



Stress levels of dominants reflect underlying conflicts with subordinates in a cooperatively breeding species

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Abstract

Maintaining dominance status had long been considered to be less stressful than subordination. However, no consistency in stress levels of dominant and subordinate individuals has been demonstrated. Tactics used to achieve and maintain dominance could be determinant. In cooperatively breeding species, conflicts between dominants and subordinates are expected since dominant individuals tend to monopolize reproduction while subordinates seldom reproduce. Reproductive skew models predict that subordinates' reproductive opportunities are either allotted or subject to competition with dominants. In the former case, no policing of subordinates by dominants is expected. In the latter, dominant should exert a control over the subordinates possibly leading to higher stress levels in dominants than in subordinates, which could be further elevated as the number of potential competitors in the group increases. In the present study, we aimed to test these hypotheses by assessing individual's stress level using the neutrophils to lymphocytes ratio (N:L) in a wild cooperatively breeding rodent, the Alpine marmot (*Marmota marmota*). We found that dominants exhibit higher N:L ratio than subordinates and that dominants' N:L ratio increases with the number of unrelated same-sex subordinates in the group. We conclude that controlling unrelated subordinates is stressful for dominants, as expected under tug-of-war models. These stress patterns reveal conflicting relationships between dominants and subordinates over the reproduction and social status acquisition. This study highlights the influence of the nature, strength, and direction of conflicts on stress levels.

Significance Statement

In cooperatively breeding species, reproductive skew models predict that subordinates' reproductive opportunities are either allotted or subject to competition with dominants and, thus, can modulate the relative stress level between dominants and subordinates. In the first case, no policing of subordinates by dominants is expected, while in the second, dominant should exert a control over the subordinates which should lead to higher stress level in dominants than in subordinates, and particularly when subordinates are unrelated to the dominants. In Alpine marmots, we found that dominants exhibit higher stress level than subordinates and dominants' stress level increased with the number of unrelated same-sex subordinates. These patterns are in agreement with the predictions of the tug-of-war models of reproductive skew and indicate that controlling subordinates is costly for dominants.

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Introduction

Group living leads to major conflicts over resource partitioning (Krause and Ruxton 2002; Hennessy et al. 2009) and dominance hierarchies evolved to avoid the resultant costs of overt competition and aggression among group members (Enquist and Leimar 1990). Agonistic interactions arising from social conflicts are known to activate the stress response through the stimulation of the hypothalamic-pituitary-adrenocortical axis, which result in adrenal glucocorticoids secretion (hereafter GC) typically cortisol and

corticosterone (von Holst 1998). Early experiments in captive rodents and primates showed higher levels of GC in winners (so-called dominants) compared to losers (so-called subordinates) at the end of a confrontation (Bronson and Eleftheriou 1964; Louch and Higginbotham 1967; Manogue et al. 1975). Thus, Creel (2001) hypothesized that, in hierarchical societies, social dominance should be less stressful than subordination. However, other studies indicate no consistent relationship between GC levels and social rank among mammalian species (Sapolsky 1983; Abbott 1987; Creel 2005). These contradictory findings suggest that differential stress level in subordinates and dominants may be ascribed to other factors than purely their social rank, which complicate the conventional view of social stress and our understanding of the mechanisms underlying the evolution of social hierarchies (Creel et al. 2013).

Although higher stress level in dominants than in subordinates may arise from their different investment in specific behaviors, such as reproductive activity (Saltzman et al. 1994; Smith and French 1997) or defense against intruders (e.g., Cooney 2002; Garvy et al. 2015), variations between dominants and subordinates can also originate from different tactics to achieve and maintain social status (Abbott et al. 2003; Goymann and Wingfield 2004; Creel et al. 2013). Dominants appear less stressed than subordinates in groups where subordinates endure high rates of physical or psychological stressors, where fewer sources of social support are available, and where relatedness between dominants and subordinates is low (Abbott et al. 2003). In contrast, in relatively nonaggressive groups in which assessing dominance mostly depends on rare instances of aggression at times of vacated dominant positions and where the maintenance of dominance requires little threat or intimidation, dominants may be more stressed than subordinates (Abbott et al. 2003). For example, in adult male olive baboons (*Papio anubis*), for which violent actions are key to reach dominance and where threat and intimidation are necessary to its maintenance, basal cortisol concentration of dominants is nearly 50% lower than that of subordinates (Sapolsky 1983). Conversely, subordinate female common marmosets (*Callithrix jacchus*) living in a relatively nonaggressive society (Lazaro-Perea 2001) had lower basal plasma cortisol levels than dominant females (Saltzman et al. 1998).

Despite the fact that, in such cooperatively breeding societies, severe conflicts between dominants and subordinates are to be expected (Young et al. 2006), aggressive interactions are rarely observed between group members (Creel et al. 1992, 1997). Indeed, in such despotic societies, a pair of dominant individuals tends to monopolize reproduction while subordinates only obtain a small share of reproduction (Clutton-Brock et al. 1998, 2010). The reproductive skew theory offers one potential explanation for this low level of declared conflicts: each group member is allotted or gains inclusive fitness

equal to or exceeding their expectation from reproducing on their own (Nonacs and Hager 2011). Under transactional models, reproductive concession by dominants rewards cooperative behaviors of subordinates (Johnstone and Cant 1999; Buston et al. 2007). Conversely, tug-of-war models assume that reproductive opportunities are obtained by subordinates from dominants through competition (Reeve 1998; Reeve and Shen 2006). Under the former, no policing of subordinates by dominants is expected and stress levels of dominants and subordinates should be comparable while under the later, dominants should exert a control over subordinates which should lead to higher stress level in dominants than in subordinates and their stress level should increase with the number of potential competitors in the group (Creel 2001; Goymann et al. 2003). Accordingly, the stress level of dominants should increase with the size of the social group (e.g. Pride 2005), and more specifically, with the number of sexually mature same-sex subordinates. Moreover, competition between dominants and subordinates should be all the more acute when the indirect fitness benefits obtained through helping are low (Hatchwell and Sharp 2006; Meade and Hatchwell 2010; Nam et al. 2010). As a consequence, the presence of unrelated subordinates in family groups may further increase the stress level of dominants (Arnold and Dittami 1997; Goymann and Wingfield 2004; Galvao-Coelho et al. 2012).

Here, we aimed to test whether predictions of transactional or of tug-of-war models regarding the stress level of dominants and subordinates apply to the Alpine marmot (*Marmota marmota*). The Alpine marmot is a cooperatively breeding, ground-dwelling squirrel living in family groups composed of a dominant pair (higher hierarchical rank) that monopolizes reproduction, and of sexually mature and immature subordinates of both sexes (lower hierarchical rank) (Allainé 2000). Subordinate males act as “helpers” and have a positive effect on juvenile survival during hibernation (Allainé and Theuriat 2004). Nonetheless, there is a strong intra-sexual competition between dominants and subordinates as evidenced by a decrease in the dominants’ body condition and a higher probability of losing its reproduction and social status as the number of same-sex subordinates increases (Cohas et al. 2006; Lardy et al. 2012, 2013; Bichet et al. 2016). We used the neutrophils to lymphocytes ratio (hereafter N:L ratio) from peripheral blood as a proxy of circulating GC (Davis et al. 2008) to assess basal stress level of adult Alpine marmots outside their mating period. According to previous findings indicating that dominant Alpine marmots exert a costly control over their subordinates (Arnold and Dittami 1997; Cohas et al. 2006; Lardy et al. 2012, 2013; Bichet et al. 2016), we expect dominant marmots to exhibit higher N:L ratio than subordinates, as predicted under the tug-of-war models. Social factors, such as group size and composition, are also expected to impact dominant’s stress level. Specifically, dominants living with a higher number of same-sex sexually mature subordinates

should have higher N:L ratio, which should be further elevated and this all the more that subordinates are unrelated to the dominant.

Material and methods

Studied species

Alpine marmots are territorial, socially monogamous and cooperative breeding ground-dwelling squirrels inhabiting alpine meadows (Allainé 2000). Marmots live in family groups of two to 16 individuals composed of a dominant pair, sexually mature (≥ 2 years) and immature (1 year) subordinates of both sexes, and pups of the year (Allainé 2000). Each family group occupies a territory mainly defended by the dominant pair. Dominant pairs nearly exclusively monopolize the reproduction within family groups (Cohas et al. 2006) and actively inhibit the reproduction of the sexually mature subordinates through aggressive behaviors (Arnold and Dittami 1997; Hacklander et al. 2003). No hierarchy has been observed among subordinates (Barash 1976; Perrin 1993).

At sexual maturity (i.e., 2 years of age), subordinates of both sexes may either keep their subordinate status, attempt to become dominants in their natal groups (15% of the dominant males, 35% of the dominant females) or disperse to attempt to gain dominance in another territory (Lardy et al. 2012). An individual can never join another social group than its natal group as a subordinate (Allainé 2000). Dominance is established for several years until the dominant is evicted by another individual or dies (Lardy et al. 2011). Once an individual reaches dominance, it cannot reverse to subordinate status. Sexually mature male subordinates that delay dispersal are considered as helpers. The presence of helpers in a family group increases the survival probability of offspring during their first hibernation (Allainé and Theuriau 2004) through their role in social thermoregulation (Arnold 1988).

Field methods

Our study took place at La Grande Sassièrre Nature Reserve (2340 m a.s.l., French Alps, 45° 29' N, 65° 90' E, see Cohas et al. 2008) where a population of Alpine marmots has been monitored since 1990. As part of a long-term study, we captured marmots annually, from mid-April to mid-July using two-door live-capture traps baited with dandelion (*Taraxacum officinale*). We placed traps near the entrance of the main burrows of each group to assign trapped individuals to their family. We checked the traps every 30 min to limit the time a marmot spent in a trap and thus exposure to predators and to adverse weather. Once trapped, we placed the marmots in an opaque bag and carried them

to a nearby (maximum 500 m) handling area. There, they were placed in a calm and cool room for 5 min allowing them to recover from the stress of capture and transport before tranquilization. We tranquilized each captured individual by intramuscular injection of Zolétil 100 (Tilamine + Zolazépam, 10 mg kg⁻¹) and determined their mass, sex, and age. We assessed the social status (dominant or subordinate) through examination of sexual traits (large scrotum for males and prominent teats for females, characteristics of each sex all year round and independently of pup production). We marked each individuals with a microchip inserted percutaneously (model ID100, 0.9 cm long, < 0.1 cm in diameter, Trovan Ltd, www.Trovan.com, Identifikationssysteme, Metternicher Straße 4, 53919 Weilerswist, Germany) for permanent individual recognition and a numbered metal ear-tag. An additional colored plastic ear-tag was placed on the opposite ear of dominant individuals. The marking did not cause any bleeding. Later, we confirmed each individual's social status by observations of scent-marking behavior and territorial defense that are characteristics of dominants (Bel et al. 1999).

Each year, we determined the size and the composition of each family group combining individuals' capture histories with intensive daily observations (see Cohas et al. 2008 for details). Finally, we counted the number of pups through additional observations (see Cohas et al. 2006) and capture them within 3 days after their first emergence from the natal burrow.

Group size and composition

We characterized each family group by its size and composition. To infer the level of competition between individuals, we defined "group size" as the number of individuals 1 year old or older in the group including the dominant pair. To assess variations in the level of intra-sexual competition, we used two types of group-level measurements. First, we used the number of sexually mature same-sex subordinates present in the group (i.e., ≥ 2 years old). Second, we determined the numbers of same-sex unrelated and mature related subordinates to the dominant. A subordinate was considered as "related" (94.1% of subordinates for the dominant females and 93.7% for the dominant males) if it was born during the dominance tenure (i.e. son/daughter of the dominant) and as "unrelated" (5.9% of subordinates for the dominant females and 6.3% for the dominant males) if born when another dominant was holding the territory.

Assessment of basal stress level through measures of neutrophils to lymphocytes (N:L) ratio

We measured the N:L ratio as a proxy of basal glucocorticoids which is a good indicator of the level of environmental stress

to which an individual was exposed. We chose to measure the N:L ratio because it is more likely to reflect the basal stress level of captured animals, than measuring plasma GC concentration itself. Indeed, plasma GC rises critically within 2 to 5 min following capture and restraint in wild-caught animals (Romero and Romero 2002; Romero and Reed 2005; Johnstone et al. 2012), making it extremely difficult to obtain reliable baseline measures of stress level under field conditions. An understanding of the effect of stress hormones on leukocyte profiles comes from biomedical studies on mammals (Ottaway and Husband 1994; Brenner et al. 1998). GC stimulates an influx of neutrophils from tissues into the blood (Bishop et al. 1968); concomitantly, it causes a migration of lymphocytes from the blood circulation to other compartments (Cohen 1972; Fauci 1975; Dhabhar 2002). Thus, a rise of plasma GC caused by stress increases the N:L ratio (Davis et al. 2008). Unlike the hormonal response to acute stress, the initial leukocyte response begins over a time span of hours (between 1 and 4 h; Burguez et al. 1983; Davis 2005; López-Olvera et al. 2007). We measured N:L ratio from 298 blood samples drawn within 30 min after capture from the great saphenous vein of 171 sexually mature individuals (i.e., 2 years and older) trapped in the 36 family groups monitored from 2009 to 2015. This sampling was done during a period ranging from the gestation of females to the weaning of pups. Immediately upon collection, a drop of blood was smeared onto a slide and air dried. We used the May Grünwal Giemsa staining method (Brown 1993) for differential counting of blood cells using an aerospray stainer (Aerospray Hematology Slide/Cytocentrifuge 7150, ELITechGroup, Wescor, France). The smears were screened by a single observer using a light microscope with 10× ocular and 100× oil immersion lenses until up to 100 leukocytes. Neutrophils and lymphocytes were determined according to Hawkey and Dennett's (1989) criteria and counted. Furthermore, to distinguish between stress and immune response effects on N:L ratio (Davis et al. 2008), we controlled for other parameters specific of an immune response: the leukocytes concentration and the number of eosinophils and monocytes (see Supplementary material S1).

Statistical analyses

Do dominants have higher stress level than subordinates?

To investigate whether the N:L ratio differed between dominants and subordinates, we used the N:L ratio ($N = 298$ from 81 dominants and 90 subordinates) as the dependent variable and the social status as an explanatory variable in a Generalized Linear Mixed Model (GLMM) with a logarithm link and a variance given by a gamma distribution, due to the overdispersion of our data. The gamma distribution was chosen a priori by fitting the observed distribution of the N:L ratio

using the R package `fitdistrplus` (Delignette-Muller and Dutang 2015). We further checked a posteriori the distribution of the residuals to assess the fit of the selected model to the observed data. Additionally, we entered potential confounding variables such as the sex, the body mass and the age of the individual as well as the year and the date of capture as explanatory variables with all the continuous variables standardized (by subtracting to each value the mean of the variable and dividing it by the squared variance of the variable). Additive effects of all these variables as well as the first order interactions between the year and the date of capture and between all individual variables and the social status were considered. To control for a potential “territory” effect and pseudo-replication due to N:L ratio being measured several times (median = 1.00, mean = 2.01, min = 1, max = 5) on a given animal over years, we included the territory and the identity of the individuals as random intercepts.

Does dominants' stress level vary with group size and composition?

To investigate if the N:L ratio of a dominant individual was influenced by the size and the level of competition in its family group, we used the N:L ratio of dominant individuals ($N = 196$ from 79 individuals) as the response variable in a generalized linear model (GLM) with a logarithm link and a variance given by a gamma distribution. Because the random intercepts of the territory and the identity of the individual were estimated close to 0 in this case, leading to convergence failure, we discarded them for this model. We built three different models. In the first, we included the group size as an explanatory variable; in the second, the number of sexually mature same-sex subordinates; and in the third, the numbers of related and unrelated same-sex subordinates. In each model, we entered the same confounding variables as above (sex, body mass, age, the date and the year of capture and their first order interaction) as explanatory variables.

Statistical analyses were performed with R 3.3.1 (R Development Core Team 2016). The function “`glmer`” in the package “`lme4`” (Bates et al. 2015) was used to fit GLMMs with a negative binomial distributions (Venables and Ripley 2002). The function “`glm`” in the package “`stats`” was used to perform GLMs (R Development Core Team 2016). We set the level of significance to $\alpha = 0.05$ and parameter estimates are given as mean \pm SE.

Data availability Datasets will be available under https://www.researchgate.net/publication/323550862_Data_for_Stress_levels_of_dominants_reflect_underlying_conflicts_with_subordinates_in_a_cooperatively_breeding_species upon request to the corresponding author.

Results

Do dominants have higher stress level than subordinates?

Dominant individuals had a higher N:L ratio than subordinate individuals ($\beta = 0.60 \pm 0.15$, $t = 4.13$, $p < 0.001$, marginal $R^2 = 0.25$, conditional $R^2 = 0.52$, Fig. 1, Table 1) and N:L ratio did not depend on the sex of the dominant individual ($\beta = 0.03 \pm 0.22$, $t = 0.13$, $p = 0.89$). Further, dominants have higher N:L ratio than their same-sex subordinates (female $\beta = 0.54 \pm 0.20$, $t = 2.65$, $p = 0.008$; male $\beta = 0.79 \pm 0.22$, $t = 3.65$, $p < 0.001$).

Does dominants' stress level vary with group size and composition?

The N:L ratio of dominant individuals was not correlated with the group size ($\beta = 0.003 \pm 0.03$, $t = 0.12$, $p = 0.90$, $R^2 = 0.17$, Table 2) and this independently of the sex of the dominant (interaction between sex and group size: $\beta = -0.06 \pm 0.05$, $t = -0.17$, $p = 0.24$).

The dominants' N:L ratio was not correlated with the number of same-sex subordinates ($\beta = 0.09 \pm 0.08$, $t = 1.11$, $p = 0.27$, $R^2 = 0.17$, Table 2) and this independently of the sex of

Table 1 Effect of the social status on the N:L ratio. Model parameters were obtained once all non-significant first order interactions were removed. Significant effects are in bold

Fixed effects	Estimate \pm SE	<i>t</i> value	<i>p</i> value
Intercept	1.63 \pm 0.44	3.73	< 0.001
Social status (dominant)	0.60 \pm 0.15	4.13	< 0.001
Sex (male)	0.14 \pm 0.13	1.02	0.31
Body mass	-0.79 \pm 0.19	-4.11	< 0.001
Age	0.23 \pm 0.07	3.17	0.002
Date of capture	-0.57 \pm 0.17	-3.42	< 0.001
Year 2012	0.74 \pm 0.23	3.26	0.001*
Year 2013	0.46 \pm 0.23	2.04	0.04*
Year 2014	0.46 \pm 0.29	1.59	0.11*
Year 2015	0.70 \pm 0.29	2.43	0.01*
Year 2012: Date of capture	0.75 \pm 0.26	2.86	0.004**
Year 2013: Date of capture	1.04 \pm 0.29	3.66	< 0.001**
Year 2014:Date of capture	0.68 \pm 0.35	1.95	0.05**
Year 2015:Date of capture	0.88 \pm 0.34	2.62	0.01**

*Wald-test for the year effect: $\chi^2 = 11.5$, $df = 4$, $p = 0.022$; **Wald-test for the interactive effect between the year and the date of capture: $\chi^2 = 18.7$, $df = 4$, $p < 0.001$: first-order interaction

the dominant (interaction between sex and number of same-sex subordinates: $\beta = -0.11 \pm 0.15$, $t = -0.72$, $p = 0.47$).

Fig. 1 Residual N:L ratio as a function of social status. The open circles represent the observed values and the closed circles represent the estimated N:L ratio surrounded by their standard errors. The scale of the y-axis is logarithmic

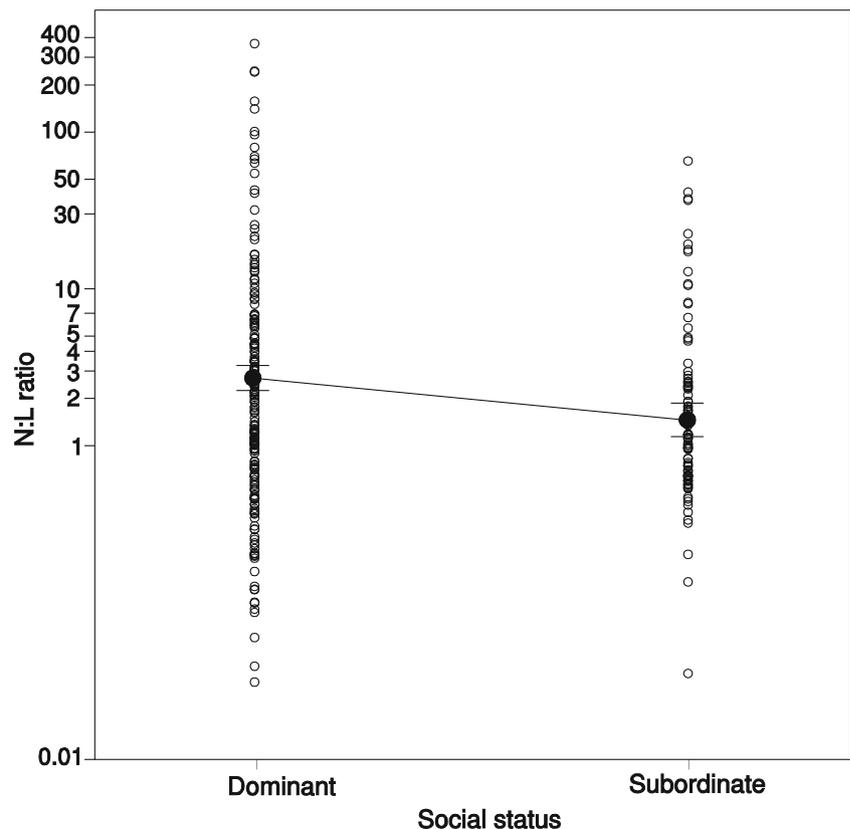


Table 2 Effects of group size and composition on the dominants' N:L ratio. Model parameters were obtained once all non-significant first order interactions were removed. Significant effects are in bold

Models	Model 1			Model 2			Model 3		
	Estimate ± SE	t value	p value	Estimate ± SE	t value	p value	Estimate ± SE	t value	p value
Intercept	0.41 ± 0.42	0.98	0.33	0.38 ± 0.41	0.93	0.36	0.23 ± 0.40	0.56	0.58
Social variables:	0.003 ± 0.03	0.12	0.90	–	–	–	–	–	–
Group size	–	–	–	0.09 ± 0.08	1.11	0.27	–	–	–
Number of same-sex subordinates	–	–	–	–	–	–	0.04 ± 0.08	0.48	0.63
Number of related same-sex subordinates	–	–	–	–	–	–	0.51 ± 0.24	2.18	0.03
Number of unrelated same-sex subordinates	–	–	–	–	–	–	0.21 ± 0.06	3.38	0.001
Age	0.17 ± 0.06	2.84	0.005	0.15 ± 0.06	2.58	0.01	0.21 ± 0.06	3.38	0.001
Sex (male)	0.26 ± 0.11	2.27	0.02	0.26 ± 0.11	2.29	0.02	0.22 ± 0.11	1.92	0.06
Body mass	–0.31 ± 0.23	–1.39	0.17	–0.32 ± 0.23	–1.41	0.16	–0.26 ± 0.22	–1.18	0.24
Date of capture	–0.57 ± 0.21	–2.63	0.009	–0.60 ± 0.22	–2.80	0.006	–0.63 ± 0.21	–3.00	0.003
Year 2012	0.89 ± 0.29	3.10	0.002	0.94 ± 0.29	3.25	0.001	0.86 ± 0.29	3.02	0.003
Year 2013	0.78 ± 0.29	2.69	0.008	0.85 ± 0.29	2.90	0.004	0.84 ± 0.28	2.95	0.004
Year 2014	0.43 ± 0.37	1.17	0.24	0.46 ± 0.37	1.24	0.22	0.47 ± 0.36	1.31	0.19
Year 2015	0.79 ± 0.34	2.33	0.02	0.81 ± 0.34	2.40	0.02	0.67 ± 0.33	2.01	0.05
Year 2012:Date of capture	0.73 ± 0.35	2.07	0.04	0.78 ± 0.35	2.21	0.03	0.71 ± 0.35	2.02	0.05
Year 2013:Date of capture	0.93 ± 0.39	2.39	0.02	1.03 ± 0.39	2.63	0.01	0.99 ± 0.38	2.58	0.01
Year 2014: Date of capture	0.57 ± 0.44	1.30	0.20	0.59 ± 0.44	1.34	0.18	0.59 ± 0.43	1.39	0.17
Year 2015: Date of capture	0.92 ± 0.41	2.24	0.03	0.94 ± 0.41	2.32	0.02	0.83 ± 0.40	2.07	0.04

While the N:L ratio of dominant individuals was not correlated with the number of same-sex sons/daughters ($\beta = 0.04 \pm 0.08$, $t = 0.48$, $p = 0.63$, Fig. 2a, Table 2), it increased with the number of same-sex unrelated subordinates ($\beta = 0.51 \pm 0.24$, $t = 2.18$, $p = 0.03$, $R^2 = 0.19$, Fig. 2b, Table 2). Again, the dominants' N:L ratio was not correlated with their sex (interaction between sex and number of same-sex sons/daughters: $\beta = -0.17 \pm 0.15$, $t = -1.13$, $p = 0.26$; interaction between sex and number of same-sex unrelated subordinates: $\beta = 0.19 \pm 0.47$, $t = 0.40$, $p = 0.69$).

Discussion

We showed that dominant males and females had a higher N:L ratio (indicating higher stress level) than subordinate individuals in our Alpine marmot population (Fig. 1). Moreover, the N:L ratio of the dominant individuals of both sexes varied neither with the size of the group nor with the number of same sex subordinates but it increased with the number of same sex unrelated subordinates (Table 2). Our data support that dominants thus exert a costly control over their subordinates to prevent them from reproducing in agreement with the tug-of-war models. As expected from kin selection (Hatchwell and Sharp 2006), the costs associated with such control increase with lower relatedness between group members. These findings demonstrate that, although social hierarchy is thought to have evolved to limit the costs associated with conflicts

among group members, this hierarchy at best reduces the costs of intra-group competition.

That dominant marmots show higher N:L ratio than subordinates corroborates previous findings in several cooperatively breeding vertebrates (see Creel 2001). However, these results stand in stark contrast with other studies showing no clear association between social rank and stress level or even a higher stress level in subordinates than in dominants (Table 3). The social organization alone is likely insufficient to explain the diversity of associations between social status and levels of GC observed in cooperative breeders (Table 3). Indeed, the discrepancies between social rank and stress levels in cooperative breeders could rather be explained by crucial differences in the nature of social relationships between group members (Abbott et al. 2003; Sapolsky 2005; Creel et al. 2013). Cooperatively breeding species strongly differ in the size and composition of social groups, especially in terms of relatedness between group members, type of hierarchy, pattern of dominance acquisition and maintenance (Table 3). However, in almost all cooperative breeders, reproduction tends to be monopolized by dominants (Clutton-Brock et al. 2010) and the reproductive skew theory predicts that the nature of the relationships between dominants and subordinates around the share of reproduction varies from peace (transactional models) to war (tug-of-war models) (Johnstone 2000).

In this study, N:L ratio of dominants increases only with the number of same-sex unrelated subordinate individuals, extending previous findings in the same species showing a

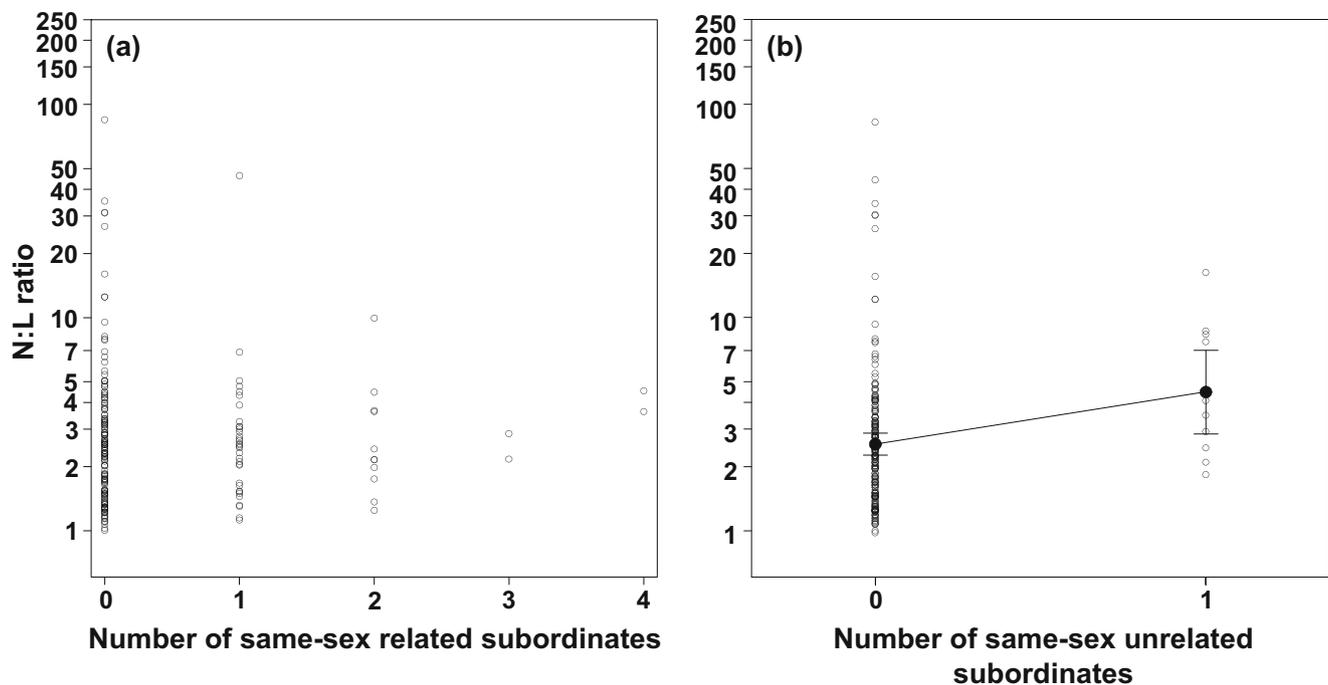


Fig. 2 Residual N:L ratio as a function of the number of same-sex related (a) and unrelated (b) subordinates. The open circles represent the observed values and the closed circles represent the estimated N:L ratio surrounded by their standard errors. The scale of the y-axis is logarithmic

Table 3 Stress levels of dominant (D) and subordinate (S) individuals in wild cooperatively breeding vertebrates and their society characteristics

Species	Stress status	Female	Hormones	Source of hormone sample	Period studied	References			
Mammals									
African wild dog (<i>Lycoon pictus</i>)	D > S	D > S	Cortisol	Feces	All year round	Creel et al. 1996			
Alpine marmot (<i>Marmota marmota</i>)	D > S	D > S	Corticosterone	Feces	All year round	Creel et al. 1997			
	Unclear	–	Corticosterone	Plasma	Mating season	Arnold and Dittami 1997			
	–	S > D	Corticosterone and cortisol	Plasma	Gestation, after unclear	Hacklander et al. 2003			
Banded mongoose (<i>Mungos mungo</i>)	–	D = S (prior to and 1st trimester of gestation), S > D (2nd and 3rd trimesters of gestation)	Glucocorticoid	Feces	Prior and during gestation	Sanderson et al. 2015			
Common dwarf mongoose (<i>Helogale parvula</i>)	D = S (basal), S > D (acute)	D > S (basal+acute)	Cortisol	Urine	all year round	Creel et al. 1996			
Ethiopian wolf (<i>Canis simensis</i>)	D > S	–	Glucocorticoid	Feces	All year round	van Kesteren et al. 2012			
Golden lion tamarins (<i>Leontopithecus rosalia</i>)	D = S	D = S	Cortisol	Feces	All year round	Bales et al. 2005			
Gray wolf (<i>Canis lupus</i>)	D > S	–	Cortisol	Feces	All year round	Bales et al. 2006			
Iberian wolf (<i>Canis lupus signatus</i>)	D > S	D > S	Glucocorticoid	Feces	January 1999 to July 2000	Sands and Creel 2004			
Meerkats (<i>Suricata suricatta</i>)	D > S (immigrant), D = S (natal)	D > S	Cortisol (probability of detection)	Plasma	June to August	Barja et al. 2008			
	–	D = S	Glucocorticoid	Feces	All year round	Carlson et al. 2004			
	–	D = S (only the pregnant)	Glucocorticoid	Feces	All year round	Young et al. 2008			
Ring-tailed lemur (<i>Lemur catta</i>)	–	–	Glucocorticoid	Feces	From pre-conception to the end of the lactation	Barrette et al. 2012			
	–	D > S	Cortisol	Feces	All year round	Cavigelli 1999			
	D = S	D > S	Cortisol	Feces	Lactation	Cavigelli et al. 2003			
	–	–	Glucocorticoid	Feces	All year round	Gould et al. 2005			
	–	D = S	Glucocorticoid	Feces	All year round	Pride 2005			
Birds									
Cockaded Woodpecker (<i>Picoides borealis</i>)	D = S (basal+acute)	D = S (basal+acute)	Corticosterone	Plasma	All	Malheg et al. 2009			
Florida scrub jay (<i>Aphelocoma coerulescens</i>)	D = S	D > S	Corticosterone	Plasma	All year round	Schoech et al. 1991			
HARRIS Hawk (<i>Parabuteo unicinctus</i>)	D = S (basal+acute)	D = S (basal+acute)	Corticosterone	Plasma	All year round	Schoech et al. 1997			
	D = S	D = S	Corticosterone	Plasma	October–August, from the non-breeding period to the feeding period	Mays et al. 1991			
Superb starling (<i>Lampromornis superbus</i>)	S > D (dry years), S < D (wet years)	S > D (dry years), S < D (wet years)	Glucocorticoid corticosterone	Plasma	Dry season (December–February) corresponding to the pre-breeding period	Rubenstein 2007b			
Species	Typical group size	Group composition	Relatedness	Immigrant as subordinates	Dispersal	Dominance	Reproductive skew	Helper sex	
		Male Female	Male Female	Male Female	Male Female	Male Female			
Mammals									
African wild dog (<i>Lycoon pictus</i>)	3–20	Multi	Mixed	Yes	Yes	Single	Queue, challenge	High males, medium females (8%)	Both
	6	Multi	Family	No	Yes	Single	Dispersal	High	Male

Table 3 (continued)

Alpine marmot (<i>Marmota marmota</i>)	20	Multi	Multi	High	High	No	No	Yes	Yes	Hierarchy	Queue	Low	Both
Banded mongoose (<i>Mungos mungo</i>)	9–30	Multi	Multi	Family	Family	No	Yes	Yes	Yes	Single	Queue, dispersal	High	Mostly females
Common dwarf mongoose (<i>Helogale parvula</i>)	6	Multi	Bi	Family	Mixed	No	Yes	Yes	Yes	Single	Queue, dispersal (females only)	High	Both
Ethiopian wolf (<i>Canis simensis</i>)	3	Bi	Uni	Brothers	–	No	Yes	No	No	Bi	Queue	Medium (10% other)	Both
Golden lion tamarins (<i>Leontopithecus rosalia</i>)	5–8	Multi	Multi	Family	Family	Yes	Yes	Yes	Yes	Single	Dispersal, queue	Medium (8%)	Both
Gray wolf (<i>Canis lupus</i>)	5–8	Multi	Multi	Family	Family	Yes	Yes	Yes	Yes	Single	Dispersal	Medium (8%)	Both
Iberian wolf (<i>Canis lupus signatus</i>)	15	Multi	Multi	Family	Family	No	Yes	No	No	Single	Queue	Medium (20% other)	Both
Meerkats (<i>Suricata suricatta</i>)	12–17	Multi	Multi	Mixed	Family	Yes	Yes	No	No	Hierarchy	Queue	Low	Mostly female
Ring-tailed lemur (<i>Lemur catta</i>)													
Birds													
Cockaded Woodpecker (<i>Picoides borealis</i>)	2–5	Bi	Single	Family	Family	No	No	Yes	Yes	Single	Dispersal	High	Male
Florida scrub jay (<i>Aphelocoma coerulescens</i>)	2–6	Bi	Bi	Family	Family	No	Yes	Yes	Yes	Single	Dispersal	High	Both
Harri's Hawk (<i>Parabuteo unicinctus</i>)	2.7	Bi	Bi	Mixed	Family	Yes	Yes	Yes	Yes	Single	Dispersal	High	Both (mostly male)
Superb starling (<i>Lamprolornis superbus</i>)	26	Multi	Multi	Family	Mixed	No	Yes	Yes	Yes	Hierarchy	Queue	Medium (25%)	Both
Species													
	Subordinate reproduction			Aggression against subordinates			Reproduction-related aggression		Dominant preferentially aggressive towards unrelated subordinates	References			
Male		Female		Male	Female			Male					
Mammals													
African wild dog (<i>Lycodon pictus</i>)	Yes	No	No	No	No	Yes	Yes	Unknown	Unknown	Unknown	Queue	Medium (25%)	Both
Alpine marmot (<i>Marmota marmota</i>)	Rare (unrelated and extra-group)	No (very rare case, daughter of the dominant)	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes	Queue	Medium (25%)	Both
Banded mongoose (<i>Mungos mungo</i>)	Yes	Yes	Yes	Yes	No	Yes (males)		No	No	No	Queue	High	Both
Common dwarf mongoose (<i>Helogale parvula</i>)	No	No	Yes	Yes	Yes	Yes	Yes	No	No	No	Queue	High	Both
Ethiopian wolf (<i>Canis simensis</i>)	Yes, outside the group	No	Unknown	Yes	(eviction)	No	Yes	Unknown	Unknown	Unknown	Queue	High	Both
Golden lion tamarins (<i>Leontopithecus rosalia</i>)	Yes	Yes (10% only the daughters of the dominant)	No	Yes	Yes (afterbirth)	No	Yes	Yes	Yes	–	Queue	High	Both

Table 3 (continued)

Gray wolf (<i>Canis lupus</i>)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No	Mech 1974; Gese and Mech 1991
Iberian wolf (<i>Canis lupus signatus</i>)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No	Mech 1974; Gese and Mech 1991
Meerkats (<i>Suricata suricatta</i>)	No (extra-group only)	Yes	Yes	Clutton-Brock et al. 2001; Griffin et al. 2003; Russell et al. 2003; Kutsukake and Clutton-Brock 2006; Young et al. 2006; Spong et al. 2008; Thavarajah et al. 2014						
Ring-tailed lemur (<i>Lemur catta</i>)	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	Kappeler 1990, 1993, Sussman 1991, 1992; Gould 1992; Jolly et al. 1993; Sauther 1993; Sauther and Sussman 1993; Nakamichi and Koyama 1997, 2000; Jolly 1998; Gould et al. 2003
Birds										
Cockaded Woodpecker (<i>Picoides borealis</i>)	Yes	Yes	Yes	No	Yes	Yes	Yes	No	No	Lape 1990; Walters 1990; Haig et al. 1993, 1994; Khan 1999; Khan and Walters 2002
Florida scrub jay (<i>Aphelocoma coerulescens</i>)	No	No	Yes	No	No	Yes	No	Yes	No	Stallcup and Woolfenden 1978; Woolfenden and Fitzpatrick 1986, 1994; Mumme et al. 1989; Balcombe 1989; Hailman et al. 1994; Townsend et al. 2011; Tringali and Bowman 2012
Harri's Hawk (<i>Parabuteo unicinctus</i>)	No	No	No	no	No	No	No	Yes (the beta male is unrelated)	–	Bednarz 1987, 1988; Dawson and Mannan 1991
Superb starling (<i>Lamprolornis superbus</i>)	Yes (inside and outside group)	Yes	No	No	No	No	No	–	–	Rubenstein 2006, 2007a, b; Rubenstein and Shen 2009; Keen et al. 2013

positive association between acute stress level of dominant males (measured as circulating GC levels) and the numbers of non-sons in their group (Arnold and Dittami 1997). All together, these results support the tug-of-war models. In both transactional and tug-of-war models, the lower the subordinates' relatedness to the dominant, the higher the amount of reproduction the dominant is likely to concede to the subordinate due to the low indirect fitness benefits expected by the subordinate (Reeve et al. 1998; Johnstone and Cant 1999; Reeve and Shen 2006; Buston et al. 2007). Nonetheless, under the transactional models, the dominants concede reproduction peacefully to unrelated subordinates to retain them in the group; while under the tug-of-war models, dominants and their unrelated subordinates compete for reproduction (Johnstone 2000; Buston and Zink 2009; Clutton-Brock et al. 2010). The observed increase in N:L ratio clearly supports the idea that dominants exert a stressful control over unrelated subordinates, suggesting that control over their subordinates is costly for the dominants. In line, dominants of both sexes preferentially direct aggressive behaviors towards their same-sex unrelated subordinates (Arnold and Dittami 1997; Hacklander et al. 2003).

Temporal variation in the relationships, and more specifically the nature and strength of the conflicts, between dominants and subordinates can explain part of the variability of the stress patterns observed within and between species (Table 3). In cooperative breeders, dominants have to secure their dominant position all year round and to suppress subordinates' reproduction during the reproductive period, which is likely to influence the differential in stress levels of dominant and subordinates. In this study, individuals were mainly sampled during the period of time where females were lactating and dominant females had higher N:L ratios than their same-sex subordinates. However, Hacklander et al. (2003) found, in the same species, that GC levels were lower in dominant females than in their female subordinates during gestation. As in the Alpine marmot females, temporal variations in the stress hormone levels of dominant female meerkats (*Suricata suricatta*) were observed during their reproductive cycle with dominants presenting higher GC levels than subordinates all year round, except during the pre-conception and gestation periods (Table 3, Carlson et al. 2004; Young et al. 2006). This is likely the result of dominant females initiating significantly more agonistic interactions towards subordinate females, and especially towards unrelated subordinates to suppress their reproduction (Hacklander et al. 2003; Kutsukake and Clutton-Brock 2006; Young et al. 2006). In both meerkats and Alpine marmots, this increase in aggressive interactions towards subordinates during the gestation period causes a chronic elevation of GC in subordinates, which in turn leads to an impaired function of the hypothalamic-pituitary-gonadal axis and to failures to conceive and to abortions in subordinates (Hacklander et al. 2003; Young et al. 2006). The reverse differential in stress levels of dominants and subordinates

during the gestation compare to the rest of the year could indicate that, when conflicts between individuals arise, the individuals initiating aggression are likely to be less stressed than the ones that received it, in agreement with stress pattern found in confrontation experiments (e.g. Blanchard et al. 1995) and under captive environments (e.g., Faulkes and Abbott 1997).

Finally, methodological shortcomings may also explain inconsistent findings in the relationships between social rank and stress level observed in cooperative breeding species. Stress level has been evaluated by authors using different stress markers (cortisol or/and corticosterone) measured in different matrices (plasma, urine, feces) and each of these measures are subjected to specific limitations (Johnstone et al. 2012). For instance, assessing stress level by measuring circulating glucocorticoids is not appropriate for most free-living mammals because these hormone levels varies within a few minutes in response to capture and handling, an effect that seems to be taxa-specific (Romero and Reed 2005). Other confounding factors arising from reproductive or nutritional status may contribute to the apparent inconsistent results (reviewed in Johnstone et al. 2012). In the present study, we used the N:L ratio to assess the stress level of free ranging marmots of two contrasted social status. This method also has limitations. Notably N:L ratio is potentially affected by any factor, other than stress, modifying immune status. However, it has been preferred here as it provides an overall retrospective assessment of individual's stress integrating both baseline and acute response to environmental stressors (Davis et al. 2008).

For the past decades, the increasing number of studies on stress of free-ranging vertebrates revealed complex patterns between social living, dominance rank and stress levels. A careful examination of the nature, strength, and direction of conflicts over reproduction combining physiological and behavioral aspects in cooperatively breeding species and more generally over resources in social species is a necessary step to better understand the observed variability of stress patterns and ultimately the mechanisms shaping the evolution of sociality.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The fieldwork conducted was undertaken after deliverance of the permit number AP n82010/121 by the Préfecture de la Savoie. AC and SL are authorized for experimentation with animals, issued by the French Ministry of Agriculture and Fisheries (diplomas n8R45GRETAF110 and OETRY20090520). The protocol has been approved by the ethical committee of the University of Claude Bernard Lyon 1 (n8BH2012-92 V1).

References

- Abbott DH (1987) Behaviorally mediated suppression of reproduction in female primates. *J Zool* 213:455–470
- Abbott DH (1993) Social conflict and reproductive suppression in marmoset and tamarin monkeys. In: Mason WA, Mendoza SP (eds) *Primate Social Conflict*. SUNY Press, Albany, pp 331–368
- Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland T Jr, Sapolsky RM (2003) Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm Behav* 43:67–82. [https://doi.org/10.1016/S0018-506X\(02\)00037-5](https://doi.org/10.1016/S0018-506X(02)00037-5)
- Allainé D (2000) Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behav Process* 51:21–34. [https://doi.org/10.1016/S0376-6357\(00\)00116-9](https://doi.org/10.1016/S0376-6357(00)00116-9)
- Allainé D, Theuriu F (2004) Is there an optimal number of helpers in alpine marmot family groups? *Behav Ecol* 15:916–924. <https://doi.org/10.1093/beheco/arl096>
- Arnold W (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *J Comp Physiol B* 158:151–156. <https://doi.org/10.1007/BF01075828>
- Arnold W, Dittami J (1997) Reproductive suppression in male alpine marmots. *Anim Behav* 53:53–66. <https://doi.org/10.1006/anbe.1996.0277>
- Balcombe J (1989) Non-breeder asymmetry in Florida scrub jays. *Evol Ecol* 3:77–79. <https://doi.org/10.1007/BF02147933>
- Bales KL, French JA, Hostetler CM, Dietz JM (2005) Social and reproductive factors affecting cortisol levels in wild female golden lion tamarins (*Leontopithecus rosalia*). *Am J Primatol* 67:25–35. <https://doi.org/10.1002/ajp.20167>
- Bales KL, French JA, McWilliams J, Lake RA, Dietz JM (2006) Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Horm Behav* 49:88–95. <https://doi.org/10.1016/j.yhbeh.2005.05.006>
- Barash D (1976) Social-behavior and individual differences in free-living alpine marmots (*Marmota marmota*). *Anim Behav* 24:27–35. [https://doi.org/10.1016/S0003-3472\(76\)80096-6](https://doi.org/10.1016/S0003-3472(76)80096-6)
- Barja I, Silvan G, Illera JC (2008) Relationships between sex and stress hormone levels in feces and marking behavior in a wild population of Iberian wolves (*Canis lupus signatus*). *J Chem Ecol* 34:697–701. <https://doi.org/10.1007/s10886-008-9460-0>
- Barrette M-F, Monfort SL, Festa-Bianchet M, Clutton-Brock TH, Russell AF (2012) Reproductive rate, not dominance status, affects fecal glucocorticoid levels in breeding female meerkats. *Horm Behav* 61:463–471. <https://doi.org/10.1016/j.yhbeh.2011.12.005>
- Bates D, Maechler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Bednarz JC (1987) Pair and group reproductive success, polyandry, and cooperative breeding in Harris' Hawks. *Auk* 104:393–404
- Bednarz JC (1988) Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). *Science* 239:1525–1527
- Bel MC, Coulon J, Sreng L, Allainé D, Bagnères AG, Clément JL (1999) Social signals involved in scent-marking behavior by cheek-rubbing in alpine marmots (*Marmota marmota*). *J Chem Ecol* 25:2267–2283. <https://doi.org/10.1023/A:1020869706956>
- Bichet C, Allainé D, Sauzet S, Cohas A (2016) Faithful or not: direct and indirect effects of climate on extra-pair paternities in a population of alpine marmots. *Proc R Soc B* 283:20162240. <https://doi.org/10.1098/rspb.2016.2240>
- Bishop CR, Athens JW, Boggs DR, Warner HR, Cartwright GE, Wintrobe MM (1968) Leukokinetic studies .13. A non-steady-state kinetic evaluation of mechanism of cortisone-induced granulocytosis. *J Clin Invest* 47:249–260. <https://doi.org/10.1172/JCI105721>
- Blanchard DC, Spencer RL, Weiss SM, Blanchard RJ, McEwen B, Sakai RR (1995) Visible burrow system as a model of chronic social stress—behavioral and neuroendocrine correlates. *Psychoneuroendocrinology* 20:117–134. [https://doi.org/10.1016/0306-4530\(94\)E0045-B](https://doi.org/10.1016/0306-4530(94)E0045-B)
- Brenner I, Shek PN, Zamecnik J, Shephard RJ (1998) Stress hormones and the immunological responses to heat and exercise. *Int J Sports Med* 19:130–143. <https://doi.org/10.1055/s-2007-971895>
- Bronson F, Eleftheriou B (1964) Chronic physiological effects of fighting in mice. *Gen Comp Endocrinol* 4:9–14. [https://doi.org/10.1016/0016-6480\(64\)90033-4](https://doi.org/10.1016/0016-6480(64)90033-4)
- Brown AB (1993) *Hematology: principles and procedures*, Sixth Edition. Lea & Febiger, Philadelphia, pp 453
- Burguez P, Ousey J, Cash R, Rosedale P (1983) Changes in blood neutrophil and lymphocyte counts following administration of cortisol to horses and foals. *Equine Vet J* 15:58–60
- Buston PM, Reeve HK, Cant MA, Vehrencamp SL, Emlen ST (2007) Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Anim Behav* 74:1643–1654. <https://doi.org/10.1016/j.anbehav.2007.03.003>
- Buston PM, Zink AG (2009) Reproductive skew and the evolution of conflict resolution: a synthesis of transactional and tug-of-war models. *Behav Ecol* 20:672–684. <https://doi.org/10.1093/beheco/arp050>
- Cant MA (2000) Social control of reproduction in banded mongooses. *Anim Behav* 59:147–158. <https://doi.org/10.1006/anbe.1999.1279>
- Cant MA (2003) Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*). *J Zool* 259:115–121. <https://doi.org/10.1017/S0952836902003011>
- Cant MA, Nichols HJ, Johnstone RA, Hodge SJ (2014) Policing of reproduction by hidden threats in a cooperative mammal. *P Natl Acad Sci USA* 111:326–330. <https://doi.org/10.1073/pnas.1312626111>
- Cant MA, Otali E, Mwanguhya F (2001) Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). *J Zool* 254:155–162. <https://doi.org/10.1017/S0952836901000668>
- Carlson AA, Young AJ, Russell AF, Bennett NC, McNeilly AS, Clutton-Brock T (2004) Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Horm Behav* 46:141–150. <https://doi.org/10.1016/j.yhbeh.2004.01.009>
- Cavigelli SA (1999) Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Anim Behav* 57:935–944. <https://doi.org/10.1006/anbe.1998.1054>
- Cavigelli SA, Dubovick T, Levash W, Jolly A, Pitts A (2003) Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*). *Horm Behav* 43:166–179. [https://doi.org/10.1016/S0018-506X\(02\)00031-4](https://doi.org/10.1016/S0018-506X(02)00031-4)
- Clutton-Brock TH, Brotherton PNM, Russell AF, O'Riain MJ, Gaynor D, Kansky R, Griffin A, Manser M, Sharpe L, McIlrath G, Small T, Moss A, Monfort S (2001) Cooperation, control, and concession in meerkat groups. *Science* 291:478–481. <https://doi.org/10.1126/science.291.5503.478>
- Clutton-Brock TH, Gaynor D, Kansky R, MacColl ADC, McIlrath G, Chadwick P, Brotherton PNM, O'Riain JM, Manser M, Skinner JD

- (1998) Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc R Soc Lond B* 265:185–190
- Clutton-Brock TH, Hodge SJ, Flower TP, Spong G, Young A (2010) Adaptive suppression of subordinate reproduction in cooperative mammals. *Am Nat* 176:664–673. <https://doi.org/10.1086/656492>
- Cohas A, Yoccoz NG, Bonenfant C, Goossens B, Genton C, Galant M, Kempenaers B, Allainé D (2008) The genetic similarity between pair members influences the frequency of extrapair paternity in alpine marmots. *Anim Behav* 76:87–95. <https://doi.org/10.1016/j.anbehav.2008.01.012>
- Cohas A, Yoccoz NG, Da Silva A, Goossens B, Allainé D (2006) Extrapair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. *Behav Ecol Sociobiol* 59:597–605. <https://doi.org/10.1007/s00265-005-0086-8>
- Cohen J (1972) Thymus-derived lymphocytes sequestered in bone-marrow of hydrocortisone-treated mice. *J Immunol* 108:841–844
- Cooney R (2002) Colony defense in Damaraland mole-rats, *Cryptomys damarensis*. *Behav Ecol* 13:160–162. <https://doi.org/10.1093/beheco/13.2.160>
- Courchamp F, Macdonald DW (2001) Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Anim Conserv* 4:169–174. <https://doi.org/10.1017/S1367943001001196>
- Courchamp F, Rasmussen GSA, Macdonald DW (2002) Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav Ecol* 13:20–27. <https://doi.org/10.1093/beheco/13.1.20>
- Creel S (2001) Social dominance and stress hormones. *Trends Ecol Evol* 16:491–497. [https://doi.org/10.1016/S0169-5347\(01\)02227-3](https://doi.org/10.1016/S0169-5347(01)02227-3)
- Creel S, Creel N, Wildt D, Monfort S (1992) Behavioral and endocrine mechanisms of reproductive suppression in Serengeti dwarf mongooses. *Anim Behav* 43:231–245. [https://doi.org/10.1016/S0003-3472\(05\)80219-2](https://doi.org/10.1016/S0003-3472(05)80219-2)
- Creel S, Creel NM (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim Behav* 50:1325–1339. [https://doi.org/10.1016/0003-3472\(95\)80048-4](https://doi.org/10.1016/0003-3472(95)80048-4)
- Creel S, Creel NM, Mills MGL, Monfort SL (1997) Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behav Ecol* 8:298–306. <https://doi.org/10.1093/beheco/8.3.298>
- Creel S, Creel NM, Monfort SL (1996) Social stress and dominance. *Nature* 379:212–212. <https://doi.org/10.1038/379212a0>
- Creel S, Dantzer B, Goymann W, Rubenstein DR (2013) The ecology of stress: effects of the social environment. *Funct Ecol* 27:66–80. <https://doi.org/10.1111/j.1365-2435.2012.02029.x>
- Creel SF (2005) Dominance, aggression, and glucocorticoid levels in social carnivores. *J Mammal* 86:255–264. <https://doi.org/10.1644/BHE-002.1>
- Creel SR, Waser PM (1991) Failures of reproductive suppression in dwarf mongooses (*Helogale parvula*): accident or adaptation? *Behav Ecol* 2:7–15. <https://doi.org/10.1093/beheco/2.1.7>
- Davis AK (2005) Effect of handling time and repeated sampling on avian white blood cell counts. *J Field Ornithol* 76:334–338
- Davis AK, Maney DL, Maerz JC (2008) The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Funct Ecol* 22:760–772. <https://doi.org/10.1111/j.1365-2435.2008.01467.x>
- Dawson JW, Mannan RW (1991) Dominance hierarchies and helper contributions in Harris' hawks. *Auk* 108:649–660. <https://doi.org/10.2307/4088105>
- De Luca DW, Ginsberg JR (2001) Dominance, reproduction and survival in banded mongooses: towards an egalitarian social system? *Anim Behav* 61:17–30. <https://doi.org/10.1006/anbe.2000.1559>
- de Villiers MS, Richardson PRK, van Jaarsveld AS (2003) Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). *J Zool* 260:377–389. <https://doi.org/10.1017/S0952836903003832>
- Delignette-Muller ML, Dutang C (2015) Fitdistrplus: an R package for fitting distributions. *J Stat Softw* 64:1–34
- Dhabhar FS (2002) A hassle a day may keep the doctor away: stress and the augmentation of immune function. *Integr Comp Biol* 42:556–564. <https://doi.org/10.1093/icb/42.3.556>
- Dietz J (1993) Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Anim Behav* 46:1067–1078. <https://doi.org/10.1006/anbe.1993.1297>
- Enquist M, Leimar O (1990) The evolution of fatal fighting. *Anim Behav* 39:1–9. [https://doi.org/10.1016/S0003-3472\(05\)80721-3](https://doi.org/10.1016/S0003-3472(05)80721-3)
- Fauci A (1975) Mechanisms of corticosteroid action on lymphocyte subpopulations 1. Redistribution of circulating T-lymphocytes and B-lymphocytes to bone-marrow. *Immunology* 28:669–680
- Faulkes CG, Abbott DH (1997) The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In: Solomon NG, French JA (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 302–334
- Frame LH, Malcolm JR, Frame GW, Van Lawick H (1979) Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967–1978. *Z Für Tierpsychol* 50:225–249. <https://doi.org/10.1111/j.1439-0310.1979.tb01030.x>
- French J, Inglett B (1989) Female female aggression and male indifference in response to unfamiliar intruders in lion tamarins. *Anim Behav* 37:487–497. [https://doi.org/10.1016/0003-3472\(89\)90095-X](https://doi.org/10.1016/0003-3472(89)90095-X)
- Galvao-Coelho NL, Silva HPA, Cordeiro De Sousa MB (2012) The influence of sex and relatedness on stress response in common marmosets (*Callithrix jacchus*). *Am J Primatol* 74:819–827. <https://doi.org/10.1002/ajp.22032>
- Garvy KA, Hellmann JK, Ligocki IY, Reddon AR, Marsh-Rollo SE, Hamilton IM, Balshine S, O'Connor CM (2015) Sex and social status affect territorial defence in a cooperatively breeding cichlid fish, *Neolamprologus savoryi*. *Hydrobiologia* 748:75–85. <https://doi.org/10.1007/s10750-014-1899-0>
- Gese E, Mech L (1991) Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. *Can J Zool* 69:2946–2955. <https://doi.org/10.1139/z91-415>
- Gilchrist JS (2006) Reproductive success in a low skew, communal breeding mammal: the banded mongoose, *Mungos mungo*. *Behav Ecol Sociobiol* 60:854–863. <https://doi.org/10.1007/s00265-006-0229-6>
- Gilchrist JS, Otali E, Mwanguhya F (2004) Why breed communally? Factors affecting fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*). *Behav Ecol Sociobiol* 57:119–131. <https://doi.org/10.1007/s00265-004-0837-y>
- Gould L (1992) Alloparental care in free-ranging *Lemur catta* at Berenty reserve, Madagascar. *Folia Primatol* 58:72–83. <https://doi.org/10.1159/000156611>
- Gould L, Sussman RW, Sauther ML (2003) Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly reserve, Madagascar: a 15-year perspective. *Am J Phys Anthropol* 120:182–194. <https://doi.org/10.1002/ajpa.10151>
- Gould L, Ziegler TE, Wittwer DJ (2005) Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly reserve, Madagascar. *Am J Primatol* 67:5–23. <https://doi.org/10.1002/ajp.20166>
- Goymann W, East ML, Wachter B, Höner OP, Möstl E, Hofer H (2003) Social status does not predict corticosteroid levels in postdispersal male spotted hyenas. *Horm Behav* 43:474–479. [https://doi.org/10.1016/S0018-506X\(03\)00032-1](https://doi.org/10.1016/S0018-506X(03)00032-1)
- Goymann W, Wingfield JC (2004) Allostatic load, social status and stress hormones: the costs of social status matter. *Anim Behav* 67:591–602. <https://doi.org/10.1016/j.anbehav.2003.08.007>

- Griffin AS, Pemberton JM, Brotherton PNM, McIlrath G, Gaynor D, Kansky R, O'Riain J, Clutton-Brock TH (2003) A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behav Ecol* 14:472–480. <https://doi.org/10.1093/beheco/arg040>
- Hacklander K, Mostl E, Arnold W (2003) Reproductive suppression in female alpine marmots, *Marmota marmota*. *Anim Behav* 65:1133–1140. <https://doi.org/10.1006/anbe.2003.2159>
- Haig S, Belthoff J, Allen D (1993) Examination of population structure in red cockaded woodpeckers using DNA profiles. *Evolution* 47:185–194. <https://doi.org/10.2307/2410128>
- Haig S, Walters J, Plissner J (1994) Genetic evidence for monogamy in the cooperatively breeding red cockaded woodpecker. *Behav Ecol Sociobiol* 34:295–303. <https://doi.org/10.1007/BF00183480>
- Hailman JP, McGowan KJ, Woolfenden GE (1994) Role of helpers in the sentinel behaviour of the Florida scrub jay (*Aphelocoma c. coerulescens*). *Ethology* 97:119–140. <https://doi.org/10.1111/j.1439-0310.1994.tb01034.x>
- Hatchwell BJ, Sharp SP (2006) Kin selection, constraints, and the evolution of cooperative breeding in long-tailed tits. *Adv Stud Behav* 36:355–395
- Hawkey CM, Dennett TB (1989) A colour atlas of comparative veterinary haematology. Normal and abnormal blood cells in mammals, birds and reptiles, Wolfe publishing limited, Ipswich
- Hennessy MB, Kaiser S, Sachser N (2009) Social buffering of the stress response: diversity, mechanisms, and functions. *Front Neuroendocrinol* 30:470–482. <https://doi.org/10.1016/j.yfrne.2009.06.001>
- Henry MD, Hankerson SJ, Siani JM, French JA, Dietz JM (2013) High rates of pregnancy loss by subordinates leads to high reproductive skew in wild golden lion tamarins (*Leontopithecus rosalia*). *Horm Behav* 63:675–683. <https://doi.org/10.1016/j.yhbeh.2013.02.009>
- Johnstone CP, Lill A, Reina RD (2012) Does habitat fragmentation cause stress in the agile antechinus? A haematological approach. *J Comp Physiol B* 182:139–155. <https://doi.org/10.1007/s00360-011-0598-7>
- Johnstone RA (2000) Models of reproductive skew: a review and synthesis (invited article). *Ethology* 106:5–26. <https://doi.org/10.1046/j.1439-0310.2000.00529.x>
- Johnstone RA, Cant MA (1999) Reproductive skew and the threat of eviction: a new perspective. *Proc R Soc Lond B* 266:275–279
- Jolly A (1998) Pair-bonding, female aggression and the evolution of lemur societies—keynote address. *Folia Primatol* 69(Suppl 1):1–13. <https://doi.org/10.1159/000052693>
- Jolly A, Rasamimanana HR, Kinnaird MF, O'Brien TG, Crowley HM (1993) Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In: Kappeler PM, Ganzhorn JU (eds) *Lemur social systems and their ecological basis*. Springer, Boston, pp 85–100
- Kappeler PM (1990) Female dominance in *Lemur catta*: more than just female feeding priority? *Folia Primatol* (Basel) 55:92–95. <https://doi.org/10.1159/000156504>
- Kappeler PM (1993) Variation in social structure—the effects of sex and kinship on social interactions in 3 lemur species. *Ethology* 93:125–145
- Keen SC, Meliza CD, Rubenstein DR (2013) Flight calls signal group and individual identity but not kinship in a cooperatively breeding bird. *Behav Ecol* 24:1279–1285. <https://doi.org/10.1093/beheco/art062>
- Khan MZ (1999) Ultimate and proximate explanations of helping behavior in the red-cockaded woodpecker (*Picoides borealis*). PhD thesis, Virginia Polytechnic Institute and State University
- Khan MZ, Walters JR (2002) Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). *Behav Ecol Sociobiol* 51:336–344. <https://doi.org/10.1007/s00265-001-0441-3>
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- Kutsukake N, Clutton-Brock TH (2006) Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats *Suricata suricatta*. *Behav Ecol Sociobiol* 59:541–548. <https://doi.org/10.1007/s00265-005-0079-7>
- Lape JJ (1990) Mate guarding in the red-cockaded woodpecker. MSc thesis, North Carolina State University
- Lardy S, Allainé D, Cohas A (2013) Intrasexual competition and female dominance in a singular breeding mammal, the alpine marmot. *Anim Behav* 86:1155–1163. <https://doi.org/10.1016/j.anbehav.2013.09.017>
- Lardy S, Cohas A, Desouhant E, Tafani M, Allainé D (2012) Paternity and dominance loss in male breeders: the cost of helpers in a cooperatively breeding mammal. *PLoS One* 7:e29508. <https://doi.org/10.1371/journal.pone.0029508>
- Lardy S, Cohas A, Figueroa I, Allainé D (2011) Mate change in a socially monogamous mammal: evidences support the “forced divorce” hypothesis. *Behav Ecol* 22:120–125. <https://doi.org/10.1093/beheco/arq168>
- Lazaro-Perea C (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Anim Behav* 62:11–21. <https://doi.org/10.1006/anbe.2000.1726>
- López-Olvera JR, Marco I, Montano J, Casas-Díaz E, Lavín S (2007) Effects of acepromazine on the stress response in southern chamois (*Rupicapra pyrenaica*) captured by means of drive-nets. *Can J Vet Res* 71:41–51
- Louch C, Higginbotham M (1967) Relation between social rank and plasma corticosterone levels in mice. *Gen Comp Endocrinol* 8:441–449. [https://doi.org/10.1016/S0016-6480\(67\)80006-6](https://doi.org/10.1016/S0016-6480(67)80006-6)
- Malcolm JR, Marten K (1982) Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav Ecol Sociobiol* 10:1–13. <https://doi.org/10.1007/BF00296390>
- Malueg AL, Walters JR, Moore IT (2009) Do stress hormones suppress helper reproduction in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*)? *Behav Ecol Sociobiol* 63:687–698. <https://doi.org/10.1007/s00265-008-0702-5>
- Manogue KR, Leshner AI, Candland DK (1975) Dominance status and adrenocortical reactivity to stress in squirrel monkeys (*Saimiri sciureus*). *Primates* 16:457–463. <https://doi.org/10.1007/BF02382742>
- Mays N, Vleck C, Dawson J (1991) Plasma luteinizing-hormone, steroid-hormones, behavioral role, and nest stage in cooperatively breeding Harris hawks (*Parabuteo unicinctus*). *Auk* 108:619–637
- McNutt JW (1996) Sex-biased dispersal in African wild dogs, *Lycaon pictus*. *Anim Behav* 52:1067–1077. <https://doi.org/10.1006/anbe.1996.0254>
- Meade J, Hatchwell BJ (2010) No direct fitness benefits of helping in a cooperative breeder despite higher survival of helpers. *Behav Ecol* 21:1186–1194. <https://doi.org/10.1093/beheco/arq137>
- Mech LD (1974) *Canis lupus*. *Mamm Species* 37:1–6. <https://doi.org/10.2307/3503924>
- Müller CA, Manser MB (2007) “Nasty neighbours” rather than “dear enemies” in a social carnivore. *Proc R Soc Lond B* 274:959–965. <https://doi.org/10.1098/rspb.2006.0222>
- Müller CA, Manser MB (2008) Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. *Ethology* 114:174–185. <https://doi.org/10.1111/j.1439-0310.2007.01455.x>
- Mumme RL, Koenig WD, Ratnieks FLW (1989) Helping behaviour, reproductive value, and the future component of indirect fitness. *Anim Behav* 38:331–343. [https://doi.org/10.1016/S0003-3472\(89\)80094-6](https://doi.org/10.1016/S0003-3472(89)80094-6)
- Nakamichi M, Koyama N (1997) Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty reserve, Madagascar. *Int J Primatol* 18:73–93. <https://doi.org/10.1023/A:1026393223883>

- Nakamichi M, Koyama N (2000) Intra-troop affiliative relationships of females with newborn infants in wild ring-tailed lemurs (*Lemur catta*). *Am J Primatol* 50:187–203. [https://doi.org/10.1002/\(SICI\)1098-2345\(200003\)50:3<187::AID-AJP2>3.0.CO;2-Q](https://doi.org/10.1002/(SICI)1098-2345(200003)50:3<187::AID-AJP2>3.0.CO;2-Q)
- Nam K-B, Simeoni M, Sharp SP, Hatchwell BJ (2010) Kinship affects investment by helpers in a cooperatively breeding bird. *Proc R Soc Lond B* 277:3299–3306. <https://doi.org/10.1098/rspb.2010.0737>
- Nonacs P, Hager R (2011) The past, present and future of reproductive skew theory and experiments. *Biol Rev* 86:271–298. <https://doi.org/10.1111/j.1469-185X.2010.00144.x>
- Ottaway C, Husband A (1994) The influence of neuroendocrine pathways on lymphocyte migration. *Immunol Today* 15:511–517. [https://doi.org/10.1016/0167-5699\(94\)90206-2](https://doi.org/10.1016/0167-5699(94)90206-2)
- Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. *Behav Ecol Sociobiol* 25: 227–233. <https://doi.org/10.1007/BF00302922>
- Perrin C (1993) Organisation socio-spatiale et distribution des activités chez la marmotte alpine (*Marmota marmota* Linné 1758). PhD thesis, Université Paris 7
- Pride E (2005) Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behav Ecol* 16:550–560. <https://doi.org/10.1093/beheco/ari025>
- Core Team R (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <http://www.R-project.org>
- Randall DA, Pollinger JP, Wayne RK, Tallents LA, Johnson PJ, Macdonald DW (2007) Inbreeding is reduced by female-biased dispersal and mating behavior in Ethiopian wolves. *Behav Ecol* 18: 579–589. <https://doi.org/10.1093/beheco/arm010>
- Rasa A (1973) Intra-familial sexual repression in the dwarf mongoose *Helogale parvula*. *Naturwissenschaften* 60:303–304. <https://doi.org/10.1007/BF00624455>
- Reeve HK (1998) Game theory, reproductive skew, and nepotism. In: Dugatkin LA, Reeve HK (eds) *Game theory and animal behaviour*. Oxford University Press, Oxford, pp 118–145
- Reeve HK, Emlen ST, Keller L (1998) Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav Ecol* 9:267–278. <https://doi.org/10.1093/beheco/9.3.267>
- Reeve HK, Shen SF (2006) A missing model in reproductive skew theory: the bordered tug-of-war. *P Natl Acad Sci U S A* 103:8430–8434. <https://doi.org/10.1073/pnas.0603005103>
- Romero LM, Reed JM (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comp Biochem Physiol* 140:73–79. <https://doi.org/10.1016/j.cbpb.2004.11.004>
- Romero LM, Romero RC (2002) Corticosterone responses in wild birds: The importance of rapid initial sampling. *Condor* 104:129–135. [https://doi.org/10.1650/0010-5422\(2002\)104\[0129,CRIWBT\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2002)104[0129,CRIWBT]2.0.CO;2)
- Rood JP (1978) Dwarf mongoose helpers at the den. *Z Tierpsychol* 48: 277–287. <https://doi.org/10.1111/j.1439-0310.1978.tb00260.x>
- Rood JP (1980) Mating relationships and breeding suppression in the dwarf mongoose. *Anim Behav* 28:143–150. [https://doi.org/10.1016/S0003-3472\(80\)80019-4](https://doi.org/10.1016/S0003-3472(80)80019-4)
- Rood JP (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Anim Behav* 39:566–572. [https://doi.org/10.1016/S0003-3472\(05\)80423-3](https://doi.org/10.1016/S0003-3472(05)80423-3)
- Rubenstein DR (2006) The evolution of the social and mating systems of the plural cooperatively breeding superb starling, *Lamprotornis superbus*. PhD thesis, Cornell University
- Rubenstein DR (2007a) Female extrapair mate choice in a cooperative breeder: trading sex for help and increasing offspring heterozygosity. *Proc R Soc Lond B* 274:1895–1903. <https://doi.org/10.1098/rspb.2007.0424>
- Rubenstein DR (2007b) Stress hormones and sociality: integrating social and environmental stressors. *Proc R Soc Lond B* 274:967–975. <https://doi.org/10.1098/rspb.2006.0051>
- Rubenstein DR, Shen S-F (2009) Reproductive conflict and the costs of social status in cooperatively breeding vertebrates. *Am Nat* 173: 650–661. <https://doi.org/10.1086/597606>
- Russell AF, Brotherton PNM, McIlrath GM, Sharp LL, Clutton-Brock TH (2003) Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behav Ecol* 14:486–492. <https://doi.org/10.1093/beheco/arg022>
- Saltzman W, Schult-Darken N, Scheffler G, Wegner F (1994) Social and reproductive influences on plasma-cortisol in female marmoset monkeys. *Physiol Behav* 56:801–810. [https://doi.org/10.1016/0031-9384\(94\)90246-1](https://doi.org/10.1016/0031-9384(94)90246-1)
- Saltzman W, Schultz-Darken NJ, Wegner FH, Wittwer DJ, Abbott DH (1998) Suppression of cortisol levels in subordinate female marmosets: reproductive and social contributions. *Horm Behav* 33:58–74. <https://doi.org/10.1006/hbeh.1998.1436>
- Sanderson JL, Nichols HJ, Marshall HH, Vitikainen EIK, Thompson FJ, Walker SL, Cant MA, Young AJ (2015) Elevated glucocorticoid concentrations during gestation predict reduced reproductive success in subordinate female banded mongooses. *Biol Lett* 11: 20150620. <https://doi.org/10.1098/rsbl.2015.0620>
- Sands J, Creel S (2004) Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Anim Behav* 67:387–396. <https://doi.org/10.1016/j.anbehav.2003.03.019>
- Sapolsky RM (1983) Endocrine aspects of social instability in the olive baboon (*Papio anubis*). *Am J Primatol* 5:365–379. <https://doi.org/10.1002/ajp.1350050406>
- Sapolsky RM (2005) The influence of social hierarchy on primate health. *Science* 308:648–652. <https://doi.org/10.1126/science.1106477>
- Sauther ML (1993) Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In: Kappeler PM, Ganzhorn JU (eds) *Lemur social systems and their ecological basis*. Springer US, New York, pp 135–152
- Sauther ML, Sussman RW (1993) A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: Kappeler PM, Ganzhorn JU (eds) *Lemur social systems and their ecological basis*. Springer US, New York, pp 111–121
- Schaffner CM, French JA (2004) Behavioral and endocrine responses in male marmosets to the establishment of multimale breeding groups: evidence for non-monopolizing facultative polyandry. *Int J Primatol* 25:709–732. <https://doi.org/10.1023/B:IJOP.0000023582.34854.43>
- Schoech S, Mumme R, Moore M (1991) Reproductive endocrinology and mechanisms of breeding inhibition in cooperatively breeding Florida scrub jays (*Aphelocoma c. coerulescens*). *Condor* 93:354–364. <https://doi.org/10.2307/1368951>
- Schoech SJ, Mumme RL, Wingfield JC (1997) Corticosterone, reproductive status, and body mass in a cooperative breeder, the Florida scrub-jay (*Aphelocoma coerulescens*). *Physiol Zool* 70:68–73
- Sillero-Zubiri C, Gottelli D (1995) Spatial organization in the Ethiopian wolf *Canis simensis*—large packs and small stable home ranges. *J Zool* 237:65–81
- Sillero-Zubiri C, Gottelli D, Macdonald DW (1996) Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behav Ecol Sociobiol* 38:331–340. <https://doi.org/10.1007/s002650050249>
- Sillero-Zubiri C, Macdonald DW (1998) Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *J Zool* 245:351–361. <https://doi.org/10.1111/j.1469-7998.1998.tb00110.x>
- Smith TE, French JA (1997) Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets (*Callithrix kuhli*). *Am J Primatol* 42:253–267. [https://doi.org/10.1002/\(SICI\)1098-2345\(1997\)42:4<253::AID-AJP1>3.0.CO;2-W](https://doi.org/10.1002/(SICI)1098-2345(1997)42:4<253::AID-AJP1>3.0.CO;2-W)

- Snyder PA (1974) Behavior of *Leontopithecus rosalia* (golden-lion marmoset) and related species: a review. *J Hum Evol* 3:109–122. [https://doi.org/10.1016/0047-2484\(74\)90194-8](https://doi.org/10.1016/0047-2484(74)90194-8)
- Spiering PA, Somers MJ, Maldonado JE, Wildt DE, Gunther MS (2010) Reproductive sharing and proximate factors mediating cooperative breeding in the African wild dog (*Lycaon pictus*). *Behav Ecol Sociobiol* 64:583–592. <https://doi.org/10.1007/s00265-009-0875-6>
- Spong GF, Hodge SJ, Young AJ, Clutton-Brock TH (2008) Factors affecting the reproductive success of dominant male meerkats. *Mol Ecol* 17:2287–2299. <https://doi.org/10.1111/j.1365-294X.2008.03734.x>
- Stallcup J, Woolfenden G (1978) Family status and contributions to breeding by Florida scrub jays. *Anim Behav* 26:1144–1156. [https://doi.org/10.1016/0003-3472\(78\)90104-5](https://doi.org/10.1016/0003-3472(78)90104-5)
- Sussman R (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly reserve, Madagascar. *Am J Phys Anthropol* 84:43–58. <https://doi.org/10.1002/ajpa.1330840105>
- Sussman R (1992) Male life-history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int J Primatol* 13:395–413. <https://doi.org/10.1007/BF02547825>
- Thavarajah NK, Fenkes M, Clutton-Brock TH (2014) The determinants of dominance relationships among subordinate females in the cooperatively breeding meerkat. *Behaviour* 151:89–102. <https://doi.org/10.1163/1568539X-00003124>
- Townsend AK, Bowman R, Fitzpatrick JW, Dent M, Lovette IJ (2011) Genetic monogamy across variable demographic landscapes in cooperatively breeding Florida scrub-jays. *Behav Ecol* 22:464–470. <https://doi.org/10.1093/beheco/arq227>
- Tringali A, Bowman R (2012) Plumage reflectance signals dominance in Florida scrub-jay, *Aphelocoma coerulescens*, juveniles. *Anim Behav* 84:1517–1522. <https://doi.org/10.1016/j.anbehav.2012.09.025>
- van Kesteren F, Sillero-Zubiri C, Millar R, Argaw K, Macdonald DW, Paris M (2012) Sex, stress and social status: patterns in fecal testosterone and glucocorticoid metabolites in male Ethiopian wolves. *Gen Comp Endocrinol* 179:30–37. <https://doi.org/10.1016/j.ygcen.2012.07.016>
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer-Verlag, New York
- von Holst D (1998) The concept of stress and its relevance for animal behavior. *Adv Stud Behav* 27:1–131
- Walters JR (1990) Red-cockaded woodpeckers: a “primitive” cooperative breeder. In: Stacey PB, Koenig WD (eds) Cooperative breeding in birds: long term studies of ecology and behaviour. Cambridge University Press, Cambridge, pp 67–102
- Woolfenden GE, Fitzpatrick JW (1986) Sexual asymmetries in the life history of the Florida scrub jay. In: Rubenstein DI, Wrangham RW (eds) Ecological aspects of social evolution: birds and mammals. Princeton University Press, Princeton, pp 87–107
- Woolfenden GE, Fitzpatrick JW (1994) The Florida scrub jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton
- Young AJ, Carlson AA, Monfort SL, Russell AF, Bennett NC, Clutton-Brock T (2006) Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *P Natl Acad Sci USA* 103:12005–12010. <https://doi.org/10.1073/pnas.0510038103>
- Young AJ, Monfort SL, Clutton-Brock TH (2008) The causes of physiological suppression among female meerkats: a role for subordinate restraint due to the threat of infanticide? *Horm Behav* 53:131–139. <https://doi.org/10.1016/j.yhbeh.2007.09.005>