and Macdonald 1987; Salas 1999) that are the most comparable because they were carried out at 2 sites in the same ecosystem (seasonally flooded tropical savannas), used similar methods, and were \leq 50 km apart. Nonetheless, despite these similarities, the 2 habitats clearly differed. One was on a ranch with patchy distribution of water holes and was strongly affected by the wet-dry seasonality (Herrera and Macdonald 1987), and the other on a ranch where well-managed dikes with floodgates maintained a more spatially homogeneous and more constant resource base (grass and

water) throughout the year (Congdon 2007; E. R. Congdon, pers. obs.; Salas 1999). At ecological densities of up to 173 individuals/km² (Congdon 2007; Table 1) group sizes varied between 6 and 11 adults, but in the study with a density of $>$ 200 individuals/km², groups attained a mean size of 16 individuals (Salas 1999; Table 1). These larger groups also were found in a social situation where floaters—apparently unaffiliated animals, mostly males—were more common than at the site with lower population density (Herrera and Macdonald 1987; Table 1). M. J. Corriale (pers. obs.) also reports group sizes at the site in Argentina that are similar to those of Salas (1999; Table 1). Although no data on population density are available for the Argentinean location, the habitat is obviously highly productive, and water and grass are available year-round, suggesting that population density can be high. An association of higher densities with larger group sizes has been reported in other rodents (Lucia et al. 2008; Randall et al. 2005).

The greater proportion of floaters found at the high population density studied by Salas (1999) also can influence sex ratio within groups, which could have profound implications for sexual selection and aggression among males as they queue for dominance. However, although the sex ratio in the study by Salas (1999) was high (1:2.0, male:female), it was not the highest reported (Table 1). The occurrence and impact of floater males in this system is not well understood.

Optimal group size for a population typically is dependent on costs and benefits associated with the particular habitat. As in most other large mammalian herbivores living in open habitats, capybara group living has been associated with predation (Ebensperger 2001; Ebensperger and Blumstein 2006). This pattern is corroborated by individual vigilance rates, which correlate negatively with group size (Yáber and Herrera 1994). Vigilance patterns also are affected by sex and social status; females in larger groups show lower rates of alertness, but subordinate males do not enjoy this benefit (Yáber and Herrera 1994).

The ultimate measure of the selective advantage of group living is reproductive success, and although capybaras do not

seem to breed successfully outside of a group, the evidence that individuals in larger groups do better is inconclusive. Individual female breeding success (average number of pups surviving to about 6 months of age per female) was correlated with the number of females (up to 7) in the group (Herrera and Macdonald 1987), whereas a similar correlation was not statistically significant in the higher-density situation (Salas 1999). However, all groups in the study by Salas (1999) were larger than groups in the study by Herrera and Macdonald (1987). Salas (1999) suggests that many females in her larger groups were young adults, which tend to be less successful at breeding (Ojasti 1973). Communal nursing commonly occurs (Macdonald 1981; Salas 1999) and could be 1 benefit of group living for female capybaras. Females also tend to breed synchronously, and the young form nursery groups almost immediately after birth, which also likely provides advantages in terms of protection from predators and infanticidal males (E. R. Congdon, Drexel University, pers. obs.). We have not seen evidence of reproductive suppression among females.

Ample evidence exists that grouping also seems to benefit grazers in their foraging. For example, it has been argued that the maintenance of a “grazing lawn” can be achieved only by a group, because the animals optimize grass growth by grazing at specific intervals in the same general area (Arsenault and Owen Smith 2002; Gordon 1988; McNaughton 1979). Karki et al. (2000) reported that grazing not only stimulates grass growth but also results in greater diversity and increased nutritional content of grasses. Use of space while grazing by capybaras is likely to fit this pattern (Barreto and Herrera 1998).

A capybara territory is defended by all adult members of a group and encompasses a patch of grassland, a shrubby piece of higher ground, and a section of a body of water (Herrera and Macdonald 1989). In a study where territory and home range could be directly compared, they appeared to be generally equivalent (Herrera and Macdonald 1989). Home-range size correlated with group size (Herrera and Macdonald 1989; Salas 1999), with a slightly higher within-home-range density at the site of Salas (1999). In the Llanos of Colombia home ranges varied between 10 and 56 ha (Perea and Ruiz 1977), but in the Brazilian Pantanal a wide range of home-range sizes has been described, with a minimum size of 12 ha and maximum of 200 ha (Schaller and Crawshaw 1981; Table 1). The higher end of the latter range of home-range sizes is likely to include temporary excursions and, as such, we would not consider these as home range. Thus, in this species, an increase in density, while increasing group size, appears to increase territory size only marginally, leading to an increased within-home-range density. This increased density could be 1 of the proximate cues for changes in dispersal.

DISPERSAL AND PHILOPATRY

Patterns of dispersal and philopatry play an important role in the social and genetic structure of populations (Chepko-Sade and Halpin 1987; Lucia et al. 2008; Storz 1999). In

capybaras a mark–recapture study of dispersal presented evidence that sexes dispersed equally. For example, a group of 6 juvenile capybaras (3 males and 3 females) initially captured in the same location were recaptured together again as adults 3.5 km (7 home-range widths) away, suggesting that they dispersed as a group (Herrera 1992a). This pattern also has been supported by circumstantial evidence in behavioral studies where, on several occasions, a young male was observed moving away from his group accompanied by a number of subadults (Herrera and Macdonald 1989). At the high-density location studied by Salas (1999; Table 1), where the focus was on philopatry rather than dispersal, some juvenile females stayed in their natal groups whereas all juvenile males disappeared (Salas 1999). Congdon (2007) conducted a detailed study of natal dispersal in the same site a few years later, when density had dropped somewhat (Table 1), and found almost complete male-biased dispersal. Behavioral data failed to support group dispersal in that population (Congdon 2007). Young males destined to disperse were not more likely to follow older males than were young females, nor were young males ever seen away from their natal group in pairs or groups (Congdon 2007). This pattern of philopatry (females philopatric, males dispersing) predicts that females in groups will be related but males will not, a pattern generally supported by genetic evidence from the same population (E. A. Herrera, pers. obs.). Thus, at high densities, the sex bias of dispersal increases.

In addition to differences in density, variation in dispersal patterns could be related to the spatial distribution of a key territory component, water. At the site of Herrera and Macdonald (1987, 1989) water is distributed in isolated ponds or a few rivers separated by some distance. As capybaras disperse they would be forced to continue until they reached the next pond; thus to some extent distribution of water might dictate dispersal distance. The maximum dispersal distance detected at this site was 5.6 km (Herrera 1992a). At the site studied by Salas (1999) and Congdon (2007) sources of water were more continuous and linearly distributed so dispersers could travel along canals, going almost directly from 1 territory to the next, thereby spending only limited time in more inhospitable habitats. The maximum dispersal distance detected at this site was approximately 3 km, and some capybaras dispersed to social groups immediately adjacent to their natal territory (Congdon 2007). Therefore, at 2 sites with similar densities but differences in water and grass distribution, a patchier resource distribution correlated with larger dispersal distance, lack of sex bias, and possible group dispersal (Congdon 2007; Herrera 1992a). The decision by females to disperse might have been dictated, at least in part, by a lack of resources in their original territories. These differences in dispersal distance patterns could have significant impact on genetic structure of the population. Further analyses of the factors most likely responsible for these site differences are needed. However, logistics and the wide distribution of capybara populations place constraints on the feasibility of such studies.

CONCEPTUAL ISSUES

Variation in behavior always has been a focus of behavioral ecology, in part because natural selection can only act on heritable variation. Studies on proximate mechanisms of intraspecific variation in social structure in mammals have focused on the physiological underpinnings, particularly on hormonal correlates (Cushing et al. 2001; Maher 2000; Roberts et al. 1998a). Nothing at present is known about the physiological mechanisms underlying social variation in capybaras. Clearly, studies of endocrine mechanisms and possible epigenetic effects (Fish et al. 2004; Francis et al. 1999; Weaver et al. 2004) are needed. For example, nongenetic maternal effects, which are a type of epigenetic effect, can influence variation in social behavior across multiple generations, as reported for rats (*Rattus norvegicus*—Francis et al. 1999).

Other studies of intraspecific variation, focused more on ultimate causation, have emphasized ecological and habitat characteristics as the most important factors influencing social variation (Maher and Burger 2011 [this issue]). The most commonly cited factors are food abundance and distribution. The resource dispersion hypothesis (Slobodchikoff 1984), optimal group size model, and other related models (e.g., Crook 1965) all predict that food dispersion affects social structure, and results of studies on many mammalian species generally have supported this prediction (Kruuk and Parish 1987; Travis et al. 1995; Verdolin 2009; Yamigawa and Hill 1998). However, capybaras might be somewhat different because water, rather than food, could be their most important limited resource.

Additional factors that must be taken into account in examining variation in social behavior are costs and benefits. For example, consider the interactions among dispersal and variation in population density, resource distribution, and size of social groups within a population. In terms of benefits, sex-biased dispersal and immigration of new individuals into established groups would increase gene flow and decrease inbreeding (Schwartz and Armitage 1980; Storz 1999).

With regard to costs, both individual and inclusive fitness can decline if individuals delay dispersal and this results in delayed age of 1st reproduction (McGraw and Caswell 1996; Oli and Armitage 2003, 2008). In contrast, if individuals disperse to avoid competition due to overcrowding in their home territory, these individuals should search for smaller groups in which competition will not be as great. Thus, if a dispersing individual encounters only large groups in the vicinity of its natal territory and has to travel long distances to find a smaller group, the costs of dispersal can be so high that it becomes more beneficial to forego or delay dispersal. The resulting philopatry would have the effect of increasing genetic relatedness, a requisite for the occurrence of kin selection, which could then promote or maintain higher levels of sociality. One problem, of course, is the possibility of inbreeding and inbreeding depression, but this effect could be reduced in several ways. For example, even if 1 sex is philopatric (e.g., females), the arrival of unrelated immigrants

of the opposite sex (e.g., males) can result in new genes entering the group (Storz 1999). Such immigration was observed in capybaras at least once when a newcomer ousted the dominant male of an established group (Herrera and Macdonald 1993). Moreover, the level of inbreeding in any population or group will depend in large part on the turnover rate of the immigrant sex and the ability of immigrants to mate with unrelated females (Schwartz and Armitage 1980; Storz 1999). Thus, the dynamic interplay between the philopatric sex and the dispersing sex can critically affect levels of inbreeding and genetic structuring of populations.

In addition to intergroup transfers and immigration of unrelated individuals, other ways of ameliorating the possibly detrimental effects of inbreeding can be identified, such as occasional matings with individuals from neighboring groups. This situation has been documented in Gunnison's prairie dogs, a species with social organization somewhat similar to that of capybaras (Travis et al. 1996). However, behavioral observations of capybaras have not detected extragroup copulations, and genetic tests that could shed further light on this issue are still in progress. Another alternative solution to the problem of inbreeding when dispersal is delayed is the evolution of cooperative breeding, with 1 pair of breeders supplemented by helpers (Solomon and French 1997). This outcome also would be facilitated and maintained by kin selection. However, in capybaras >1 female typically mates in each group (i.e., no reproductive suppression), which does not fit the typical pattern of cooperative breeding. Although capybara females cooperatively nurse and rear the young in nursery groups, males compete for dominance status, including access to females, and cooperate only by defending the territory, which also can be interpreted as selfish because they are direct beneficiaries of this behavior.

If neighboring groups are small, dispersing individuals could settle in neighboring territories and dispersal costs would likely be lower. This situation also raises interesting social possibilities because dispersers then might have an increased likelihood of continuing to encounter and interact socially with relatives, which could lead to decreased aggression between neighboring groups (perhaps similar to a dear enemy phenomenon—Fisher 1954; Wilson 1975) and to larger and more complex social networks. Although the relatedness of the individuals involved is not known, dispersing capybaras sometimes settled in territories adjacent to their natal territory (Congdon 2007); however, cooperation between groups was not observed.

The complexity and reciprocity of the interactions discussed above suggest that no single factor in isolation should be considered as key to understanding intraspecific variation in social behavior and organization. Rather, any change in the physical or social environment might initiate a chain reaction affecting many other factors that can influence various aspects of the social system of a species. Moreover, different species can have different dynamics, depending on which resources are most important in their biology and on details of their social organization. Some species, including capybaras (at

least in populations that have been studied), can have an established social organization (e.g., group living, group territoriality, linear dominance hierarchies, and polygyny), whereas others might be much more flexible (woodchucks [Maher 2006] and pronghorns [Maher 2000]). However, even in species with established social organization, significant phenotypic plasticity still can impact fitness.

The preponderance of evidence suggests that capybaras have been selected for phenotypic plasticity in their social structure. This plasticity is perhaps most striking when one considers the availability of water sources, a major resource for this species. In Venezuelan populations during the wet season capybaras are found in territorial social groups (as described previously), and aggression toward neighboring group members is common (Herrera and Macdonald 1987). In contrast, during the dry season water sources dry up, and capybaras can be found in groups of hundreds gathered around the few remaining water holes (Macdonald 1981; Ojasti 1973). In addition to seasonal variation in water availability, stochastic variation in rainfall and drought exists, and water management practices of different ranches also vary. Additionally, spatial structure of water sources varies (i.e., isolated ponds at some sites versus more continuous and linearly structured bodies of water), which seems to influence numerous social parameters, including group size, dispersal patterns, territoriality, and interactions among groups. Thus, all of these preceding water-related differences can affect variation in capybara social structure.

Intraspecific variation based on seasonal rainfall was documented in impalas (*Aepyceros melampus*—Jarman and Jarman 1979). Specifically, during the dry season female groups are smaller and individuals are more dispersed (i.e., greater distances among group members). At the same time, males have smaller territories during the dry season compared to the wet season. All of these effects appeared to be a result of differences in food availability and distribution between dry and wet seasons (Jarman and Jarman 1979). Similar changes in behavior related to wet and dry seasons occur in feral asses (*Equus asinus*), but the relationship of this response to food resources was not reported (Woodward 1979).

Hunting or harvesting also can be a relevant factor in intraspecific social variation among capybaras. Specifically, hunting and particularly harvesting can affect group size, sex ratio, age structure, and genetic relationships within groups, and these changes can have cascading effects on other aspects of the social system and life history (Allendorf et al. 2008; Festa-Bianchet 2003; FitzGibbon 1998; Tuytens and Macdonald 2000). Such effects have been documented in other species. For example, in pronghorns hunting pressures result in a shift from male territoriality to living in multimale, multifemale groups (Deblinger and Alldredge 1989). Additionally, group composition was biased toward more females and young in a hunted as compared to a nonhunted population (Maher and Mitchell 2000). However, other behavior patterns were not affected, possibly because hunting pressure was low. Hunting also affects breeding systems in elephant seals

(*Mirounga leonina*—Bonner 1989) and white-tailed deer (*Odocoileus virginianus*—Miller and Ozoga 1997). At high population densities coyotes, (*Canis latrans*) live in groups with yearlings as helpers; however, hunting disrupts groups and results in male–female pairs and solitary individuals (Andelt 1985).

In parts of their range capybaras are hunted either for their meat (as in Venezuela) or their hides (as in Argentina). In Venezuela, although poaching occurs, the authorized harvests are managed and occur during a particular time of each year. Large males are favored (E. R. Congdon, Drexel University, E. A. Herrera, and V. Salas, pers. obs.), which could lead to changes in sex ratio, group composition, group sizes, possibly dispersal patterns, and drastic disruption of social groups once every year. Comparative studies of harvested and nonharvested capybara populations are needed.

The complexity of interactive factors that potentially affect social structure also suggests that studies of intraspecific variation should include at least 3 different levels of analysis: differences among individuals within a group, differences among groups in a population, and differences among populations. Of these, individual variation might be most important because it can determine the behavior of groups, which in turn affects population differences. Most studies on intraspecific variation concentrate on population differences, which can obscure variation among individuals and among groups; more emphasis on variation within groups and populations could contribute to our understanding of the origins of variation in social behavior and organization among populations.

FINAL REMARKS

Capybara social behavior has a number of constant features: group living, stable social units, group territoriality, and a male-only dominance hierarchy. Other aspects are more plastic, such as group size, proportion of floaters, and patterns of dispersal and philopatry. This review shows that when resources are more abundant and homogeneous in time and space, density increases and is associated with larger groups, a greater proportion of mostly male floaters, and more male-biased dispersal. The variation observed in group size in relation to ecology—that is, larger groups in more-productive and hence more densely populated regions—has been described for several other species of rodents (Lucia et al. 2008; Randall et al. 2005). A high level of phenotypic plasticity has allowed capybaras to exploit a number of habitats, ranging from riparian forests to seasonally flooded savannas, from northwestern Colombia to Argentina, and from tropical climates to more temperate zones where temperatures can reach the freezing point. Additionally, their adaptability probably helped to make them resilient to hunting, including both poaching and commercial harvesting, thereby making it possible for capybaras to serve as important commercial sources of meat and hides (Ojasti 1991). Despite the many studies already conducted on capybara behavior, many

questions remain, particularly with regard to the importance of sexual selection, extent of female choice, role of scent-marking in social dynamics, role of infanticide, and patterns of group formation. The high level of phenotypic plasticity in social behavior of capybaras, along with high fertility, may explain how capybaras have stayed off the threatened species list and adapted to different types of habitats, despite extreme habitat destruction and excessive levels of hunting in some areas.

RESUMEN

Los capibaras (*Hydrochoerus hydrochaeris*) son histrocósmorfos del Nuevo Mundo de gran tamaño, comunes en las sabanas inundables de Sur América tropical y subtropical. En este artículo, hacemos una revisión de la estructura y dinámica social de los capibaras en gran parte de su ámbito geográfico. En todos los lugares donde han sido estudiados, los capibaras viven en grupos. Estos grupos son unidades sociales estables compuestas por adultos de ambos sexos (con sesgo hacia las hembras) con sus crías. Las interacciones entre los machos se caracterizan por una jerarquía de dominancia lineal en la que el macho dominante obtiene la mayoría de los apareamientos. Los grupos varían en tamaño entre 6 y 16 adultos, en relación a características del hábitat y densidad de la población. A densidades altas, los tamaños de grupo y la proporción de animales flotantes, principalmente machos, aumenta. En una localidad con baja densidad, la dispersión ocurre en grupos de ambos sexos, mientras en otra localidad de mayor densidad, los machos dispersan mientras las hembras son filopátricas. Discutimos también asuntos conceptuales relacionados con la variación social intra-específica en general y la de los capibaras en particular.

ACKNOWLEDGMENTS

We thank, 1st of all, L. Hayes for his kind invitation to participate in this special feature. Comments by C. Maher, B. Blake, and 2 anonymous reviewers were very helpful. The research of ERC was supported by an International Dissertation Enhancement Grant from the National Science Foundation, by a Fullbright Scholarship, and by a grant from the Whitney R. Harris World Ecology Center at the University of Missouri–St. Louis. The research of VS was supported by a Raul Leoni Scholarship, Overseas Research Student Award (CVCP), Cambridge Overseas Trust, Weis-Fogh Fund, CONICIT, Perry Fund from Queens' College Cambridge, and Cambridge Philosophical Society. EAH appreciates the support from the Deanery for Research and Development (DID) at Universidad Simón Bolívar, Caracas, Venezuela. We are grateful to the management and staff at Hato El Cedral and Hato El Frio in Venezuela for their invaluable cooperation and assistance in conducting this research.

LITERATURE CITED

- ALHO, C. J. R., AND N. L. RONDON. 1987. Habitat, population density and social structure of capybaras (*Hydrochoerus hydrochaeris*) in the Pantanal, Brazil. *Revista Brasileira de Zoologia* 4:139–149.
- ALLENDORF, F. W., P. R. ENGLAND, G. LUIKHHART, P. A. RITCHIE, AND N. RYMAN. 2008. Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution* 23:327–337.
- ANDELT, W. F. 1985. Behavioral ecology of coyotes in South Texas. *Wildlife Monographs* 94:1–45.
- ARMITAGE, K. B. 1977. Social variety in the yellow-bellied marmot: a population behavioral system. *Animal Behaviour* 25:585–593.
- ARSENAULT, R., AND N. OWEN SMITH. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313–318.
- AZCÁRATE, T. 1980. Sociobiología y manejo del capibara, *Hydrochoerus hydrochaeris*. *Doñana Acta Vertebrata* 7:1–228.
- BARRETO, G. R., AND E. A. HERRERA. 1998. Foraging patterns of capybaras in a seasonally flooded savanna of Venezuela. *Journal of Tropical Ecology* 14:87–98.
- BEDOYA, M. 2008. Selección de pareja en hembras de chigüire, *Hydrochoerus hydrochaeris*. Tesis de Licenciatura [undergraduate thesis], Biología, Universidad Simón Bolívar, Caracas, Venezuela.
- BONNER, W. N. 1989. The natural history of seals. Christopher Helm, London, United Kingdom.
- CHEPKO-SADE, B. D., AND Z. T. HALPIN. 1987. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois.
- CONGDON, E. R. 2007. Natal dispersal and new group formation in capybaras (*Hydrochoerus hydrochaeris*) in a seasonally flooded savanna of Venezuela. Ph.D. dissertation, University of Missouri at Saint Louis, Saint Louis, Missouri.
- COSTA, D. S., AND T. A. R. PAULA. 2006. Testosterone level, nasal gland volume and Lydig cell morphometry in capybaras (*Hydrochoerus hydrochaeris*). *Arquivos Brasileiros de Medicina Veterinária Zootécnica* 58:1086–1091.
- CROOK, J. H. 1965. The adaptive significance of avian social organizations. *Symposia of the Zoological Society of London* 14:181–281.
- CUSHING, B. S., J. O. MARTIN, L. J. YOUNG, AND C. S. CARTER. 2001. The effects of peptides on partner preference formation are predicted by habitat in prairie voles. *Hormones and Behavior* 39:48–58.
- DEBLINGER, R. R., AND A. W. ALLDREDGE. 1989. Management implications of variation in pronghorn social behavior. *Wildlife Society Bulletin* 17:82–87.
- EBENSPERGER, L. A. 2001. A review of the evolutionary causes of rodent group-living. *Acta Theriologica* 46:115–144.
- EBENSPERGER, L. A., AND D. T. BLUMSTEIN. 2006. Sociality in New World hystricognath rodents is linked to predators and burrow digging. *Behavioral Ecology* 17:410–418.
- FERRON, J., AND J.-P. OULLET. 1989. Temporal and intersexual variation in the use of space with regard to social organization in the woodchuck (*Marmota monax*). *Canadian Journal of Zoology* 67:1642–1649.
- FESTA-BIANCHET, M. 2003. Exploitative wildlife management as a selective pressure for the life history evolution of large mammals. Pp. 191–208 in *Animal behavior and wildlife conservation* (M. Festa-Bianchet and M. Apollonio, eds.). Island Press, Washington, D.C.
- FISH, E. W., ET AL. 2004. Epigenetic programming of stress responses through variations in maternal care. *Annals of the New York Academy of Sciences* 1036:167–180.
- FISHER, J. 1954. Evolution and bird sociality. Pp. 71–83 in *Evolution as a process* (J. Huxley, A. C. Hardy, and E. B. Ford, eds.). Allen & Unwin, London, United Kingdom.

- FITZGIBBON, C. 1998. The management of subsistence harvesting; behavioral ecology of hunters and their mammalian prey. Pp. 449–473 in *Behavioral ecology and conservation biology* (T. Caro, ed.). Oxford University Press, New York.
- FRANCIS, D., J. DIORIO, D. LIU, AND M. J. MEANEY. 1999. Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science* 286:1155–1158.
- GORDON, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. *Journal of Applied Ecology* 25: 1–10.
- HEANEY, L. R. 1984. Climate influence on life-history tactics and behavior of North American tree squirrels. Pp. 43–78 in *The biology of ground-dwelling squirrels* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.
- HERRERA, E. A. 1992a. Growth and dispersal in capybaras, *Hydrochaeris hydrochaeris*. *Journal of Zoology* (London) 228:307–316.
- HERRERA, E. A. 1992b. Size of testes and scent glands in capybaras, *Hydrochaeris hydrochaeris* (Rodentia: Cavimorpha). *Journal of Mammalogy* 73:871–875.
- HERRERA, E. A., AND D. W. MACDONALD. 1987. Group stability and the structure of a capybara population. *Symposia of the Zoological Society of London* 5:115–130.
- HERRERA, E. A., AND D. W. MACDONALD. 1989. Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). *Journal of Animal Ecology* 58:667–679.
- HERRERA, E. A., AND D. W. MACDONALD. 1993. Aggression, dominance and mating success in capybaras. *Behavioral Ecology* 4: 114–119.
- JARMAN, P. J., AND M. V. JARMAN. 1979. The dynamics of ungulate social organization. Pp. 185–220 in *Serengeti: dynamics of an ecosystem* (A. R. E. Sinclair and M. Norton-Griffiths, eds.). University of Chicago Press, Chicago, Illinois.
- KARKI, J. B., Y. V. JHALA, AND P. P. KHANNA. 2000. Grazing lawns in Terai grasslands, Royal Bardia National Park, Nepal. *Biotropica* 32:423–429.
- KOKKO, H., AND R. JOHNSTONE. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London, B. Biological Sciences* 266:571–578.
- KOMDEUR, J., A. HUFFSTADT, W. PRAST, G. CASTLE, R. MILETO, AND J. WATTEL. 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Animal Behaviour* 49:695–708.
- KRUUK, H., AND T. PARISH. 1987. Changes in the size of groups and ranges of the European badger, *Meles meles*, in an area in Scotland. *Journal of Animal Ecology* 56:351–364.
- LAYNE, J. N. 1954. The biology of the red squirrel *Tamiasciurus hudsonicus* (Bangs), in central New York. *Ecological Monographs* 24:227–267.
- LONSTEIN, J. S., AND J. G. DEVRIES. 1999. Sex differences in the parental behaviour of adult virgin prairie voles: independence from gonadal hormones and vasopressin. *Journal of Neuroendocrinology* 11:441–449.
- LÓPEZ, M., M. G. MUÑOZ, AND E. A. HERRERA. 2008. Reproductive morphology of capybaras, *Hydrochoerus hydrochaeris* (Rodentia: Hystricognathi): no evidence for sperm competition? *Mammalian Biology* 73:241–244.
- LÓPEZ-BARBELLA, S. 1987. Una contribución al conocimiento de la fisiología de la reproducción del chigüire, *Hydrochoerus hydrochaeris*. Trabajo de Ascenso, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela.
- LOTT, D. F. 1979. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266–325.
- LUCIA, K. E., B. KEANE, L. D. HAYES, Y. K. LIN, R. L. SCHAEFER, AND N. G. SOLOMON. 2008. Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behavioral Ecology* 19:774–783.
- MACDONALD, D. W. 1981. Dwindling resources and the social behaviour of capybaras, (*Hydrochoerus hydrochaeris*) (Mammalia). *Journal of Zoology* (London) 194:371–391.
- MAHER, C. R. 2000. Quantitative variation in ecological and hormonal variables correlate with spatial organization of pronghorn (*Antilocapra americana*). *Behavioral Ecology and Sociobiology* 47:327–338.
- MAHER, C. R. 2004. Intrasexual territoriality in woodchucks (*Marmota monax*). *Journal of Mammalogy* 85:1087–1094.
- MAHER, C. R. 2006. Social organization in woodchucks (*Marmota monax*) and its relationship to growing season. *Ethology* 112:313–324.
- MAHER, C. R., AND J. R. BURGER. 2011. Intraspecific variation in space use, group size, and mating systems of caviomorph rodents. *Journal of Mammalogy* 92:54–64.
- MAHER, C. R., AND C. D. MITCHELL. 2000. Effects of selective hunting on group composition and behavior patterns of pronghorn, *Antilocapra americana*, males in Montana. *Canadian Field-Naturalist* 114:264–270.
- MCGRAW, J. B., AND H. CASWELL. 1996. Estimation of individual fitness from life-history data. *American Naturalist* 147:47–64.
- MCKNAUGHTON, S. J. 1979. Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* 124:863–886.
- MEIER, P. T. 1992. Social organization of woodchucks (*Marmota monax*). *Behavioral Ecology and Sociobiology* 31:393–400.
- MILLER, K. V., AND J. J. OZOGA. 1997. Density effects on deer sociobiology. Pp. 136–150 in *The science of overabundance in deer ecology and population management* (W. J. McShea, H. B. Underwood, and J. H. Rappole, eds.). Smithsonian Institution Press, Washington, D.C.
- MOREIRA, J. R., D. W. MACDONALD, AND J. R. CLARKE. 1997. The testis of capybaras (*Hydrochoerus hydrochaeris*). *Journal of Mammalogy* 78:1096–1100.
- OJASTI, J. 1973. Estudio biológico del chigüire o capibara. FONAIAP, Caracas, Venezuela.
- OJASTI, J. 1991. Human exploitation of capybaras. Pp. 236–252 in *Neotropical wildlife use and conservation* (J. Robinson and K. H. Redford, eds.). University of Chicago Press, Chicago, Illinois.
- OLI, M. K., AND K. B. ARMITAGE. 2003. Sociality and individual fitness in yellow-bellied marmots: insights from a long-term study (1962–2001). *Oecologia* 136:543–550.
- OLI, M. K., AND K. B. ARMITAGE. 2008. Indirect benefits do not compensate for the loss of direct fitness in yellow-bellied marmots. *Journal of Mammalogy* 89:874–881.
- PEREA, J. T., AND S. M. RUIZ. 1977. Organización social y hábitos territoriales del chigüiro. Tesis de Grado [undergraduate thesis]), Universidad Nacional de Colombia, Bogotá, Colombia.
- RANDALL, J. A., K. ROGOVIN, P. G. PARKER, AND J. A. EIMES. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behavioral Ecology* 16:961–973.
- ROBERTS, R. L., B. S. CUSHING, AND C. S. CARTER. 1998a. Intraspecific variation in the induction of female sexual receptivity in prairie voles. *Physiology and Behavior* 64:209–212.
- ROBERTS, R. L., J. R. WILLIAMS, A. K. WANG, AND C. S. CARTER. 1998b. Cooperative breeding and monogamy in prairie voles: influences of the sire and geographic variation. *Animal Behaviour* 55:1131–1140.

- SALAS, V. 1999. Social organisation of capybaras in the Venezuelan Llanos. Ph.D. dissertation, Cambridge University, Cambridge, United Kingdom.
- SCHALLER, G. B., AND P. G. CRAWSHAW. 1981. Social organization in a capybara population. *Säugetierkundliche Mitteilungen* 29:3–16.
- SCHWARTZ, O. A., AND K. B. ARMITAGE. 1980. Genetic variation in social mammals: the marmot model. *Science* 207:665–667.
- SLOBODCHIKOFF, C. N. 1984. Resources and the evolution of social behavior. Pp. 227–251 in *A new ecology: novel approaches to interactive systems* (P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, eds.). John Wiley & Sons, Inc., New York.
- SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecological Monographs* 38:31–63.
- SOLOMON, N. G., AND J. A. FRENCH (EDS.). 1997. *Cooperative breeding in mammals*. Cambridge University Press, Cambridge, United Kingdom.
- STORZ, J. F. 1999. Genetic consequences of mammalian social structure. *Journal of Mammalogy* 80:553–569.
- SWIHART, R. K. 1992. Home range attributes and spatial structure of woodchuck populations. *Journal of Mammalogy* 73:604–618.
- TANG-MARTÍNEZ, Z. 2003. Emerging themes and future challenges: forgotten rodents, neglected questions. *Journal of Mammalogy* 84:1212–1227.
- TRAVIS, S. E., C. N. SLOBODCHIKOFF, AND P. KEIM. 1995. Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology* 76:1794–1803.
- TRAVIS, S. E., C. N. SLOBODCHIKOFF, AND P. KEIM. 1996. Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. *Behavioral Ecology* 7:95–100.
- TUYTTENS, F. A. M., AND D. W. MACDONALD. 2000. Consequences of social perturbation for wildlife management and conservation. Pp. 315–329 in *Behaviour and conservation* (L. M. Gosling and W. J. Sutherland, eds.). Cambridge University Press, Cambridge, United Kingdom.
- VERDOLIN, J. L. 2009. Gunnison's prairie dog (*Cynomys gunnisoni*): testing the resource dispersion hypothesis. *Behavioral Ecology and Sociobiology* 63:789–799.
- WEAVER, I. C. G., ET AL. 2004. Epigenetic programming by maternal behavior. *Nature Neuroscience* 7:847–854.
- WILSON, E. O. 1975. *Sociobiology*. Harvard University Press, Cambridge, Massachusetts.
- WOODWARD, S. L. 1979. The social system of feral asses. *Zeitschrift für Tierpsychologie* 49:304–316.
- YAMIGAWA, J., AND D. HILL. 1998. Intraspecific variation in the social organization of Japanese macaques: past and present scope of field studies in natural habitats. *Primates* 39:257–273.
- YÁBER, M. C., AND E. A. HERRERA. 1994. Vigilance, group size and social status in capybaras. *Animal Behaviour* 48:1301–1307.

Special Feature Editor was Barbara H. Blake.