

Towards an integrative model of sociality in caviomorph rodents

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In the late 1990s and early 2000s it was recognized that behavioral ecologists needed to study the sociality of caviomorph rodents (New World hystricognaths) before generalizations about rodent sociality could be made. Researchers identified specific problems facing individuals interested in caviomorph sociality, including a lack of information on the proximate mechanisms of sociality, role of social environment in development, and geographical or intraspecific variation in social systems. Since then researchers have described the social systems of many previously understudied species, including some with broad geographical ranges. Researchers have done a good job of determining the role of social environments in development and identifying the costs and benefits of social living. However, relatively little is known about the proximate mechanisms of social behavior and fitness consequences, limiting progress toward the development of integrative (evolutionary-mechanistic) models for sociality. To develop integrative models behavioral ecologists studying caviomorph rodents must generate information on the fitness consequences of different types of social organization, brain mechanisms, and endocrine substrates of sociality. We review our current understanding and future directions for research in these conceptual areas. A greater understanding of disease ecology, particularly in species carrying Old World parasites, is needed before we can identify potential links between social phenotypes, mechanism, and fitness.

Key words: behavioral endocrinology, caviomorphs, disease ecology, fitness consequences, neuroanatomy, sociality

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In the late 1990s and early 2000s the Neotropical and temperate South American caviomorph rodents (New World hystricognaths) were identified as understudied organisms, particularly in terms of social systems, that is, sociality and mating systems (Ebensperger 1998; Tang-Martinez 2003). At that time researchers recognized that several of the caviomorph species were social (Ebensperger 1998, 2001), but general statements about social evolution of rodents could not be made without more research (Ebensperger 1998). Caviomorphs occur in a diverse range of habitats and include species that are arboreal (Adler 2011 [this issue]), semiaquatic (Macdonald et al. 2007), semifossorial (Ebensperger and Blumstein 2006; Lacey and Ebensperger 2007), and subterranean (Lacey and Ebensperger 2007). Some species have wide geographical ranges with different populations experiencing very different ecological conditions (Lacey and Ebensperger 2007). In some cases even the same populations experience very different environmental conditions temporally (Ebensperger and Hurtado 2005). Thus, research on caviomorph rodents will improve our understanding of the evolutionary ecology of mammalian sociality. Additionally, caviomorph rodents provide interesting comparisons with the better-studied North American species (marmots and murids) and African bathygerid rodents (Tang-Martinez 2003).

Tang-Martinez (2003) identified several understudied aspects of caviomorph social systems, including the proximate mechanisms of sociality, the role of social environment in development, and geographical or intraspecific variation in social systems. Some progress has been made on these and other issues identified by Ebensperger (1998) as crucial to understanding the evolution of caviomorph social systems. Social systems have been described in species representing several caviomorph families, including the octodontids (Ebensperger et al. 2008; Lacey and Ebensperger 2007),



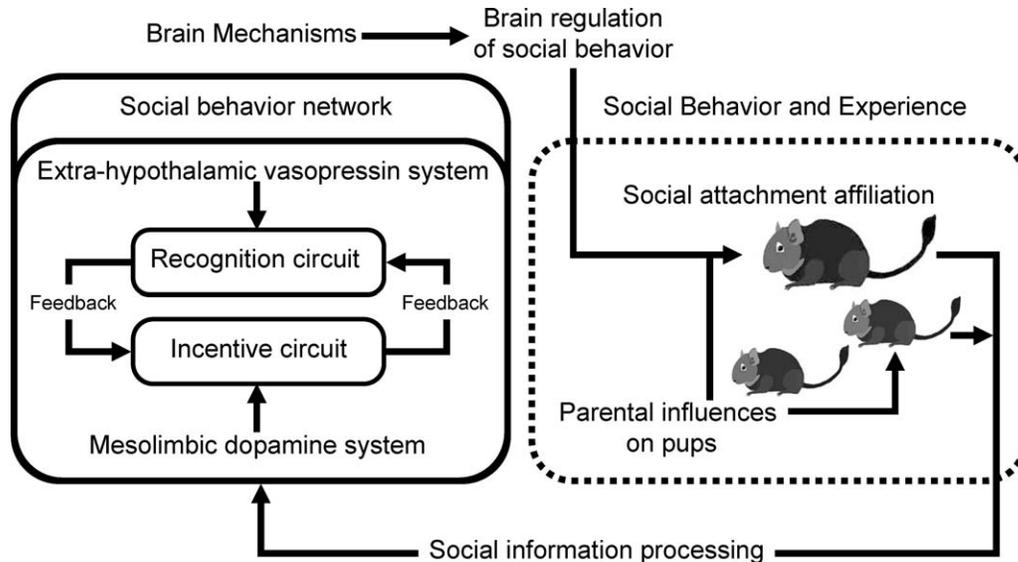


FIG. 1.—Model linking brain mechanisms with social behaviors and experience in caviomorph rodents. Pictures of degus are adapted from Suárez and Mpodozis (2009).

capibaras (Herrera et al. 2011 [this issue]; Macdonald et al. 2007), cavies (Taraborelli and Moreno 2009), ctenomyids (Lacey and Ebensperger 2007), and echimyids (Freitas et al. 2008; Santos and Lacey 2011 [this issue]). As is the case in other rodents, many of the caviomorphs are solitary (Adler 2011 [this issue]). However, a larger percentage of caviomorphs exhibit communal breeding strategies, that is, females rear offspring together (Ebensperger et al. 2002; Silk 2007). In recent years researchers studying cavies (Adrian et al. 2008; Kaiser et al. 2003; Sachser et al. 1999; Salvador and Fernandez 2008; Trillmich et al. 2006, 2008) and other species (Ebensperger et al. 2007; Gruss et al. 2006) have identified some conditions of the early social environment influencing juvenile development and behavior. Ecological factors, including the distribution of resources such as food (Lacey and Ebensperger 2007; Lacey and Wiczorek 2003; Macdonald et al. 2007; Maher and Burger 2011 [this issue]), predation risk (Ebensperger and Blumstein 2006; Lacey and Ebensperger 2007; Lacey and Sherman 2007; Macdonald et al. 2007), and soil conditions associated with digging burrows (Ebensperger and Blumstein 2006; Ebensperger and Cofré 2001; Lacey and Ebensperger 2007; Lacey and Sherman 2007) have been identified as potential causes for the formation of social groups. With regard to evolution and adaptive significance, behavioral ecologists have identified numerous costs and benefits of social living (Ebensperger and Bozinovic 2000; Ebensperger and Wallem 2002; Izquierdo and Lacey 2007; Quirici et al. 2008; Vásquez 1997). To a much lesser extent we have quantified some of the consequences to reproductive fitness of social behavior (Ebensperger et al. 2007; Hayes et al. 2009; Lacey 2004; Sachser et al. 1999; Trillmich et al. 2008).

Despite these advances we still lack a comprehensive understanding of caviomorph rodent sociality and, in fact, of all rodents in general (<5% of species have been studied

extensively). To reach a comprehensive understanding and come in line with current paradigms researchers studying caviomorphs need to take more integrative research approaches. Integrative approaches build upon traditional models by incorporating predictions for how genetic, physiological (including endocrine), or neuroanatomical variation—factors upon which selection can act to shape social phenotypes—underlie intraspecific variation in social systems. The relationship between these internal mechanisms and social traits (e.g., social systems) is bidirectional. For example, social behaviors and variation in social systems can affect physiological and neuroendocrine mechanisms (Young et al. 2006). Understanding the bidirectional nature of these mechanistic factors and the role of ecological variation on their expression is also crucial to predicting the fitness consequences (and thus, evolutionary significance) of social phenotypes. Social attachment in rodents appears to involve primarily 2 brain systems (Young 2009; Fig. 1). The extrahypothalamic vasopressin system, a recognition circuit, can mediate conspecific recognition and thus allow appropriate social behaviors to be expressed. Information about the identity of another individual from the extrahypothalamic vasopressin system can modify (or even initiate) responses within the mesolimbic dopamine system (an incentive circuit; Fig. 1). Feedback from the incentive circuit can then dictate the direction and intensity of the interactions. These relationships provide a basic and comparative framework for our current understanding of the brain substrates and endocrine or physiological bases of rodent social behavior.

Developing integrative models for caviomorph sociality will require that we overcome several major challenges, including a few already highlighted by Tang-Martinez (2003). For example, interpopulation comparisons of sociality are limited to a few species (L. A. Ebensperger, and L. D. Hayes, pers. obs.; Herrera et al. 2011 [this issue]; Taraborelli

and Moreno 2009). Evidence for intraspecific variation in foraging behavior (Quispe et al. 2009), space use (Cutrera et al. 2006), and social behavior (Taber and Macdonald 1992; Taraborelli and Moreno 2009) suggests that differences in environmental conditions can result in variation in caviomorph social structure, similar to that observed in *Microtus* (Tang-Martinez 2003). It is not our intention to write an extensive review of the ecological sources of variation in caviomorph rodent social systems (Ebensperger 2001; Ebensperger and Blumstein 2006; Lacey and Sherman 2007; Maher and Burger 2011 [this issue]). However, understanding how this ecological variation influences neuroanatomical and neuroendocrine mechanisms in the expression of social phenotypes is critical to advancing theory (Owens 2006). Currently, we know very little about brain mechanisms underlying social behavior, gene regulation (sensu Young and Wang 2004), and genomics (Gallardo et al. 2004). Finally, our understanding of sociality in caviomorphs is biased toward only a few of the >250 species. Most of work has been done with capybaras (*Hydrochoerus hydrochaeris*), cavies (Caviidae), coruros (*Spalacopus cyanus*), degus (*Octodon degus*), and social tuco-tucos (*Ctenomys sociabilis*). In the caviomorphs interspecific variation in behavior and habitat selection (arboreal, semifossorial, and subterranean) is considerable. Consequently, the development of an integrative model of caviomorph sociality will require information from more species.

A good starting point for the development of an integrative model for caviomorph social systems is to identify and prioritize future research. An exhaustive review of all the neural, physiological, and genetic mechanisms underlying social behavior is beyond the scope of this paper. Thus, we identify a subset of research foci within the framework of our own collective research expertise that we believe will contribute to an integrative model of intraspecific caviomorph sociality and allow for broader interspecific comparisons among caviomorphs and better-studied taxa (North American murids and sciurids). Specifically, we review our current understanding of and propose future directions for research on brain mechanisms of social systems (e.g., neuropeptide receptor expression), behavioral endocrinology, and fitness consequences of sociality. Additionally, we suggest how research on disease ecology would provide a link between social phenotypes, mechanism, and fitness.

BRAIN MECHANISMS

Current understanding.—It is an important challenge to behavioral ecologists studying caviomorph sociality to develop an understanding of the brain mechanisms underlying social phenotypes. Such information is crucial for predicting variation upon which natural selection can act and which, therefore, could explain some of the diversity of social systems observed in the caviomorph rodents.

To date, much of our understanding has come from work on voles in the genus *Microtus*. Behavioral neuroscientists

studying voles have made remarkable progress in understanding the neuroanatomical variation underlying diversity in social behavior. In socially monogamous prairie voles (*M. ochrogaster*) the oxytocin receptor and arginine vasopressin receptors 1a and 1b are concentrated in reward and reinforcement regions of the brain (nucleus accumbens or incentive circuit region). In nonmonogamous species, such as the meadow vole (*M. pennsylvanicus*), fewer of these receptors are found in the reward and reinforcement regions (Young and Wang 2004). Viral vector gene transfer experiments, used to transfer genes from *M. ochrogaster* to nonmonogamous species, demonstrate a causal link between receptor expression and social behavior. Changes in the regional expression of a single gene can have a profound effect on the social behavior of individuals within a species (Lim et al. 2004; but see Fink et al. 2006). These neuropeptide receptors are evolutionarily conserved for their structure and expression in some vertebrate and invertebrate lineages, although their regulation is quite diverse (Donaldson and Young 2008; Insel and Young 2000).

Some brain mechanisms influencing social phenotypes have been described in cavies, degus, and tuco-tucos. In studies similar to those on voles Beery et al. (2008) used receptor autoradiography to identify differences in the distributions of oxytocin receptors and arginine vasopressin 1a receptors in the brains of social tuco-tucos (*C. sociabilis*) and solitary Patagonian tuco-tucos (*C. haigi*). Oxytocin receptor binding occurred in the piriform cortex, and binding of the thalamus and arginine vasopressin 1a receptor occurred in the olfactory bulbs of social tuco-tucos but not Patagonian tuco-tucos. Oxytocin receptor binding was higher in the lateral septum and hippocampus of Patagonian tuco-tucos than social tuco-tucos. Binding in the central amygdala also was greater in social *Ctenomys*, suggesting that social-group formation is facilitated by reduced social anxiety in this species. Differences also exist in binding of oxytocin receptor and arginine 1a vasopressin receptor in *Ctenomys* and *Cavia porcellus* (Beery et al. 2008; Tribollet et al. 1992). Although it has not been tested extensively, the neuroendocrine pathways by which these neuropeptides act to shape social interactions in Ctenomyidae and Caviidae could be species-specific.

The vomeronasal system is thought to reinforce many aspects of social-sexual behaviors such as sex discrimination and aggression (Brennan and Keverne 2004; Kelliher 2007). The neuroepithelium of the vomeronasal system is the vomeronasal organ, which sends primary axons to the 2 principal subdomains for the accessory olfactory bulb, the rostral and caudal (Suárez and Mpodozis 2009). The rostral accessory bulb responds to pheromones in a general sexual context, and the caudal accessory bulb is active during intrasexual interactions. Unlike the murid rodents, degus exhibit considerable intraspecific variation (including sexual dimorphism) in the accessory bulb subdomains (Suárez and Mpodozis 2009). These observations suggest that the rostral and caudal subdomains regulate distinct functions. In degus the rostral accessory bulb is twice as large as the caudal

accessory bulb, which might be related to intersexual pheromonal sampling with body contact, as might occur during copulation. These observations support the hypothesis that sexual dimorphism in caviomorph sensory systems may emerge from sexual selection and not from species-specific adaptations.

Tang-Martinez (2003) argued that we need to better understand how the social environment influences development. In an integrative approach such an understanding would involve describing the neural pathways that are affected by variation during early social development. Moreover, epigenetic effects are established early in a rodent's life experience and are potentially reversible in adulthood (Weaver et al. 2004). Epigenetic modifications of specific genomic regions in response to variation in environmental conditions (maternal licking or grooming frequency) might serve as a major source of variation in behavioral phenotypes (Weaver et al. 2004). In other words, maternal effects could result in the transmission of adaptive responses across generations and affect chromatin structure by altering the hippocampal glucocorticoid receptors involved in maternal-offspring imprinting. Such influences could lead to alterations in social phenotypes (Weaver et al. 2004).

To date, research on cavies and degus has yielded some insight into how maternal behavior influences offspring development. Two studies in parallel (Ziabreva et al. 2003a, 2003b) demonstrated that adverse emotional experience during early postnatal development alters aminergic function within the degu brain. Repeated separation from the mothers and exposure to an unfamiliar environment results in the upregulation of monoaminergic systems of male and female pups, specifically dopamine and 5-hydroxytryptamine receptor density in the CA1 hippocampal region (Ziabreva et al. 2003a). Acoustic signals from mothers suppressed the upregulation of dopamine and 5-hydroxytryptamine receptors in some regions of the hippocampus (Ziabreva et al. 2003a). No significant changes were observed in the receptor density of gamma-aminobutyric acid (GABA_A) or in GABAergic systems, both of which modulate emotional and motivational aspects of degu behavior (Ziabreva et al. 2003a). The same pattern of neuroreceptor changes was found in the prefrontal cortex, but only in female pups (Ziabreva et al. 2003b). It is possible that the sex-specific responses to neonatal environmental change include an interaction of gonadal hormones with the function of hypothalamic pituitary axis activating "social buffering" and monoaminergic systems (Ziabreva et al. 2003a, 2003b).

Research on cavies and degus suggests that important neurological consequences to maternal separation exist during early offspring development, which could, in turn, influence social behavior (Fig. 1). Tamborski et al. (1990) determined that adverse emotional experiences influence the plasticity and adaptability of postnatal development of the brain of guinea pigs (*C. porcellus*). In this species maternal separation during weaning increased dopamine turnover (ratio of metabolites to dopamine), but only in novel situations, including exposure to

another individual or new environment. Imbalances of the dopamine receptors in degus resulting from chronic social isolation after weaning affect locomotor activities in novel environments (Braun et al. 2003). These studies demonstrate that mother-offspring vocalizations during early offspring development are correlated with neuroanatomical features in guinea pigs and degus.

In mammals, the consequences of early aversive environmental stimuli on brain function can be improved or prevented by the interaction with the mother via her vocalizations or other sensory signals (Fleming et al. 1999). Moreover, receptor changes in limbic structures can be suppressed by maternal calls (Ziabreva et al. 2003a). Suppression is mediated by the emotional rather than acoustic features of this auditory stimulus (Ziabreva et al. 2003a). These results support the hypothesis that mothers function as regulators of the socio-emotional environment of some caviomorphs during early postnatal development (Ziabreva et al. 2003a). Altogether, these results suggest that maternal care and vocalizations in rodents act as an emotional buffer, influencing the development and possibly adult social behavior of offspring.

Variation in brain size has been hypothesized to correlate with the diversity of social systems observed in mammals (Dunbar 1998). The social brain hypothesis posits that social living selects for larger brains and thus more neurons (Dunbar 1992, 1998). Evidence supporting the social brain hypothesis comes mostly from research on carnivores, primates, toothed whales (Delphinidae and Phocoenidae), and ungulates (Dunbar 1998; Dunbar and Bever 1998; Marino 1996; Pérez-Barbería and Gordon 2005; Shultz and Dunbar 2006). Alternatively, metabolic and energetic hypotheses might better explain the evolution of "brainy" rodents, including some caviomorphs (Isler and van Schaik 2006). These hypotheses predict that energy input is an issue in the maintenance of a relatively large brain and that brain mass is positively correlated with the basal metabolic rates in mammals, controlling for body-size effects. These hypotheses have been supported by the variation in brain mass of a large sample of 347 mammalian species (Isler and van Schaik 2006). Other factors such as neocortex size, activity period, and range size predict mammalian brain size (Dunbar and Shultz 2007). Group size and brain size, respectively, are influenced by ecological and life-history factors.

Future directions.—We need to describe the brain mechanisms underlying social behaviors in more caviomorph species before we can even approach an integrative model that includes neural pathways. Once this descriptive work is completed to some large extent, comparative studies with well-resolved phylogenies should be used. Such methods can be used to answer questions about the origins of novel anatomical traits and establish links between brain mechanisms and social behaviors across species. They also can be used to determine if similar brain mechanisms across rodent species can be linked to common habitat features (e.g., openness of habitat). Finally, given the remarkable diversity in body size and brain size of caviomorph rodents, comparative

approaches also could be useful in testing the predictions of the social brain hypothesis (Vassallo and Echeverría 2009).

An integrative model requires that we determine if intraspecific differences exist in neuroanatomy and social behavior. Intraspecific differences in social systems have been observed in some caviomorphs (Taraborelli and Moreno 2009; E. A. Lacey, University of California, Berkeley, pers. comm.; L. A. Ebensperger, pers. obs.), and some murid rodents (Hayes 2000; Roberts et al. 1998; Schradin et al. 2010; Schradin and Pillay 2005; Solomon and Crist 2008; Young and Wang 2004). The potential causes of intraspecific variation include divergence in neuroanatomical pathways due to differential selection pressures or selection for phenotypic plasticity in neuroanatomy. Widely distributed caviomorphs such as *coruros* or *degus* may provide excellent models for determining the effect of ecological variation on neuroanatomical features underlying social behaviors. To advance our understanding we need to develop field studies to quantify interpopulational variation in 3 areas, ecological conditions, social systems, and individual polymorphism for neurological characters. The inclusion of genetic comparisons in these field studies is crucial in determining the relative significance of divergence and plasticity as mechanisms for social evolution in caviomorphs.

Researchers studying the neurobiology of caviomorph rodents could take numerous other directions. Future tests of the social brain hypothesis must consider the nature of social bonds (including variables such as parental influences on pups, attachment, social affiliation, and social information processing) that define reciprocal relationship between brain mechanisms and social behavior (Young 2009). Research focusing on changes in connectivity between nodes of the emergent neural network (Young 2009) is crucial because this link generates the variability in social phenotypes (Curtis et al. 2007; Young 2009; Fig. 1).

Finally, the different social behaviors of mammals are regulated by a dynamic neural activity pattern, widely distributed in brain anatomy and under endocrine control (Goodson and Kabelik 2009). This pattern consists of interconnected nodes in its functional “neural context.” These nodes provide specific networks that also are interconnected (Goodson and Kabelik 2009; Newman 1999). This theoretical idea of an integrated, complex network with neuroanatomical features invites us to think beyond the discrete neuroanatomical structures, segregated and hierarchical. Additionally, it also contributes to our understanding of the neural context, focusing mainly on the pattern of neural activity that determines the social behavior network (Goodson and Kabelik 2009).

BEHAVIORAL ENDOCRINOLOGY

Current understanding.—An integrative understanding of caviomorph social systems requires an understanding of mechanisms underlying proximate causes. In this sense, hormones provide the link between genetic and ecological mechanisms that result in specific behavioral patterns (Nelson

2005). Researchers studying hormonal regulation of caviomorph social systems (mainly using *cavies* and *degus*) have focused on 2 main areas, the study of sexual hormones as determinants of aggression, breeding activity, and mating behavior, and the effects of various social contexts on the stress response. Studies on *cavies* have relied on laboratory experiments and observations. In contrast, studies on *degus* have used a combination of laboratory and field approaches.

A diversity of mating systems, including monogamy (*Galea*—Hohoff et al. 2002), polygyny (*Cavia aperea*—Sachser et al. 1999), and promiscuity (*Galea musteloides*—Sachser et al. 1999) have been documented in the *cavies*. This diversity of mating systems provides a mating system gradient in which comparative studies are possible. Laboratory observations reveal an increasing ratio of testis size to body size among species with the most promiscuous mating system (Sachser et al. 1999; Schwarz-Weig and Sachser 1996). In a comparison of domestic and wild guinea pigs, Künzl and Sachser (1999) observed that affiliative behavior was coupled with increasing levels of testosterone in the domestic forms and that stress response (as determined from blood cortisol levels) decreases with domestication. The relatively high social tolerance of domestic guinea pigs was associated with greater promiscuity. Thus, increasing levels of testosterone in domestic guinea pigs are not associated with male aggression but are more related to a promiscuous mating system. This “domestic” pattern contrasts with that of wild guinea pigs, whose mating system is characterized by female-defense polygyny and opportunistic male territoriality (Asher et al. 2008). In a context of sexual preferences females of domestic lines prefer to associate with males having relatively low basal levels of testosterone and that more quickly find a platform during a swim test (Bauer et al. 2008a). In addition, these males are less aggressive and maintain body mass during breeding season (Machatschke et al. 2008). Male testosterone is not influenced by social interactions with females, and females avoid aggressive males because of the potential negative fitness consequences to themselves and (or) their future offspring (Bauer et al. 2008a; Machatschke et al. 2008).

Cavies also have been studied in a context of social stress regulation. Prior to weaning, male and female guinea pig pups produce less cortisol after exposure to their mothers than after exposure to unfamiliar females (Hennessy et al. 2002). However, only males maintain this ability beyond the preweaning stage and well into preadolescent and nonbreeding adult stages (Hennessy et al. 2006). The prebreeding social environment also has subsequent, long-term effects on male stress responses. Maken and Hennessy (2009) studied the stress response of males at puberty to the social conditions experienced prior to puberty. They observed that single males housed with 2 unrelated females of similar age had different endocrine responses to preferred and unpreferred females. The presence of preferred females and not other females was linked to reduced cortisol levels in males at puberty. These results are intriguing because they demonstrate a selective social buffering effect on the plasma cortisol response in a

nonmonogamous species. Understanding these effects is important because stressors experienced during early ontogeny, and before breeding, could impact individual sensitivity to stress responses during subsequent life stages. For example, environmental or social stressors experienced during early development could influence dispersal and philopatry (de Fraipont et al. 2000) and consequently social structure. More generally, differences in the physiology and social behavior of domestic and wild cavies provide outstanding opportunities to conduct integrative studies to understand the evolution of various social and breeding strategies in caviomorphs.

In degus the annual breeding season (austral winter–spring) is marked by important changes in glucocorticoids and testosterone levels. Glucocorticoids (cortisol) increase in the females during late pregnancy and peak during lactation, suggesting that this period of the life cycle is the most energetically expensive (Kenagy et al. 1999). In males testosterone increases at the start of breeding, and this increase is associated with an increase in male–male aggression, social instability, and differences in male spatial behavior (Soto-Gamboa 2004, 2005; Soto-Gamboa et al. 2005). Similar to guinea pigs, male degus seem to use different mating strategies. Resident, territorial males monopolize females, possibly through female defense polygyny. These resident males are challenged by roaming, opportunistic males. Circulating testosterone levels of territorial males are higher than those of opportunistic males (Soto-Gamboa et al. 2005). In laboratory experiments reproductive males exposed to interactions with other reproductive males presented an increase in circulating testosterone levels, suggesting that male–male interactions effectively enhance the physiological response of males (Soto-Gamboa 2004). These results suggest that testosterone levels increase as response of male–male interactions, supporting the “challenge hypothesis” (Wingfield et al. 1990), and could determine mating strategies of males (Soto-Gamboa et al. 2005).

Understanding the impact of testosterone on social behavior can be difficult because testosterone can be measured as total testosterone (i.e., the concentration in the blood) and free testosterone (i.e., the amount of testosterone that is uncoupled to binding proteins). In degus the relationship between different forms of testosterone (total and free) suggests a complex endocrine regulation of male aggression. Both total and free testosterone are elevated and male–male aggressive behavior is common during the early breeding season when males seek female mating partners (Soto-Gamboa 2005). In contrast, total testosterone remains high but aggression is not evident during the late breeding season after most males have mated (Soto-Gamboa 2005). Therefore, aggression is regulated, apparently, only by free testosterone, and the remaining high levels of total testosterone during the late breeding season are not related to aggressive behavior. The observation that territorial males are characterized not only by elevated plasma testosterone levels but also by high plasma cortisol suggests that male–male interactions enhance testosterone secretion and increase social stress (Soto-Gamboa et al. 2005).

Research on murid rodents indicates that social stress experienced during early ontogeny influences the subsequent performance of adults. For example, in rats maternal licking and grooming reduces plasma adrenocorticotropin hormone and corticosterone responses of offspring. Under stress (by handling), mothers increase the amount of time spent licking and grooming pups, which in turn affects the development of the hypothalamic–pituitary–adrenal axis of pups (Meaney and Szyf 2005; Yamazaki et al. 2005). Pups exposed to chronic stress during early development experience behavioral anomalies such as anxiety and depression-like syndromes during adulthood (Gardner et al. 2009; Ladd et al. 2000). Degus exhibit behavioral and endocrine responses to social stressors during early postnatal development similar to those in rats. Upon maternal deprivation, pups of both sexes exhibit elevated glucocorticoid levels and activity (Gruss et al. 2006; Mohawk et al. 2005). However, only female offspring exhibit decreased plasma cortisol levels characteristic of an attenuated response after they are returned to their mothers (Gruss et al. 2006). Apparently, male degu pups are more sensitive than females to stressors (e.g., separation from parents) during early postnatal development.

Future directions.—The standardization of protocols to measure adrenocortical activity from glucocorticoid metabolites in cavies (Bauer et al. 2008b) and degus (Soto-Gamboa et al. 2009) has made it possible to study long-term effects of social stress under natural conditions. With these techniques available it is now possible to study the endocrine substrates of variation in social behavior and social systems. For example, degu social groups form by 2 mechanisms, natal philopatry by female offspring and the movement of offspring and adults between social groups (Ebensperger et al. 2009). Consequently, social groups consist of related and unrelated individuals (Ebensperger et al. 2004). Under these conditions individual stress responses could vary considerably, possibly explaining why group living has no effect or a negative effect on direct fitness (Ebensperger et al. 2007; Hayes et al. 2009). Understanding the physiological stress responses of degus in response to variation in social conditions has the potential to integrate some of the major costs of sociality into a general mechanistic framework (Pride 2005a). Thus, a major research focus of some of us (L. A. Ebensperger, L. D. Hayes, and M. Soto-Gamboa) is to determine the links between mechanisms of group formation, individual stress responses, and direct fitness.

Research aimed at understanding the physiological and reproductive responses of offspring to early social conditions could make major contributions to an integrative understanding of caviomorph sociality. As in guinea pigs, exposure to periodic stressors during prenatal and early postnatal development can have long-lasting effects on the adulthood survival and reproductive success of degu offspring (Blas et al. 2007; Naguib et al. 2006; Pride 2005b; Romero and Wikelski 2001). Such conditions also could affect social interactions that, in turn, can affect social structure. Among the most likely mechanisms linking stress response and fitness are the effects

on the cellular and humoral ability to mount an immune response against pathogens (Keita et al. 2007; Ndong et al. 2007), which in turn influences parasite infection (Barnard et al. 1998, 2003) and resistance (Kiank et al. 2006; Morales et al. 2006; Smith et al. 1996; but see Barnard et al. 2003). Research aimed at determining the links between stressors such as parasitism, the stress response, and fitness would increase our understanding of the evolutionary significance of intra- and interspecific variation in sociality in caviomorphs.

FITNESS CONSEQUENCES

Current understanding.—One of the challenges to developing an evolutionary-mechanistic model for caviomorph sociality is that our understanding of the reproductive fitness consequences of sociality is limited to a few species. Research usually focuses on individuals housed in the laboratory or in single natural populations. Laboratory studies on cavies (*Galea* and *Cavia*) demonstrate a link between social conditions, reproductive development, and reproductive success. For example, the presence of a male within a social unit influences the onset of maturity in cavies (*C. aperea*—Trillmich et al. 2008). In yellow-toothed cavies (*G. musteloides*) females housed with 4 males produce more surviving offspring than females housed with 1 male (Sachser et al. 1999). In this species the reproductive success of males is dependent on their social rank (Sachser et al. 1999). Together, these results suggest that group composition influences fitness. However, more research, using a range of species under natural conditions, is required before this hypothesis can be tested adequately.

Recent studies of 2 species, social tuco-tucos (*C. sociabilis*) and degus (*O. degus*), suggest that increasing sociality does not improve direct fitness and might be costly to females. In social tuco-tucos the percentage of time that pups are left unattended decreases with increasing group size (Izquierdo and Lacey 2007). The consistent presence of adult females at the nest may reduce the risk of predation or infanticide (Manning et al. 1995) and enhance the thermal environment in which pups are reared (Hayes and Solomon 2006). Thus, we might predict that the fitness of group-living females is greater than that of solitary females. In contrast to this prediction, female tuco-tucos living in groups wean significantly fewer pups (per breeding female, per year) than do solitary females (Lacey 2004). However, lifetime direct fitness of solitary and group-living females is statistically similar (Lacey 2004). Two factors might have contributed to these results: yearling females associated with groups have a higher probability of surviving to a 2nd year than solitary yearling females (Lacey 2004), and a greater proportion of lone females fail to breed (Lacey 2004).

Lactating degus indiscriminately rear offspring together in communal groups (Ebensperger et al. 2002, 2007), which often consist of kin (Ebensperger et al. 2004). Benefits of group living (e.g., reduced predation risk) have been observed (Ebensperger and Bozinovic 2000; Ebensperger

and Wallem 2002). As in social tuco-tucos, these benefits do not result in reproductive fitness advantages. In the laboratory groups of females rearing offspring together do not wean heavier offspring than solitary or singularly breeding females (Ebensperger et al. 2007). We have confirmed laboratory results with the observation that per capita direct fitness of “core” females (i.e., individuals that have considerable spatial overlap in the same burrow systems and are presumed to be caregivers) decreases with increasing number of core females per group in a natural population (Hayes et al. 2009). Per capita direct fitness and offspring survival are not affected by total group size, which includes females with only weak associations with core group members and males (Hayes et al. 2009). However, larger group size can lead to survival benefits to adults (Ebensperger and Wallem 2002) that increase the probability of breeding opportunities. Collectively, the work on degus and tuco-tucos points to the need for models that integrate cost-based predictions and neuroendocrine mechanisms (e.g., stress responses) to shed light on these neutral–negative fitness relationships (Schradin et al. 2010).

Future directions.—Current estimates of fitness consequences should be viewed as preliminary. Fitness estimates from laboratory observations and field studies based on per capita direct fitness, although useful, should be interpreted with caution. Direct measures of fitness in wild populations are required for a better understanding of fitness consequences. Estimates of both direct and indirect fitness are needed in species that live with kin (Ebensperger et al. 2004; Lacey and Ebensperger 2007; Lacey and Wiczorek 2003). Highly variable molecular markers (microsatellite primers) used to determine maternity and thus direct fitness have been developed for several species (Patagonian tuco-tuco [Lacey et al. 1999], degus [Quan et al. 2009], and coruros [Schroeder et al. 2000]). The application of these primers in field-based studies is crucial to testing predictions based on theories of kin selection and inclusive fitness (Hamilton 1964; Maynard-Smith 1964). Moreover, intraspecific variation in fitness can occur in species (coruros and degus) that occur in populations experiencing vastly different ecological conditions. Interpopulation comparisons of ecology, group size, and direct fitness (using molecular tools) would provide a strong understanding of the adaptive significance of sociality.

As the cavy research indicates (see above), reproductive fitness might not be equitable among group members, even when groups consist of kin (Gerlach and Bartmann 2002). Competition for resources or reduced maternal care (sensu Hayes and Solomon 2004) and differences in the physical condition (or status) of females could lead to interindividual variation in fitness within a group. Such variation could influence the stability of social groups. Unfortunately, per capita estimates cannot capture this variation because they assume that all females produce litters of equal size. Future work must include microsatellite primers to determine how variable fitness is among members of the same social group. Linking this variation back to neuroendocrine and neuroan-

atomical variation (see above) is an important step in developing an integrative model.

DISEASE ECOLOGY

Current understanding.—To this point we have focused on the underlying brain mechanisms and physiological sources of variation in group living and their fitness consequences, factors typically included in the discussion of integrative models of sociality. However, an all inclusive approach to understanding social variation also requires insight from disease ecology. Investigating disease dynamics in social mammals has utility in evolutionary ecology and applied fields of conservation and environmental health (Altizer et al. 2003). Parasites and pathogens, including helminths, arthropods, viruses, bacteria, and protozoa (Anderson and May 1992), are diverse and exhibit a variety of transmission modes. These include direct horizontal (contact transmitted) and vertical (parent to offspring) transmission and indirect modes via vectors or pathogen encounters in the environment. Particularly, group living can increase infection risk of contagious pathogens relative to solitary mammals due to increased contact between infected individuals and susceptible ones (Alexander 1974; Altizer et al. 2003; Møller et al. 1993). Furthermore, parasites and pathogens can drive the evolution of socially derived behaviors such as autogrooming and allogrooming (Dunbar 1991) and exclusion of unfamiliar individuals from entering social groups to reduce infection risk (Freeland 1976, 1979). Parasite infection also can induce immune responses and have consequences for fitness (Arnold and Lichtenstein 1993; Van Vuren 1996) and life history (Schwanz 2008). Thus, studies at the interface of behavioral ecology, parasitology, and immunology are needed to address contemporary questions regarding sociality, infection risk, and fitness consequences in mammals.

The general consensus is that increased infection risk by contact-transmitted parasites is a widespread burden of group-living species. A meta-analysis conducted by Côté and Poulin (1995) revealed a consistent positive trend between social-group size and parasite loads across a number of taxa, suggesting that increased infection is a cost of sociality. Specific examples of the interactions between sociality and parasitism are available in the literature on Nearctic rodents. For example, Hoogland (1979) found that parasite abundance is greater in highly social black-tailed prairie dogs (*Cynomys ludovicianus*) than in loosely colonial white-tailed prairie dogs (*C. leucurus*). In contrast, other studies on rodents (Arnold and Lichtenstein 1993; Hillegrass et al. 2008; Van Vuren 1996) failed to demonstrate significant relationships between social living and parasitism.

If parasitism is a cost of group living, increased infection levels may have profound fitness consequences in social mammals. In marmots (*Marmota*) reduced reproductive fitness has been attributed to high degrees of parasitism, which can result in slower pup growth rates and decreased overwinter survival of offspring (Arnold and Lichtenstein 1993; Van

Vuren 1996). A number of studies also have linked immune function and parasitism (Folstad and Karter 1992; Sheldon and Verhulst 1996). Social environment may influence immune quality (through stress) leading to various degrees of susceptibility to infection. For example, a trade-off between investment in immune function and sexual traits can result, particularly in males (Folstad and Karter 1992). Thus, the energetic costs of maintaining expensive, sexually selected traits (via testosterone) can influence parasite and pathogen susceptibility indirectly due to immune suppression (Sheldon and Verhulst 1996). Immune responses induced by pathogens alter physiology, are energetically costly, and subsequently might affect social interactions and fitness (see section on endocrine responses, above, for a brief discussion).

Future directions.—To our knowledge no studies of caviomorph rodents have investigated the “parasitism-as-a-cost-of-sociality hypothesis” (Côté and Poulin 1995). Unpublished data on degus by several of us (L. D. Hayes, J. R. Burger, and L. A. Ebensperger) and A. S. Chesh (Miami University) indicate that the abundance of exotic fleas (*Xenopsylla cheopis* and *Leptopsylla segnis*) on degus is not affected by social-group size or composition. Additional studies on caviomorphs are needed to determine the relationship between social organization and parasite and pathogen risk to provide insights into the generality of the patterns found by Côté and Poulin (1995). Mate selection and mating systems may be influenced by, and in return may influence, parasite loads in social species (Hamilton and Zuk 1982). Moreover, variation in maternal investment strategies such as singular versus communal nursing (Hayes 2000) may influence both horizontal transmission (mothers to mothers) and vertical transmission (mothers to offspring) of pathogens. Furthermore, plural breeders with communal care that exhibit allonursing also may assume additional infection risk from interactions between mothers and alien young (Roulin and Heeb 1999). Finally, parasites and pathogens also may influence, and be influenced by, social-group dynamics including philopatry and dispersal (Brown and Brown 1992). Thus, investigation into the interplay between sociality, immune function, and parasitism is needed to determine fitness consequences of infection in caviomorph rodents. Studies that manipulate parasite loads using parasite removal techniques (ivermectin or flea powder) can demonstrate causality and enable researchers to tease apart the links between sociality, parasitism, and fitness.

Emerging infectious diseases pose a threat to wildlife populations (Altizer et al. 2003). Group-living caviomorphs may be highly susceptible to exotic, Old World pathogens that have recently become cosmopolitan due to the introduction of Old World rats (*Rattus*) and mice (*Mus*) into the New World. Perhaps the best known example of the deleterious effects of exotic pathogens on native host populations of highly social rodents comes from prairie dogs. The introduction of plagues into North America has led to >95% mortality in infected prairie dog colonies, resulting in dramatic population declines (Cully et al. 2006). The potential for population declines as a

result of infection by exotic pathogens is high because caviomorph rodents have had little evolutionary time to develop defense mechanisms against Old World parasites. Future studies are needed to determine the presence of exotic parasites and pathogens in caviomorph populations, the effect of sociality on their transmissibility, and subsequent fitness, life-history, and immune-system consequences.

Epidemiological models have long recognized the importance of population size and density in maintaining disease epidemics (Anderson and May 1992; de Jong et al. 1995; Dietz 1988); however, social interactions within populations are rarely homogenous. Kinship and mating systems can influence these heterogeneous interactions among social animals (Altizer et al. 2003; Emlen 1997). Yet, studies that address the links between group living and parasitism have focused largely on group size as the primary measure of sociality (Brown and Brown 1986; Côté and Poulin 1995; Hoogland 1979). Therefore, it is likely that variability in interactions among individuals within a population occurs spatially and temporally, resulting in various degrees of individual susceptibility to parasites and pathogens. Thus, group-level analyses likely fail to capture the role of heterogeneous social interactions in influencing parasite and pathogen transmission. Mathematical techniques that account for variability in social interactions among individuals within a population (e.g., social network analysis—Wey et al. 2008) are needed to increase our understanding of parasite transmission and disease risk in social caviomorph rodents.

MOVING TOWARD AN INTEGRATIVE UNDERSTANDING

The recent emphasis on using integrative approaches to better understand social phenotypes has moved the field of behavioral ecology in new directions (Owens 2006). Although interesting and powerful on their own, traditional ecological models for social systems (Brashares and Arcese 2002) require the integration of genetic, neuroanatomical, and endocrine mechanisms. Understanding these mechanisms is crucial to understanding how natural selection can shape social phenotypes, particularly in species with wide geographical ranges. Future work aimed at establishing some of these mechanisms and their links to fitness is possible in some of the better-studied caviomorph species (coruros and degus). However, information on less-studied species also is needed before we can use powerful comparative approaches to determine when certain mechanisms evolved and how similarities in ecology influence the expression of mechanisms underlying social behaviors. Additionally, a better understanding of how social systems are influenced by pathogens, or influence the spread of disease, has important evolutionary and practical applications. Thus, it is important that future directions include the role of disease ecology in social caviomorph evolution. Behavioral ecologists studying caviomorphs need to work with anatomists, disease ecologists, molecular biologists, and physiologists to generate testable predictions and methods that can be integrated into field studies. In doing so, we will

overcome some of the major roadblocks to integrative research (time, expense, and lack of experience) and establish new paradigms for research.

RESUMEN

Durante los años 1990 y 2000 se planteó que antes de realizar generalizaciones sobre la sociabilidad en roedores era necesario examinar la vida social en un grupo conocido como caviomorfos (histicognatos del Nuevo Mundo). En particular, se indentificaron 3 áreas especialmente deficitarias: mecanismos proximales de la sociabilidad, importancia del ambiente social durante el desarrollo, y variación geográfica asociada a los sistemas sociales dentro de cada especie. Desde entonces se ha avanzado bastante en describir los sistemas sociales de varias especies, incluyendo algunas con rangos geográficos amplios. También ha habido progreso en relación al efecto del ambiente social durante el desarrollo, así como en identificar costos y beneficios de la vida social. Sin embargo, se ha avanzado menos en determinar los mecanismos proximales del comportamiento social, lo que ha limitado el desarrollo de una teoría integrada (mecanicista-evolutiva) para la sociabilidad. Para avanzar en este objetivo es necesario abordar al menos 3 temas principales: consecuencias reproductivas de la vida social, bases neuroanatómicas, y mecanismos endocrinos de la sociabilidad. Para facilitar esta tarea revisamos el conocimiento existente en cada una de estas áreas. Proponemos que es fundamental determinar los factores ecológicos que afectan la transmisión de parásitos y enfermedades, particularmente aquellas originarias del Viejo Mundo, para identificar nexos entre fenotipo social, mecanismos y adecuación.

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LITERATURE CITED

- ADLER, G. H. 2011. Spacing patterns and social mating systems of echimyid rodents. *Journal of Mammalogy* 92:31–38.
- ADRIAN, O., G. DEKOMIEN, J. T. EPPLER, AND N. SACHSER. 2008. Body weight and rearing conditions of males, female choice and paternities in a small mammal, *Cavia aperea*. *Ethology* 114:897–906.
- ALEXANDER, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.

- ALTIZER, S., ET AL. 2003. Social organization and disease risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution and Systematics* 34:517–547.
- ANDERSON, R. M., AND R. M. MAY. 1992. Infectious disease of humans: dynamics and control. Oxford University Press, Oxford, United Kingdom.
- ARNOLD, W., AND A. V. LICHTENSTEIN. 1993. Ectoparasite loads decrease the fitness of alpine marmots (*Marmota marmota*) but are not a cost of sociality. *Behavioral Ecology* 4:36–39.
- ASHER, M., T. LIPPMANN, J. T. EPPLER, C. KRAUS, F. TRILLMICH, AND N. SACHSER. 2008. Large males dominate: ecology, social organization, and mating system of wild cavies, the ancestors of the guinea pig. *Behavioral Ecology and Sociobiology* 62:1509–1521.
- BARNARD, C. J., J. M. BEHNKE, A. R. GAGE, H. BROWN, AND P. R. SMITHURST. 1998. The role of parasite-induced immunodepression, rank and social environment in the modulation of behaviour and hormone concentration in male laboratory mice (*Mus musculus*). *Proceedings of the Royal Society of London, B. Biological Sciences* 265:693–701.
- BARNARD, C. J., ET AL. 2003. Local variation in helminth burdens of Egyptian spiny mice (*Acomys cahirinus dimidiatus*) from ecologically similar sites: relationships with hormone concentrations and social behaviour. *Journal of Helminthology* 77:197–207.
- BAUER, B., J. DITTAMI, AND I. H. MACHATSCHKE. 2008a. Stress responses of male guinea pigs predict female preference. *Ethology* 114:677–685.
- BAUER, B., R. PALME, I. H. MACHATSCHKE, J. DITTAMI, AND S. HUBER. 2008b. Non-invasive measurement of adrenocortical and gonadal activity in male and female guinea pigs (*Cavia aperea f. porcellus*). *General and Comparative Endocrinology* 156:482–489.
- BEERY, A. K., E. A. LACEY, AND D. D. FRANCIS. 2008. Oxytocin and vasopressin receptor distributions in a solitary and a social species of tuco-tuco (*Ctenomys haigi* and *Ctenomys sociabilis*). *Journal of Comparative Neurology* 507:1847–1859.
- BLAS, J., G. R. BORTOLOTTI, J. L. TELLA, R. BAOS, AND T. A. MARCHANT. 2007. Stress response during development predicts fitness in a wild, long lived vertebrate. *Proceedings of the National Academy of Sciences* 104:8880–8884.
- BRASHARES, J. S., AND P. ARCESE. 2002. Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. *Journal of Animal Ecology* 71:626–638.
- BRAUN, K., P. KREMZ, W. WETZEL, T. WAGNER, AND G. POEGGEL. 2003. Influence of parental deprivation on the behavioral development in *Octodon degus*: modulation by maternal vocalizations. *Developmental Psychobiology* 42:237–245.
- BRENNAN, P. A., AND E. B. KEVERNE. 2004. Something in the air? New insights into mammalian pheromones. *Current Biology* 14:R81–R89.
- BROWN, C. R., AND M. B. BROWN. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonata*). *Ecology* 67:1206–1218.
- BROWN, C. R., AND M. B. BROWN. 1992. Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology* 73:1718–1723.
- CÔTÉ, I. M., AND R. POULIN. 1995. Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology* 6:159–165.
- CULLY, J. F., JR., D. E. BIGGINS, AND D. B. SEERY. 2006. Conservation of prairie dogs in areas with sylvatic plague. Pp. 157–168 in *Conservation of the black-tailed prairie dog* (J. L. Hoogland, ed.). Island Press, Washington, D.C.
- CURTIS, J. T., Y. LIU, J. ARAGONA, AND Z. WANG. 2007. Neural regulation of social behavior in rodents. Pp. 185–194 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- CUTRERA, A. P., C. D. ANTINUCCI, M. S. MORA, AND A. I. VASSALLO. 2006. Home-range and activity patterns of the South American subterranean rodent *Ctenomys talarum*. *Journal of Mammalogy* 87:1183–1191.
- DE FRAIPONT, M., J. CLOBERT, H. JOHN-ALDER, AND S. MEYLAN. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *Journal of Animal Ecology* 69:404–413.
- DE JONG, M. C. M., O. DIEKMANN, AND H. HEESTERBEEK. 1995. How does transmission of infection depend on population size? Pp. 84–94 in *Epidemic models, their structure and relation to data* (D. Mollison, ed.). Cambridge University Press, Cambridge, United Kingdom.
- DIETZ, K. 1988. Density-dependence in parasite transmission dynamics. *Parasitology Today* 4:91–97.
- DONALDSON, Z. R., AND L. J. YOUNG. 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 317:900–904.
- DUNBAR, R. I. M. 1991. Functional significance of social grooming in primates. *Folia Primatologica* 57:121–131.
- DUNBAR, R. I. M. 1992. Neocortex size as a constraint on group-size in primates. *Journal of Human Evolution* 22:469–493.
- DUNBAR, R. I. M. 1998. The social brain hypothesis. *Evolutionary Anthropology* 6:178–190.
- DUNBAR, R. I. M., AND J. BEVER. 1998. Neocortex size predicts group size in carnivores and some insectivores. *Ethology* 104:695–708.
- DUNBAR, R. I. M., AND S. SHULTZ. 2007. Evolution in the social brain. *Science* 317:1344–1347.
- EBENSPERGER, L. A. 1998. Sociality in rodents: the New World fossorial hystricognaths as study models. *Revista Chilena de Historia Natural* 71:65–77.
- 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.
- EBENSPERGER, L. A., AND F. BOZINOVIC. 2000. Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? *Behavioral Ecology and Sociobiology* 47:365–369.
- EBENSPERGER, L. A., A. S. CHESH, R. CASTRO, L. ORTIZ, J. R. BURGER, AND L. D. HAYES. 2009. Factors influencing the social dynamics of juvenile degus, *Octodon degus*. *Ethology* 115:540–554.
- EBENSPERGER, L. A., AND H. COFRÉ. 2001. On the evolution of group-living in the New World cursorial hystricognath rodents. *Behavioral Ecology* 12:227–236.
- EBENSPERGER, L. A., AND M. J. HURTADO. 2005. Seasonal changes in the time budget of degus, *Octodon degus*. *Behaviour* 142:91–112.
- EBENSPERGER, L. A., M. J. HURTADO, AND C. LEÓN. 2007. An experimental examination of the consequences of communal versus solitary breeding on maternal condition and the early postnatal growth and survival of degu, *Octodon degus*, pups. *Animal Behaviour* 73:185–194.
- EBENSPERGER, L. A., M. J. HURTADO, M. SOTO-GAMBOA, E. A. LACEY, AND A. T. CHANG. 2004. Communal nesting and kinship in degus (*Octodon degus*). *Naturwissenschaften* 91:391–395.
- EBENSPERGER, L. A., R. SOBRERO, V. CAMPOS, AND S. M. GIANNONI. 2008. Activity, range areas, and nesting patterns in the viscacha rat, *Octomys mimax*: implications for its social organization. *Journal of Arid Environments* 72:1174–1183.
- EBENSPERGER, L. A., C. VELOSO, AND P. K. WALLEM. 2002. Do female degus communally nest and nurse their pups? *Journal of Ethology* 20:143–146.

- EBENSPERGER, L. A., AND P. K. WALLEM. 2002. Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. *Oikos* 98:491–497.
- EMLEN, S. T. 1997. Predicting family dynamics in social vertebrates. Pp. 228–253 in *Behavioral ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, eds.). Blackwell Science, Oxford, United Kingdom. Vol. 10.
- FINK, S., L. EXCOFFIER, AND G. HECKEL. 2006. Mammalian monogamy is not controlled by a single gene. *Proceedings of the National Academy of Sciences* 103:10956–10960.
- FLEMING, A. S., D. H. O'DAY, AND G. W. KRAEMER. 1999. Neurobiology of mother–infant interactions: experience and central nervous system plasticity across development and generations. *Neuroscience and Biobehavioral Reviews* 23:673–685.
- FOLSTAD, I., AND A. J. KARTER. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139:603–622.
- FREELAND, W. J. 1976. Pathogens and the evolution of primate sociality. *Biotropica* 8:12–24.
- FREELAND, W. J. 1979. Primate social groups as biological islands. *Ecology* 60:719–728.
- FREITAS, J. N. S., C. N. EL-HANI, AND P. L. B. DA ROCHA. 2008. Affiliation in four echimyid rodent species based on intrasexual dyadic encounters: evolutionary implications. *Ethology* 114:389–397.
- GALLARDO, M. H., ET AL. 2004. Whole-genome duplications in South American desert rodents (Octodontidae). *Biological Journal of the Linnean Society* 82:443–451.
- GARDNER, K. L., M. W. HALE, S. L. LIGHTMAN, P. M. PLOTSKY, AND C. A. LOWRY. 2009. Adverse early life experience and social stress during adulthood interact to increase serotonin transporter mRNA expression. *Brain Research* 1305:47–63.
- GERLACH, G., AND S. BARTMANN. 2002. Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). *Behavioral Ecology* 13:408–418.
- GOODSON, J. L., AND D. KABELIK. 2009. Dynamic limbic networks and social diversity in vertebrates: from neural context to neuromodulatory patterning. *Frontiers in Neuroendocrinology* 30:429–441.
- GRUSS, M., S. WESTPHAL, C. LULEY, AND K. BRAUN. 2006. Endocrine and behavioural plasticity in response to juvenile stress in the semi-precocial rodent *Octodon degus*. *Psychoneuroendocrinology* 31:361–372.
- HAMILTON, W. D. 1964. The genetical theory of social behavior. *Journal of Theoretical Biology* 7:1–51.
- HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.
- HAYES, L. D. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour* 59:677–688.
- HAYES, L. D., ET AL. 2009. Fitness consequences of group living in *Octodon degus*, a plural breeder rodent with communal care. *Animal Behaviour* 78:131–139.
- HAYES, L. D., AND N. G. SOLOMON. 2004. Costs and benefits of communal rearing to female prairie voles (*Microtus ochrogaster*). *Behavioral Ecology and Sociobiology* 56:585–593.
- HAYES, L. D., AND N. G. SOLOMON. 2006. Mechanisms of maternal investment by communal prairie voles, *Microtus ochrogaster*. *Animal Behaviour* 72:1069–1080.
- HENNESSY, M. B., G. HORNSCHUH, S. KAISER, AND N. SACHSER. 2006. Cortisol responses and social buffering: a study throughout the life span. *Hormones and Behavior* 49:383–390.
- HENNESSY, M. B., S. K. O'LEARY, J. L. HAWKE, AND S. E. WILSON. 2002. Social influences on cortisol and behavioral responses of preweaning, periadolescent, and adult guinea pigs. *Physiology and Behavior* 76:305–314.
- HERRERA, E. A., V. SALAS, E. R. CONGDON, M. J. CORRIALE, AND Z. TANG-MARTÍNEZ. 2011. Capybara social structure and dispersal patterns: variations on a theme. *Journal of Mammalogy* 92: 12–20.
- HILLEGRASS, M. A., J. M. WATERMAN, AND J. D. ROTH. 2008. The influence of sex and sociality on parasite loads in an African ground squirrel. *Behavioral Ecology* 19:1006–1011.
- HOHOFF, C., ET AL. 2002. Monogamy in a new species of wild guinea pigs (*Galea* sp.). *Naturwissenschaften* 89:462–465.
- HOUGLAND, J. L. 1979. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: *Cynomys* spp.) coloniality. *Behaviour* 69:1–35.
- INSEL, T. R., AND L. J. YOUNG. 2000. Neuropeptides and the evolution of social behavior. *Current Opinions in Neurobiology* 10:784–789.
- ISLER, K., AND C. P. VAN SCHAİK. 2006. Metabolic costs of brain size evolution. *Biology Letters* 2:557–560.
- IZQUIERDO, G., AND E. A. LACEY. 2007. Effects of group size on nest attendance in the communally breeding colonial tuco-tuco. *Mammalian Biology* 73:438–443.
- KAISER, S., F. P. M. KRUIJVER, D. F. SWAAB, AND N. SACHSER. 2003. Early social stress in female guinea pigs induces a masculinization of adult behavior and corresponding changes in brain and neuroendocrine function. *Behavioural Brain Research* 144:199–210.
- KEITA, A. V., L. STERTMAN, Y. Q. SUN, A. LARHED, I. SJÖHOLM, AND J. D. SÖDERHOLM. 2007. Effects of chronic stress on the immune response to oral human serum albumin-conjugated starch micro-particles in rats. *Journal of Neuroimmunology* 183:33–42.
- KELLIHER, K. R. 2007. The combined role of the main olfactory and vomeronasal systems in social communication in mammals. *Hormones and Behavior* 52:561–570.
- KENAGY, G. J., N. J. PLACE, AND C. VELOSO. 1999. Relation of glucocorticoids and testosterone to the annual cycle of free-living *degus* in semiarid central Chile. *General Comparative Endocrinology* 115:236–243.
- KIANK, C., B. HOLTFRETER, A. STARKE, A. MUNDT, C. WILKE, AND C. SCHÜTT. 2006. Stress susceptibility predicts the severity of immune depression and the failure to combat bacterial infections in chronically stressed mice. *Brain, Behavior, and Immunity* 20:359–368.
- KÜNZL, C., AND N. SACHSER. 1999. The behavioral endocrinology of domestication: a comparison between the domestic guinea pig (*Cavia aperea* f. *porcellus*) and its wild ancestor, the cavy (*Cavia aperea*). *Hormones and Behavior* 35:28–37.
- LACEY, E. A. 2004. Sociality reduces individual direct fitness in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*). *Behavioral Ecology and Sociobiology* 56:449–457.
- LACEY, E. A., AND L. A. EBENSPERGER. 2007. Social structure in octodontid and ctenomyid rodents. Pp. 403–415 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- LACEY, E. A., J. E. MALDONADO, J. P. CLABAUGH, AND M. D. MATOCQ. 1999. Interspecific variation in microsatellites isolated from tuco-tucos (Rodentia: Ctenomyidae). *Molecular Ecology* 8:1753–1768.
- LACEY, E. A., AND P. W. SHERMAN. 2007. The ecology of sociality in rodents. Pp. 243–254 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.

- LACEY, E. A., AND J. R. WIECZOREK. 2003. Ecology of sociality in rodents: a tenomysid perspective. *Journal of Mammalogy* 84:1198–1211.
- LADD, C. O., R. L. HUOT, K. V. THRIVIKRAMAN, C. B. NEMEROFF, M. J. MEANEY, AND P. M. PLOTSKY. 2000. Long-term behavioral and neuroendocrine adaptations to adverse early experience. *Progress in Brain Research* 122:81–103.
- LIM, M. M., Z. WANG, D. OLAZÁBAL, X. REN, E. F. TERWILLIGER, AND L. J. YOUNG. 2004. Enhanced partner preference in promiscuous species by manipulating the expression of a single gene. *Nature* 429:754–757.
- MACDONALD, D. W., E. A. HERRERA, B. TABER, AND J. R. MOREIRA. 2007. Social organization and resource use in capybaras and maras. Pp. 393–402 in *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- MACHATSCHKE, I., B. BAUER, C. SCHRAUF, J. DITTAMI, AND B. WALLNER. 2008. Conflict-involvement of male guinea pigs (*Cavia aperea* f. *porcellus*) as a criterion for partner preference. *Behavioral Ecology and Sociobiology* 62:1341–1350.
- 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.
- MAKEN, D. S., AND M. B. HENNESSY. 2009. Development of selective social buffering of the plasma cortisol response in laboratory-reared male guinea pigs (*Cavia porcellus*). *Behavioral Neuroscience* 123:347–355.
- MANNING, C. J., D. A. DEWSBURY, E. K. WAKELAND, AND W. K. POTTS. 1995. Communal nesting and nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour* 50:741–751.
- MARINO, L. 1996. What can dolphins tell us about primate evolution? *Evolutionary Anthropology* 5:81–86.
- MAYNARD-SMITH, J. 1964. Group selection and kin selection. *Nature* 201:1145–1147.
- MEANEY, M. J., AND M. SZYF. 2005. Maternal care as a model for experience-dependent chromatin plasticity? *Trends in Neurosciences* 28:456–463.
- MOHAWK, J. A., K. CASHEN, AND T. M. LEE. 2005. Inhibiting cortisol response accelerates recovery from a photic phase shift. *American Journal of Physiology—Regulatory, Integrative and Comparative Physiology* 288:R221–R228.
- MÖLLER, A. P., R. DUFVA, AND K. ALLANDER. 1993. Parasites and the evolution of host social behavior. *Advances in the Study of Behavior* 22:65–102.
- MORALES, J., ET AL. 2006. Higher stress protein levels are associated with lower humoral and cell-mediated immune responses in pied flycatcher females. *Functional Ecology* 20:647–655.
- NAGUIB, M., A. NEMITZ, AND D. GIL. 2006. Maternal developmental stress reduces reproductive success of female offspring in zebra finches. *Proceedings of the Royal Society of London, B. Biological Sciences* 273:1901–1905.
- NDONG, D., Y. Y. CHEN, Y. H. LIN, B. VASEEHARAN, AND J. C. CHEN. 2007. The immune response of tilapia *Oreochromis mossambicus* and its susceptibility to *Streptococcus iniae* under stress in low and high temperatures. *Fish and Shellfish Immunology* 22:686–694.
- NELSON, R. J. 2005. An introduction to behavioral endocrinology. 3rd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- NEWMAN, S. W. 1999. The medial extended amygdala in male reproductive behavior: a node in the mammalian social behavior network. *Annals of the New York Academy of Sciences* 877:242–257.
- OWENS, I. P. F. 2006. Where is behavioral ecology going? *Trends in Ecology & Evolution* 21:356–361.
- PÉREZ-BARBERÍA, F. J., AND I. J. GORDON. 2005. Gregariousness increases brain size in ungulates. *Oecologia* 145:41–52.
- PRIDE, R. E. 2005a. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16:550–560.
- PRIDE, R. E. 2005b. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biology Letters* 1:60–63.
- QUAN, Y. F., M. D. MACMANES, L. A. EBENSPERGER, E. A. LACEY, AND L. D. HAYES. 2009. Isolation and characterization of polymorphic microsatellite loci from *Octodon degus*. *Molecular Ecology Resources* 9:999–1001.
- QUIRICI, V., R. A. CASTRO, J. OYARZÚN, AND L. A. EBENSPERGER. 2008. Evidence of social monitoring during foraging in a diurnal small mammal. *Animal Cognition* 11:441–448.
- QUISPE, R., C. P. VILLAVICENCIO, A. CORTÉS, AND R. VÁSQUEZ. 2009. Inter-population variation in hoarding behaviour in degus, *Octodon degus*. *Ethology* 115:465–474.
- ROBERTS, R. L., B. S. CUSHING, AND C. S. CARTER. 1998. Intraspecific variation in the induction of female sexual receptivity in prairie voles. *Physiology and Behavior* 64:209–212.
- ROMERO, L. M., AND M. WIKELSKI. 2001. Corticosterone levels predict survival probabilities of Galápagos marine iguanas during El Niño events. *Proceedings of the National Academy of Sciences* 98:7366–7370.
- ROULIN, A., AND P. HEEB. 1999. The immunological function of allosuckling. *Ecology Letters* 5:319–324.
- SACHSER, N., E. SCHWARZ-WEIG, A. KEIL, AND J. T. EPPLIN. 1999. Behavioural strategies, testis size, and reproductive success in two caviomorph rodents with different mating systems. *Behaviour* 136:1203–1217.
- SALVADOR, C. H., AND F. A. S. FERNANDEZ. 2008. Reproduction and growth of a rare, island-endemic cavy (*Cavia intermedia*) from southern Brazil. *Journal of Mammalogy* 89:909–915.
- SANTOS, J. W. A., AND E. A. LACEY. 2011. Burrow sharing in the desert-adapted torch-tail spiny rat, *Trinomys yonenaegae*. *Journal of Mammalogy* 92:3–11.
- SCHRADIN, C., B. KÖNIG, AND N. PILLAY. 2010. Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology* 79:515–521.
- SCHRADIN, C., AND N. PILLAY. 2005. Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* 86:99–107.
- SCHROEDER, J. W., R. L. HONEYCUTT, A. P. ROONEY, G. HAN, S. BEGALL, AND M. H. GALLARDO. 2000. Microsatellites from the South America coruro, *Spalacopus cyanus*. *Molecular Ecology* 9:1447–1449.
- SCHWANZ, L. E. 2008. Persistent effects of maternal parasitic infection on offspring fitness: implications for adaptive reproductive strategies when parasitized. *Functional Ecology* 22:691–698.
- SCHWARZ-WEIG, E., AND N. SACHSER. 1996. Social behaviour, mating system and testes size in cuis (*Galea musteloides*). *Zeitschrift für Säugetierkunde* 61:25–38.
- SHELDON, B. C., AND S. VERHULST. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution* 11:317–321.
- SHULTZ, S., AND R. I. M. DUNBAR. 2006. Both social and ecological factors predict ungulate brain size. *Proceedings of the Royal Society of London, B. Biological Sciences* 273:207–215.

- SILK, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 362:539–559.
- SMITH, F. V., C. J. BARNARD, AND J. M. BEHNKE. 1996. Social odours, hormone modulation and resistance to disease in male laboratory mice, *Mus musculus*. *Animal Behaviour* 52:141–153.
- SOLOMON, N. G., AND T. O. CRIST. 2008. Estimates of reproductive success for group-living prairie voles, *Microtus ochrogaster*, in high-density populations. *Animal Behaviour* 76:881–892.
- SOTO-GAMBOA, M. 2004. Formación y estabilidad de estructuras sociales en micromamíferos, su regulación hormonal y la importancia de las interacciones entre machos. Ph.D. dissertation, Pontificia Universidad Católica de Chile, Santiago, Chile.
- SOTO-GAMBOA, M. 2005. Free and total testosterone levels in the field males of *Octodon degus* (Rodentia, Octodontidae): accuracy of the hormonal regulation of behavior. *Revista Chilena de Historia Natural* 78:229–238.
- SOTO-GAMBOA, M., S. GONZALEZ, L. D. HAYES, AND L. A. EBENSPERGER. 2009. Validation of a radioimmunoassay for measuring fecal cortisol metabolites in the hystricomorph rodent, *Octodon degus*. *Journal of Experimental Zoology, A. Ecological Genetics and Physiology* 311:496–503.
- SOTO-GAMBOA, M., M. VILLALÓN, AND F. BOZINOVIC. 2005. Social cues and hormone levels in male *Octodon degus* (Rodentia): a field test of the challenge hypothesis. *Hormones and Behavior* 47:311–318.
- SUÁREZ, R., AND J. MPODOZIS. 2009. Heterogeneities of size and sexual dimorphism between the subdomains of the lateral-innervated accessory olfactory bulb (AOB) of *Octodon degus* (Rodentia: Hystricognathi). *Behavioural Brain Research* 198:306–312.
- TABER, A. B., AND D. W. MACDONALD. 1992. Communal breeding in the mara, *Dolichotis patagonum*. *Journal of Zoology (London)* 227:439–452.
- TAMBORSKI, A., J. B. LUCOT, AND M. B. HENNESSY. 1990. Central dopamine turnover in guinea pig pups during separation from their mothers in a novel environment. *Behavioral Neuroscience* 104:607–611.
- TANG-MARTÍNEZ, Z. 2003. Emerging themes and future challenges: forgotten rodents, neglected questions. *Journal of Mammalogy* 84:1212–1227.
- TARABORELLI, P., AND P. MORENO. 2009. Comparing composition of social groups, mating system and social behaviour in two populations of *Microcavia australis*. *Mammalian Biology* 74:15–24.
- TRIBOLLET, E., C. BARBERIS, M. DUBOIS-DAUPHIN, AND J. J. DREIFUSS. 1992. Localization and characterization of binding sites for vasopressin and oxytocin in the brain of the guinea pig. *Brain Research* 589:15–23.
- TRILLMICH, F., C. LAURIEN-KEHNEN, O. ADRIAN, AND S. LINKE. 2006. Age at maturity in cavies and guinea-pigs (*Cavia aperea* and *Cavia aperea f. porcellus*): influence of social factors. *Journal of Zoology (London)* 268:285–294.
- TRILLMICH, F., B. MUELLER, S. KAISER, AND J. KRAUSE. 2008. Puberty in female cavies (*Cavia aperea*) is affected by photoperiod and social conditions. *Physiology and Behavior* 96:476–480.
- VAN VUREN, D. 1996. Ectoparasites, fitness, and social behavior of yellow-bellied marmots. *Ethology* 102:686–694.
- VÁSQUEZ, R. A. 1997. Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. *Revista Chilena de Historia Natural* 70:557–563.
- VASSALLO, A. I., AND A. I. ECHEVERRÍA. 2009. Evolution of brain size in a highly diversifying lineage of subterranean rodent genus *Ctenomys* (Caviomorpha: Ctenomyidae). *Brain, Behavior and Evolution* 73:138–149.
- WEAVER, I. C. G., ET AL. 2004. Epigenetic programming by maternal behavior. *Nature Neuroscience* 7:847–854.
- WEY, T., D. T. BLUMSTEIN, W. SHEN, AND F. JORDÁN. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* 75:333–344.
- WINGFIELD, J. C., R. E. HEGNER, A. M. DUFTY, JR., AND G. F. BALL. 1990. The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist* 136:829–846.
- YAMAZAKI, A., Y. OHTSUKI, T. YOSHIHARA, S. HONMA, AND K. I. HONMA. 2005. Maternal deprivation in neonatal rats of different conditions affects growth rate, circadian clock, and stress responsiveness differentially. *Physiology and Behavior* 86:136–144.
- YOUNG, A. J., A. A. CARLSON, S. L. MONFORT, A. F. RUSSELL, N. C. BENNETT, AND T. CLUTTON-BROCK. 2006. Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences* 103:12005–12010.
- YOUNG, L. J. 2009. The neuroendocrinology of the social brain. *Frontiers in Neuroendocrinology* 30:425–428.
- YOUNG, L. J., AND Z. WANG. 2004. The neurobiology of pair bonding. *Nature Neuroscience* 7:1048–1054.
- ZIABREVA, I., G. POEGGEL, R. SCHNABEL, AND K. BRAUN. 2003a. Separation-induced receptor changes in the hippocampus and amygdala of *Octodon degus*: influence of maternal vocalizations. *Journal of Neuroscience* 23:5329–5336.
- ZIABREVA, I., R. SCHNABEL, G. POEGGEL, AND K. BRAUN. 2003b. Mother’s voice “buffers” separation-induced receptor changes in the prefrontal cortex of *Octodon degus*. *Neuroscience* 119:433–441.

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