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Sociality, glucocorticoids and direct fitness in the communally rearing rodent, *Octodon degus*

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ABSTRACT

While ecological causes of sociality (or group living) have been identified, proximate mechanisms remain less clear. Recently, close connections between sociality, glucocorticoid hormones (cort) and fitness have been hypothesized. In particular, cort levels would reflect a balance between fitness benefits and costs of group living, and therefore baseline cort levels would vary with sociality in a way opposite to the covariation between sociality and fitness. However, since reproductive effort may become a major determinant of stress responses (i.e., the cort–adaptation hypothesis), cort levels might also be expected to vary with sociality in a way similar to the covariation between sociality and fitness. We tested these expectations during three years in a natural population of the communally rearing degu, *Octodon degus*. During each year we quantified group membership, measured fecal cortisol metabolites (a proxy of baseline cort levels under natural conditions), and estimated direct fitness. We recorded that direct fitness decreases with group size in these animals. Secondly, neither group size nor the number of females (two proxies of sociality) influenced mean (or coefficient of variation, CV) baseline cortisol levels of adult females. In contrast, cortisol increased with per capita number of offspring produced and offspring surviving to breeding age during two out of three years examined. Together, our results imply that variation in glucocorticoid hormones is more linked to reproductive challenge than to the costs of group living. Most generally, our study provided independent support to the cort–adaptation hypothesis, according to which reproductive effort is a major determinant, yet temporally variable, influence on cort–fitness covariation.

Introduction

Animal social groups range from short-term associations and aggregations (e.g., foraging or roosting groups) to relatively long-term socially cohesive units (e.g., communally rearing groups) (Krause and Ruxton, 2002; Parrish et al., 1997). Among the vertebrates, considerable intra- and inter-specific variation in the number and composition of group members characterizes socially cohesive groups (Lott, 1991). Variation in sociality is thought to reflect a trade-off between current fitness benefits and costs that emerge from individuals' decision to join or leave groups (e.g., Clark and Mangel, 1986; Krause and Ruxton, 2002; Vásquez and Kacelnik, 2000). Decreased predation risk, decreased burrowing costs, enhanced access to resources, and decreased thermoregulatory costs represent benefits that may cause the formation and maintenance of social groups (Alexander, 1974; Bertram, 1978; Ebensperger, 2001; Ebensperger and Blumstein, 2006; Ebensperger and Cofré, 2001). Fitness costs may arise from group living due to increased parasitism and competition over resources (Hoogland, 1995).

While ecological causes of sociality have been well identified (e.g., Brashares and Arcese, 2002; Ebensperger and Blumstein, 2006), proximate mechanisms remain less understood. Recently however, glucocorticoid hormones (e.g., cortisol, corticosterone) have been involved in a connection between sociality and fitness (Pride, 2005a). Glucocorticoid hormones (i.e., cort) are a major component of the hypothalamus–pituitary–adrenocortical system mediating between different allostatic states, including stress responses (Bartolomucci, 2007; Landys et al., 2006). One critical metabolic function of glucocorticoids is to divert energy from long-term storage for immediate use (Sapolsky et al., 2000). Baseline and seasonal baseline levels of these hormones are associated with normal physiological function and predictable demands (Bonier et al., 2009a; Landys et al., 2006). Short-term elevation of glucocorticoids above these baseline levels (e.g., under acute stress) is generally beneficial and thus, does not

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lower lifetime reproductive success. However, if corts remain elevated beyond baseline for long periods, the associated metabolic costs may exceed available resources and lower lifetime reproductive success (Bonier et al., 2009a; Landys et al., 2006; Sapolsky, 1985). Based on these considerations, the cort–fitness hypothesis predicts that high baseline in response to environmental challenges are associated with low fitness (Bonier et al., 2009a). An extension of these arguments to sociality theory is that cort levels reflect a balance between fitness benefits and costs of group living (i.e., Pride, 2005a). If correct, cort levels should vary with sociality in a way opposite to the covariation between sociality and fitness.

More recently, the cort–fitness hypothesis has been modified into the cort–adaptation hypothesis to accommodate the fact that the relationship between cort levels and fitness may depend on the reproductive effort of individuals (Bonier et al., 2009b). The cort–adaptation hypothesis posits that high baseline cort levels (i.e., seasonal baseline) are necessary to sustain reproductive challenges (Bonier et al., 2009a,b; Landys et al., 2006). In this sense, reproductive individuals are considered to be in good condition when able to sustain elevated levels of baseline cort. Thus the predicted relationship between fitness (i.e., reproductive success) and cort levels is positive whenever reproduction is the major determinant of predictable demands relative to ecological factors (Bonier et al., 2009a). When it comes to the potential link between secretion of cort, sociality and fitness, cort levels should vary with sociality in a way similar to the covariation between sociality and fitness, especially during breeding.

Few studies have examined these predicted relationships, and results are far from conclusive. For ring-tailed lemurs (*Lemur catta*), Pride (2005a) reported a fit between a non-linear, inverted U-shaped regression between fecal cortisol and group size, and the non-linear U-shaped relation between fitness costs and group size. While important to stimulate subsequent studies, the function of fitness costs reported by Pride (2005a) was derived from theoretical (i.e., optimal group theory) considerations rather than empirical data and thus, cannot be considered a strong test of a hypothesis. In rodents fecal corticosterone in adult male gerbils does not vary with group (family) size (Rogovin et al., 2003), a pattern that agreed with the observation that reproductive success in this species is not influenced by group size (Randall et al., 2005). In birds, plasma corticosterone levels were reported to increase with colony size in cliff swallows (Raouf et al., 2006), a pattern that agreed with the observation that offspring survival decreases with colony size in some years, but not in others (Brown and Brown, 1996). Although these pioneering studies established a framework for understanding endocrine consequences of sociality in wild populations, it is still too early to claim a general understanding of a connection between group living, cort levels, and fitness patterns.

Model species and predictions

Several studies of cort variation in social mammals have focused on singular breeding species (i.e., species where breeding is monopolized by one or a few group members) (for a review see Creel, 2005), but in which comparisons of cort levels among conspecifics may be confounded by the pronounced differences in social and reproductive status that occur within groups. Thus, studies on plural breeding species (i.e., in which breeding is shared more equally among group members) provide a more direct system for examining endocrine consequences of sociality per se.

Degus are plurally breeding rodents with communal care (Silk, 2007) i.e., multiple lactating females share underground nests and rear their litters communally (Ebensperger et al., 2002, 2004, 2007). Natural populations are located throughout central Chile where females typically breed once per year in late autumn (May-June) and give birth to litters of precocial offspring in late winter to early spring (September–October) (Ebensperger and Hurtado, 2005). Most intriguingly, 85–90% of adults do not survive to their second year of age (Ebensperger et al., 2009; Meserve et al., 1993), implying that success during the first (and solely for most) breeding event has a major effect on lifetime fitness. Most critical, field and laboratory studies have revealed that direct fitness either decreases or does not change with increasing group size in degus (Ebensperger et al., 2007; Hayes et al., 2009).

In this study, we used live-trapping and radio-telemetry techniques to examine how variation in direct fitness across multiple years in a degu population track variation in cortisol (the main glucocorticoid in degus, Kenagy et al., 1999; Soto-Gamboa et al., 2005) and sociality. Based on previous evidence (Ebensperger et al., 2007; Hayes et al., 2009) we first verified the prediction that (i) direct fitness decreases with increasing group size in degus. Then we examined whether (ii) cort levels increase with the size of social groups, but (iii) decreases with increasing fitness. These observations would imply that cort levels in social degus reflect mainly the cumulative stress response to conditions in the social environment (e.g., Bonier et al., 2009a). However, (iv) an observation that cort decreases or does not vary with increasing group size, and (v) increases with increasing fitness would imply cort levels in social degus reflect a neuroendocrine connection to reproductive effort (Bonier et al., 2009b). Based on previous evidence supporting that effects of cort secretion is context dependent (Angelier et al., 2009; Breuner et al., 2008), we tested the prediction that (vi) covariation between sociality and cort levels varies across years of study (Bonier et al., 2009b).

Given that costs and benefits may not be the same for all group members (Ebensperger et al., 2007; Krause and Ruxton, 2002) and that individuals may vary in responsiveness to environmental and social challenges (e.g., Koren et al., 2008; Smith and French, 1997), (vii) we further predicted intra-group variation in cort to vary with group size. For instance, a direct association between variability in cort and group size would indicate that some individuals in larger groups are more challenged than others.

Materials and methods

Study population

The study was conducted between 2008 and 2010 on a natural population of degus at the Estación Experimental Rinconada de Maipú, a field station of Universidad de Chile. This study area is characterized by a Mediterranean climate with cold, wet winters and warm, dry summers (di Castri and Hajek, 1976). Previous studies have revealed that degus at this population face seasonal and inter annual variation in ecological conditions such as food availability and abundance of predators (Ebensperger et al., 2011; Ebensperger and Hurtado, 2005; Quirici et al., 2010).

Determination of social groups and degu abundance

Social groups were determined in September through October, months in which females are lactating. Degus are diurnally active and remain in underground burrows overnight. Thus, the main criterion used to assign degus to social groups was the sharing of burrow systems during night time (Ebensperger et al., 2004). The sharing of burrow systems was established by means of (i) night time telemetry, and (ii) burrow trapping in August-October. During burrow trapping, we defined a burrow system as a group of burrow openings surrounding a central location where individuals were repeatedly found during night time telemetry and usually spanning 1–3 m in diameter (Fulk, 1976; Hayes et al., 2007). The total number of burrow systems trapped per year at Rinconada was 43 in 2008, 48 in 2009, and 42 in 2010. These burrows were trapped an average (±SE) of 45 ± 2 days in 2008, 44 ± 1 days in 2009, and 42 ± 2 days in 2010. Eight traps (model 201 Tomahawk, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) were used per day at each burrow system. The area