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DOMINANCE, AGGRESSION, AND GLUCOCORTICOID LEVELS IN SOCIAL CARNIVORES

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In social animals, reproductive success is often related to social dominance. In cooperatively breeding birds and mammals, reproductive rates are usually lower for social subordinates than for dominants, and it is common for reproduction in subordinates to be completely suppressed. Early research with captive animals showed that losing fights can increase glucocorticoid (GC) secretion, a general response to stress. Because GCs can suppress reproduction, it has been widely argued that chronic stress might underlie reproductive suppression of social subordinates in cooperative breeders. Contradicting this hypothesis, recent studies of cooperative breeders in the wild show that dominant individuals have elevated GCs more often than do subordinates. Here, I summarize relationships between rank, aggression, and GCs from field studies of 3 cooperatively breeding carnivores: the dwarf mongoose (*Helogale parvula*), the African wild dog (*Lycaon pictus*), and the gray wolf (*Canis lupus*). In all 3 species, GC levels are higher in dominants than in subordinates for 1 or both sexes. Higher GCs are associated with higher rates or severity of aggression in some cases, but not all. As studies have accumulated, the patterns observed in these carnivores are emerging as typical for cooperative breeders.

Key words: aggression, *Canis lupus*, carnivores, cooperative breeding, dominance, glucocorticoids, *Helogale parvula*, *Lycaon pictus*, stress

Among social carnivores, a dominance hierarchy typically stratifies groups. Because dominant animals are more likely to control access to resources or win contests for them, dominants should generally have greater reproductive success or survival than subordinates. Dominance has particularly strong effects on fitness among cooperative breeders, where dominants can monopolize reproduction almost completely.

From an evolutionary perspective, it seems obvious that being dominant is better than being subordinate. However, this conclusion should not be extended to become an implicit assumption that dominance carries no costs. The conclusion that dominance has benefits is secure on the basis of many studies, but struggling for dominance may yield high benefits at high cost, while accepting subordination yields lower benefits at lower cost. If so, this might explain the perplexing willingness of social subordinates to accept their status without obvious resistance, in cases where the inclusive fitness costs of subordination are apparently large.

For example, dominance and age are highly correlated in dwarf mongooses (*Helogale parvula*), with age explaining 68% of the variance in rank (Creel et al. 1992; Rood 1990). Within each group, only the socially dominant individual of each sex is guaranteed of breeding, and examination of genetic data shows that dominant individuals produce 75–85% of all offspring raised, although they comprise only 20% of the population (Keane et al. 1994). Subordinates gain indirect fitness benefits by helping to raise the dominants' offspring, but the "offspring equivalents" accrued by helpers are substantially lower than the reproductive success attained by breeders (Creel and Waser 1994). Logically, one might expect a strong relationship between age and rank when comparing subadults or young adults to older animals, because size (and consequently fighting ability) is still increasing, but it is difficult to see why age and fighting ability should remain closely related among older adults. Nonetheless, in 13 years of study we observed no cases in which a dominant mongoose was deposed by a younger pack mate through an internal coup (Rood 1990). In the most extreme case, a 13-year-old female that was visibly senescent (for example, she had difficulty moving with the pack as it foraged) remained at the top of a hierarchy that included 7 prime-aged females. It remains a mystery why prime-aged subordinate mongooses respect the "age convention."

Packer et al. (1995; also see Wasser 1995) suggested that elevated androgens may place limits on the aggressive behavior needed to establish and maintain rank in female baboons. They argued that high androgen levels and aggression might yield high rank but also might interfere with reproduction or maternal behavior. If rank and androgen levels are indeed related, this general argument can be extended to other costs; for example, elevated androgens might compromise immune function

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(Wingfield and Ramenofsky 1999) and thus might reduce survival. Some empirical studies show an association between rank and androgen levels (e.g., Creel et al. 1997), but this relationship is highly variable (Arnold and Dittami 1997; Bercovitch 1993; Creel et al. 1992, Ginther et al. 2001).

Dominance might also carry physiological costs mediated by the hypothalamic–pituitary–adrenal axis. Animals respond to a stressor with a series of endocrine responses that increase the immediate availability of energy, in part by inhibiting physiological processes that are not required for immediate survival (Munck et al. 1984; Sapolsky 1992; Wingfield 1994). One of the primary responses to stress is an increase in the activity of the hypothalamic–pituitary–adrenocortical axis, producing an increase in the concentration of circulating adrenal glucocorticoids (GCs). In the short term (hours to days), GC elevations redirect resources to mobilize energy that can be used to resolve the stressful situation. If the stressor is not eliminated and GC levels remain chronically high (for weeks or longer), a broad range of harmful consequences ensue, including immune suppression, loss of muscle mass, and reproductive suppression (Chrousos and Gold 1992; Pottinger 1999; Sapolsky 1992).

Two major properties of the hypothalamic–pituitary–adrenal axis underlie the pathological consequences of chronic GC elevations. The 1st property is negative feedback. When a stressor produces a short-term or "acute" stress response, the elevation of GCs itself is directly responsible for terminating the GC response. As GC levels rise over the course of 5–30 min, binding to GC receptors in the brain increases in parallel to binding in other tissues. The binding of GCs to brain receptors initiates a negative feedback on the secretion of corticotropin-releasing hormone from the hypothalamus and adrenocorticotropic hormone from the anterior pituitary, which reduces the secretion of GCs. For animals whose basal GC levels are not elevated, this negative feedback loop ensures that the acute GC response is self-limiting. However, if basal GCs are elevated for long periods, negative feedback can be impaired, further exacerbating GC-related pathologies. The 2nd property is a dual receptor system. The actions of GCs at target tissues are mediated by 2 structurally and functionally distinct types of receptors, called type I (or mineralocorticoid) and type II (or glucocorticoid) receptors (de Kloet et al. 1993). When GC levels are near the normal baseline, most GCs are bound by type I receptors, which have a higher structural affinity for GCs than do type II receptors. Most of the actions triggered by binding of GCs to type I receptors are termed "permissive" because they enhance the operation of physiological pathways that are not under the direct control of GCs themselves (Munck et al. 1984; Sapolsky et al. 2000). When GC levels increase beyond the normal baseline, type I receptors become saturated, and binding shifts to type II receptors, which have lower GC affinity but are more abundant. Type II binding triggers most of the stimulatory and inhibitory effects of GCs on the immune system, the reproductive system, and other systems. It is these effects that become pathological if prolonged (Sapolsy 1992; Sapolsky et al. 2000). Thus, the harmful effects of chronic stress are largely the result of impaired negative feedback and persistent binding of GCs to type II receptors.

THE HISTORY OF "SOCIAL STRESS"

It is widely believed that social subordination is stressful; indeed the term "social stress" is often used to mean "the stress of subordination." The idea that social stress might fall more heavily on dominants than on subordinates has received less attention, but among cooperative breeders, social stress is often a cost of dominance, rather than a consequence of subordination. Although relatively few species have been studied (Table 1), examination of recent field data strongly challenges the traditional view of social stress. On the basis of logic alone, it is difficult to predict whether domination or subordination should be more stressful. Domination might be stressful simply because it requires fighting at high rates or with greater severity. On the other hand, losing a fight might be more stressful than winning 2 fights; the algebra of winning and losing cannot be resolved by logic. It requires empirical study.

For more than 30 years, we have known that aggressive or agonistic interactions can provoke large and persistent increases in GC secretion. Influential early work on this issue was conducted with captive rodents and primates, often by grouping unfamiliar individuals, observing the fights that ensued, and comparing the GC levels of winners and losers (Bronson and Eleftheriou 1964; Louch and Higginbotham 1967; Manogue 1975). In this situation, both winners and losers show a strong stress response, but the response is larger among losers. In these early studies, losers were generally called subordinates, and winners were called dominants, and these studies are the origin of the conventional view that social subordination is stressful. These were important studies of behavioral interactions and stress responses, but they do not necessarily reveal the consequences of living as a subordinate in a social group with a settled dominance hierarchy. The rate and severity of fighting are high immediately after strangers are grouped, particularly among males, which were the focus of most winner–loser studies. For example, grouped rats in one study of rank and stress fought approximately 30 times per day (Blanchard et al. 1995). After 13 days, they had an average of 17 body wounds and had lost more than 20% of their initial body mass, despite being removed from the colony on 4 days to feed for 8 h. Aggression this severe would be unusual for a social species in the wild (Creel et al. 1992, 1997). Nonetheless, winner–loser studies of captive animals are the original basis of the argument that the "stress of subordination" or "psychological castration" might underlie reproductive suppression among subordinates in cooperatively breeding species.

Given this background, what can recent field studies (Table 1) reveal about the endocrine correlates of rank in social species, particularly cooperative breeders? Here, I summarize 3 field studies of the behavioral, endocrine, and demographic correlates of rank in cooperatively breeding carnivores (dwarf mongooses [*Helogale parvula*], African wild dogs [*Lycaon pictus*], and gray wolves, *Canis lupus*). These species have similar social systems, with stable packs that typically include several adults of both sexes (although wolf packs usually have simpler structures and a pack may have only 1 adult of a given sex). A clear dominance hierarchy exists within each sex, and only the dominant

TABLE 1.—Relationships between basal glucocorticoid (GC) levels and social status within cooperatively breeding groups.[a]

Species	Sex	Relationship of rank and GC	Reproductive suppression of subordinates[b]	Captive or wild study	Source of GC sample	Notes	Reference
Rodents							
Naked mole-rat (*Heterocephalus glaber*)	F and M	Sub > Dom	High skew	Captive	Urine		Faulkes and Abbott 1997
Alpine marmot (*Marmota marmota*)	M	Dom > 3 types of sub Dom < 1 type of sub	Low skew	Wild	Blood, long and variable lag from trapping to sample	Categorized Subs by yearling—adult and son—nonson	Arnold and Dittami 1997
Primates							
Ring-tailed lemur (*Lemur catta*)	F	Dom > Sub	Low skew	Wild	Feces		Cavigelli 1999
Common marmoset (*Callithrix jacchus*)	F	Dom > Sub	High skew	Captive	Blood		Saltzmann et al. 1998
Black tufted-ear marmoset (*Callithrix kuhlii*)	F	Dom = Sub	High skew	Captive	Urine		Smith and French 1997; J. French, pers. comm.
	M	Dom > Sub	High skew	Captive	Urine		
Cotton-top tamarin (*Saguinus oedipus*)	F	Paired > Sub with male	High skew	Captive	Urine		Ziegler et al. 1995
Birds							
White-browed sparrow weaver (*Plocepasser mahali*)	F and M	Dom = Sub	Low skew	Wild	Blood	Very low GC levels for all ranks	Wingfield et al. 1991
Florida scrub jay (*Aphelocoma coerulescens*)	F	Dom > Sub	Low skew	Wild	Blood	During all nest stages	Schoech et al. 1991
	M	Dom = Sub (see notes)	Low skew	Wild	Blood	Dom > Sub at mating stage	
Harris's hawk (*Parabuteo unicinctus*)	F and M	Dom = Sub (see notes)	High skew	Wild	Blood	NS ANOVA for GC in breeders, auxiliaries, and juveniles	Mays et al. 1991
Carnivores							
Gray wolf (*Canis lupus*)	F and M	Dom = Sub (see notes)	High skew	Captive	Urine	In wild packs, Dom > Sub	McLeod et al. 1996
Gray wolf (*Canis lupus*)	F and M	Dom > Sub (see notes)	High skew	Wild	Feces	In captive packs, Dom = Sub	Sands and Creel 2004
Dwarf mongoose (*Helogale parvula*)	F	Dom > Sub	High skew	Wild	Urine	Acute GC: Dom > Sub	Creel et al. 1992, 1996
	M	Dom = Sub	High skew	Wild	Urine	Acute GC: Dom < Sub	
African wild dog (*Lycaon pictus*)	F and M	Dom > Sub	High skew	Wild	Feces		Creel et al. 1996, 1997

[a] Dom = Dominant, Sub = subordinate, NS = nonsignificant, ANOVA = analysis of variance. This table excludes studies in which individuals in different groups or on different territories are compared, for example, comparisons of unmated, monogamously mated, and polygynously mated male birds on neighboring breeding territories, and social species that are not clearly cooperative breeders.

[b] High skew refers to species in which reproductive success is highly skewed within groups (subordinates rarely breed). Low skew refers to species in which subordinates often breed.

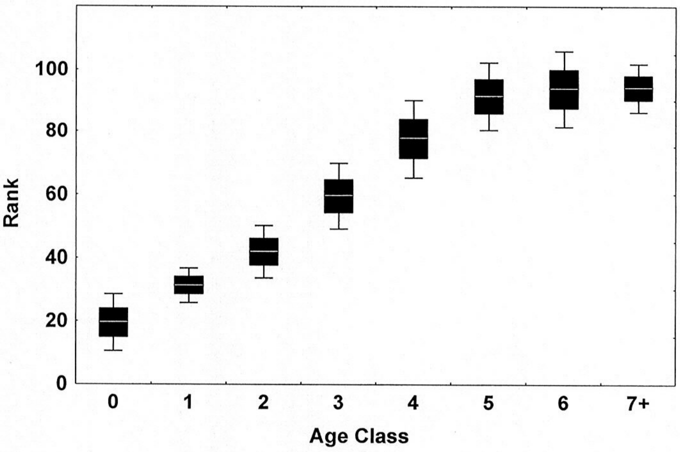


FIG. 1.—Relationship between social dominance (rank) and age (in years) for dwarf mongooses. The alpha animal in any pack had a rank of 100, with quantitative gaps between all lower ranking individuals determined by the Batchelder–Bershad–Simpson method (Jameson et al. 1999) from data on wins, losses, and rank of the opponent. Boxes show mean (central lines), 1 *SE* (boxes), and 2 *SE* (whiskers). Data are from Creel et al. (1992).

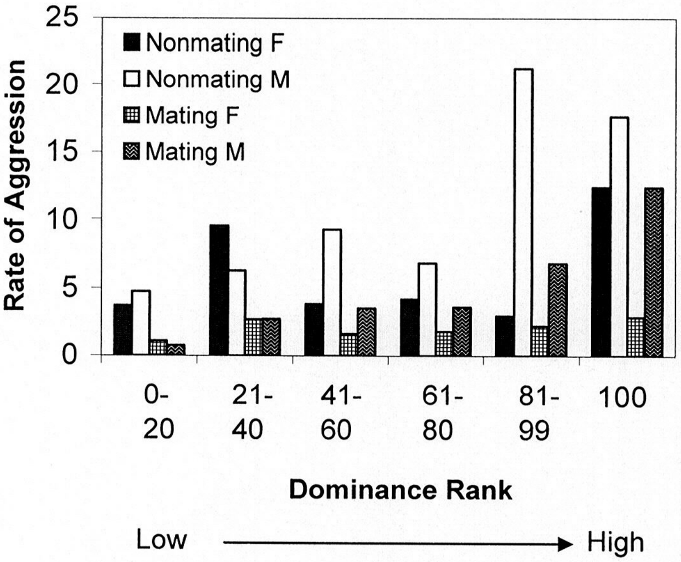


FIG. 2.—Relationship between dominance rank (see legend for Fig. 1 for details) and rates of aggression (acts/24 h) for dwarf mongooses of both sexes during the mating period and outside the mating period. High-ranking animals engage in more aggression.

individual of each sex is assured of reproducing, although subordinates of both sexes sometimes breed successfully (Creel and Creel 2002; Creel and Waser 1991). Dispersal is common for both sexes, although some individuals remain in their natal pack for their entire lives, and nondispersers can accrue inclusive fitness benefits by helping relatives to raise nondescendant kin (Creel and Waser 1994).

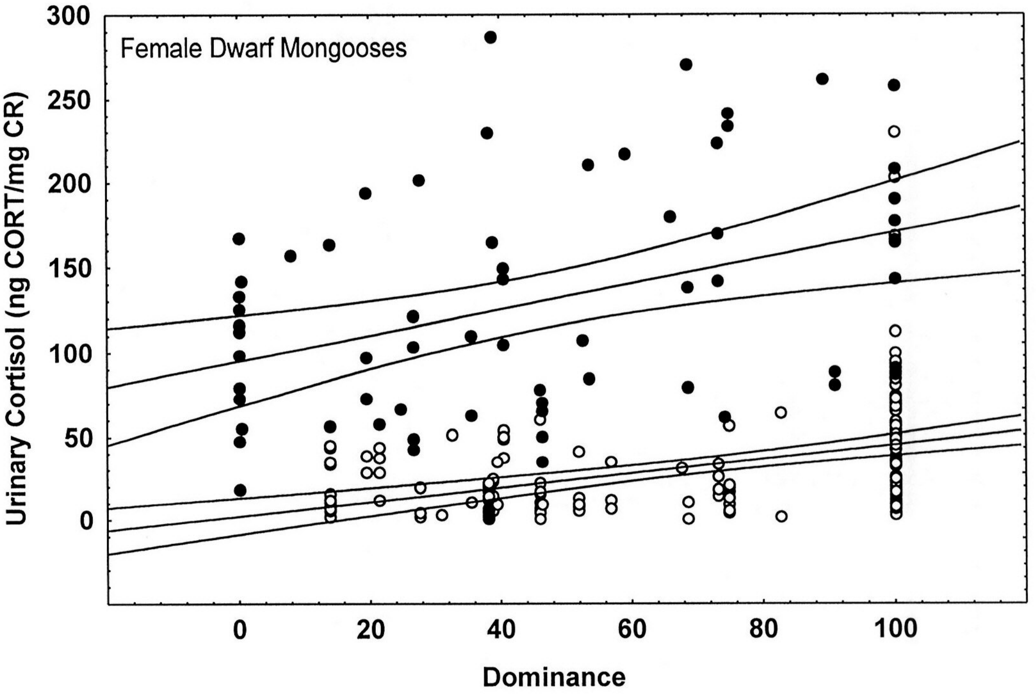
DWARF MONGOOSES

On our study area in Serengeti National Park, dwarf mongoose packs held an average of 9.0 ± 0.3 *SE* adults and yearlings, with an even sex ratio (Creel and Waser 1994; Rood 1990). Dwarf mongooses are obligately cooperative breeders. Unaided breeding pairs are rare (12 cases in 202 pack-years of observation) and almost never succeed in raising offspring to independence (mean annual reproductive success = 0.07 ± 0.07 *SE* offspring). Of 302 pregnancies, 219 (72.5%) were by alpha females, even though subordinates outnumbered alphas 3.5-fold (Creel et al. 1992). In 11 cases in which subordinates gave birth out of synchrony with the dominant female, no offspring survived to the age of emergence from the den at 4–6 weeks. In 51 cases, at least 1 subordinate gave birth in synchrony with the alpha female. The mean size of joint litters (3.2 offspring at emergence) was significantly larger than that of alpha-only litters (2.4 offspring; $t = 2.92$, $P < 0.05$). Thus, on the occasions that subordinates become pregnant, some of the offspring of subordinate females appear to survive, but only when the subordinate's litter is pooled with that of the dominant animal. Joint litters were substantially smaller than would be expected if the subordinate's contributions were equal to the alpha female's (Creel and Waser 1991). Genetic data showed that 15% of all offspring are produced by subordinate females, whereas 25% are fathered by subordinate males (Keane et al. 1994).

The demographic and morphological correlates of rank are similar for males and females, which is not surprising for a cooperative breeder with little sexual dimorphism. By itself, age explained 69% of the variance in rank across the population at large (Fig. 1). Within single packs, the relationship was even stronger: we detected no exceptions to the rule that the oldest mongoose within a specific pack was dominant. After controlling for the effects of age, body mass explained a significant portion (14%) of the variance in dominance: within an age-class, heavier mongooses tended to be dominant.

The behavioral correlates of dominance were broadly similar for males and females, but differed in some ways that might affect the endocrine correlates of rank. Dominant mongooses of both sexes engaged in aggression at significantly higher rates than did subordinates (Fig. 2) during periods of mating and nonmating. On average, dominant males fought 2.7 times more often than subordinates, whereas dominant females fought 2.0 times more often than subordinates. If fighting affects basal GCs for winners as well as losers, then we might expect to see elevated GCs in dominant dwarf mongooses of both sexes.

This expectation is met for females, but not for males. High-ranking females had higher basal urinary GC levels than subordinates, and the difference was particularly pronounced for alpha females (Fig. 3; regression, $F = 40.6$, $d.f. = 1, 99$, $P < 0.001$—Creel et al. 1996). Despite elevated basal GCs, dominant female mongooses produced higher cortisol levels than subordinates in response to the short-term stress of trapping ($F = 9.36$, $d.f. = 1, 74$, $P < 0.005$), a result that runs contrary to the general pattern that chronically elevated basal GCs weaken the acute GC response (Creel 2001). In contrast, no relationship between rank and basal urinary GCs was detected for male dwarf mongooses (despite statistical power almost identical to the test for females), but dominant males showed low peak cortisol levels in response to trap stress (Fig. 3; $F = 9.06$,



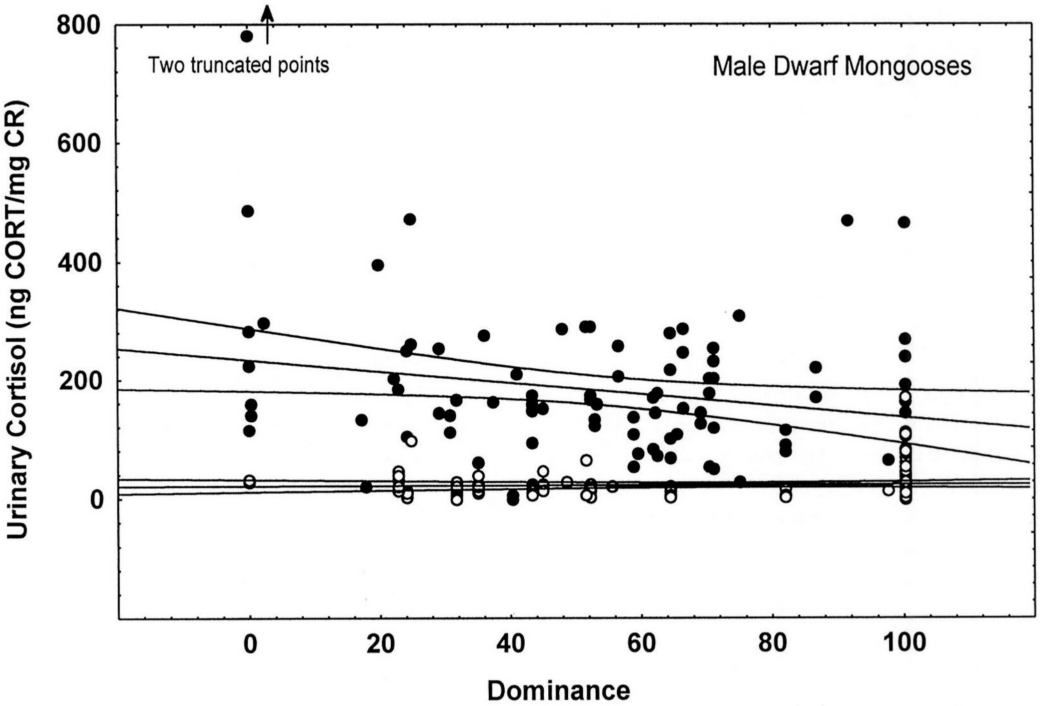


FIG. 3.—Relationships between dominance rank (see legend to Fig. 1 for details) and glucocorticoid (GC) levels in dwarf mongooses. GC levels are plotted independently for baseline samples (open circles = collected noninvasively from untrapped mongooses) and for acute stress responses (filled circles = collected from trapped mongooses). Lines show linear least-squares regressions with 95% confidence limits, with the upper regression showing acute responses and the lower regression showing basal levels.

d.f. = 1, 91, $P < 0.005$), suggesting that their acute stress response was compromised. We do not know why male and female mongooses differ so clearly in the endocrine correlates of rank, despite being monomorphic and having strong similarities in the behavioral correlates of rank. Nonetheless, this result fits a pattern that effects of rank on endocrine function are more common in females but purely behavioral mechanisms are more common in males (Creel et al. 1992).

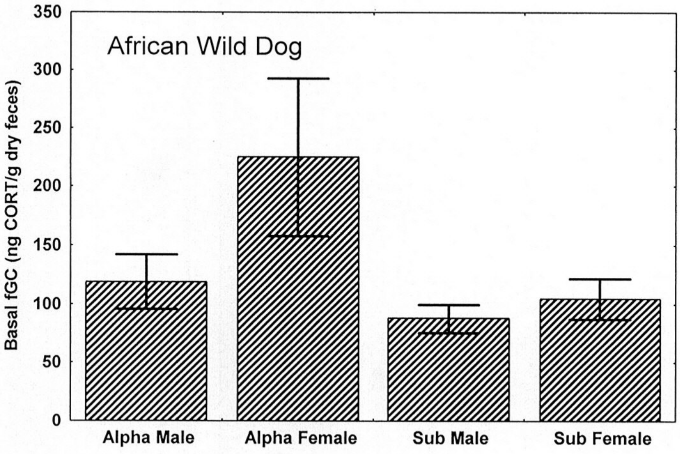


FIG. 4.—Relationship between dominance rank and basal fecal glucocorticoid (fGC) levels in African wild dogs (Sub = subordinate).

This general pattern may arise because selection for reproductive restraint is driven by reproductive constraints: without constraints, there is no selection in favor of restraint. Reproductive constraints may be greater for subordinate females simply because maternity is easier to identify than paternity. This allows alpha females to kill offspring other than their own. In contrast, alpha males are often poorly positioned to use infanticide to enforce reproductive suppression. Paternity can be mixed within litters for essentially all carnivores studied to date. If the alpha male mates more often than other males, but cannot directly determine the paternity of individual offspring, then infanticide is not a viable method of enforcing reproductive suppression (Creel and Waser 1996). It is possible that fathers can recognize their own offspring even within litters of mixed paternity, but the evidence for such capabilities is limited, and it seems very likely that confidence of paternity will be lower than confidence of maternity.

AFRICAN WILD DOGS

Wild dog packs averaged nine adults and yearlings on our study site in the Selous Game Reserve, with a range of 2–27. For all populations studied to date, pack size averaged 6.8 ± 0.8 *SE* individuals (Creel and Creel 2002). Alpha females produced 81% of 85 litters in Kruger National Park (M. G. L. Mills, pers. comm.) and 75% of 57 litters in Serengeti National Park (Burrows 1995; Malcolm and Marten 1982). In Selous, alpha females had an annual probability of breeding of 81.5% ± 7.0 *SE*, far higher than that of subordinates (6.4 ± 2.4%; $z = 7.36$, $P < 0.001$). We observed 5 cases in which no litter was produced, all in newly formed packs that deferred reproduction until the next rainy season rather than mating out of season. In stable packs, the alpha female invariably gave birth once per year, whereas 7 litters were born to subordinate females in 110 individual-years of observation. When a subordinate female gave birth, she usually did so several days after the alpha female. In Selous, as elsewhere, subordinates' pups were sometimes killed, but were sometimes creched with the dominant female's pups and raised (Frame et al. 1979; Fuller et al. 1992; van Lawick 1973). Examination of behavioral and genetic data shows that most offspring are fathered by the dominant male (Creel and Creel 2002; Girman et al. 1997). Like dwarf mongooses, wild dogs are obligately cooperative breeders: unaided pairs virtually never raise offspring to independence in any population.

Among females, the oldest individuals were usually dominant. In contrast, males of intermediate age were highest ranking because alpha males were often deposed by younger pack-mates as they aged (Creel and Creel 2002).

During nonmating periods (the great majority of the year), we detected no association between rank and fighting rate for either sex. During mating periods, alphas of both sexes fought significantly more often than did subordinates (Creel et al. 1997). Although rank and aggression were related only over a narrow time window, fecal GC levels were higher in dominant dogs year-round (Fig. 4; factorial analysis of variance including rank and sex, rank effect, $F = 6.76$, $P < 0.01$—Creel et al. 1996).

GRAY WOLVES

In Yellowstone National Park, the average size of our 3 focal packs was 8.7 adults and yearlings (range 6–12). Over 2 years, we collected 345 fecal samples and 375 h of behavioral observations on these 3 packs (Druid, Leopold, and Rose packs). Of these 345 samples, 122 came from 20 known individuals, whose social status was determined from aggressive and agonistic interactions by using the Batchelder–Bershad–Simpson method of assigning ranks (Jameson et al. 1999).

Like wild dogs and female dwarf mongooses, dominant wolves of both sexes had higher basal GC levels than did subordinates (Fig. 5). We used analysis of covariance to examine the effect of rank on GCs, controlling for the properties of the fecal samples (proportion indigestible matter, percentage water, and coefficient of variation for repeated within-sample measurements), and for variation among packs and years. GC values were log-transformed before analysis to obtain normality (Sands and Creel 2004). In the analysis of covariance, social status had a significant effect on GCs (Fig. 5; $F = 4.60$, $d.f. = 1, 96$, $P = 0.038$), with dominant animals having higher levels (1,876.0 ng cortisol/g dry feces ± 286.7 *SD*) than subordinates (1,381.8 ± 212.0 ng cortisol/g dry feces). This pattern was consistent between years (interaction, $F = 0.17$, $d.f. = 1, 96$, $P = 0.68$) and across packs (interaction, $F = 0.58$, $d.f. = 2, 96$, $P = 0.56$).

Although the endocrine correlates of rank are similar for these 3 carnivores, the behavioral correlates are more variable. For wolves, our behavioral data come from 1 pack that we observed for a total of 270 h. By using multiple regression, we tested whether the combined rate of all agonistic and aggressive behaviors was associated with GC levels, again controlling for properties of fecal samples (as above). Fecal GC levels were not detectably related to the rates of these behaviors (Fig. 6; partial correlation, $F = 2.06$, $d.f. = 3, 78$, $R^2 = 0.04$, $P < 0.12$). To test whether specific agonistic or aggressive behaviors showed a stronger relationship, we examined partial correlations between GC levels and dominance, submission, stylized aggression, and attacks. Again, we detected no relationships.

Conclusions

Noninvasive field studies of social carnivores and other cooperative breeders clearly show that elevated GC levels are often a cost of dominance. GC levels are higher in dominant wolves and wild dogs of both sexes and in female dwarf mongooses. When we 1st detected this pattern in dwarf mongooses, I was quite surprised because it opposed the prevailing view that subordination provokes a chronic elevation of GCs. However, subsequent field studies of cooperatively breeding birds, carnivores, and primates have shown that elevated GC levels in dominants are not unusual (Table 1), and this represents a substantial shift from the prior view that social stress primarily affects subordinates. We must consider the stress of domination in addition to the stress of subordination, and the selection pressures that these stressors create in social evolution. We also must identify the behavioral differences among species that predict where within the hierarchy social stress will be strongest. This is already an active field of study (Cavigelli 1999; Kotrschal et al. 1998) and 2 possibilities are that dominants have elevated GCs when a hierarchy is unstable (Sapolsky 1983) or in species in which dominants fight more often than subordinates (Creel et al. 1996).

It has also been proposed that rank might affect "allostatic load" in different ways in different species (Goymann and Wingfield 2004). Allostatic load is defined as "the cumulative cost to the body of . . . actively adjusting to both predictable and unpredictable events . . . when energy available to the organism is exceeded by demands of the environment" (McEwen and Wingfield 2003:12–13). I agree that the physical and psychosocial challenges of high and low rank are likely to vary among species, and the concept of allostatic load may be useful in understanding these differences. However, it is important that "allostatic load" does not simply become another term for stress, as in statements such as "social support and cooperation may decrease allostatic load and social conflict and competition for resources may dramatically increase it, which may be reflected in elevated glucocorticoid concentrations" (Goymann and Wingfield 2003:592). In the research summarized here, the focal questions were "How do GC levels correlate with rank?" and "What behaviors are associated with patterns of GC secretion?" To answer these questions, it is not advantageous to condense behavioral data into an omnibus variable such as allostatic load.

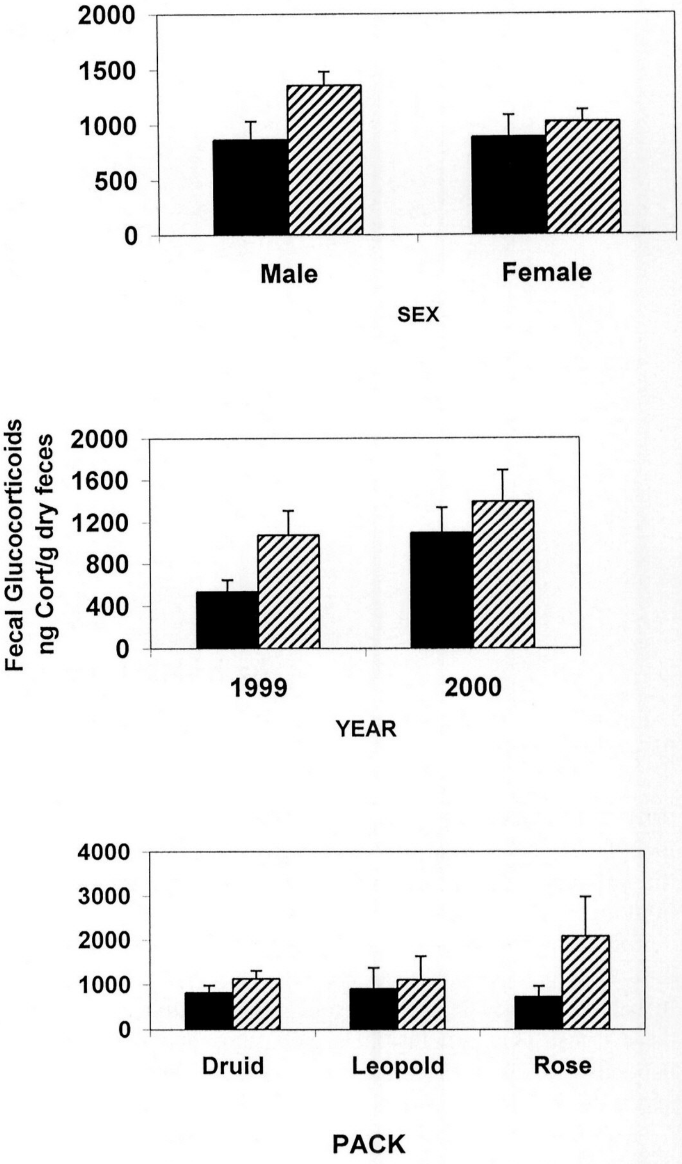


FIG. 5.—Relationship between dominance rank and basal fecal glucocorticoid levels in wolves. Glucocorticoid concentrations were higher in dominant wolves (hatched bars) than in subordinates (black bars), a pattern that was consistent for both sexes, in both years of study, in each of 3 packs studied.

Seeking to explain elevated GCs in dominant animals, and based largely on data from dwarf mongooses, I have argued that higher rates of aggression among alphas might be the cause (Creel et al. 1996). With data from wild dogs and wolves, this explanation has become less convincing. Wild dogs fight at higher rates only during the mating period, which lasts just a few weeks, yet the GC levels of alphas are higher year-round. For wolves, rates of agonistic and aggressive behavior were not detectably related to GC levels. Although dominant wolves win more often, they do not engage in agonistic or aggressive behavior more often than subordinates. This leads us to an interesting logical conundrum. If we applied the same logic as the original studies that concluded that losing fights is stressful, we would be forced to conclude that winning fights is more stressful than losing at the same rate, which seems quite unlikely. More likely, some aspects of maintaining social status are not easily captured in simple measures of the frequency and outcome of agonistic interactions (as argued by Sapolsky [1990] Virgin and Sapolsky [1997]). Rank is a good predictor of GC levels in cooperatively breeding carnivores. Nonetheless, it is still not clear whether GC levels are causally related to rank itself, or to behavioral correlates of rank. The pattern of wins and losses is effective in evaluating social dominance, which in turn is a good predictor of GC levels. Unfortunately, this same pattern of wins and losses is not clearly and consistently related to GC levels in some species (e.g., wolves). Although social stress is often a cost of dominance for cooperative breeders, the behavioral aspects of social status that

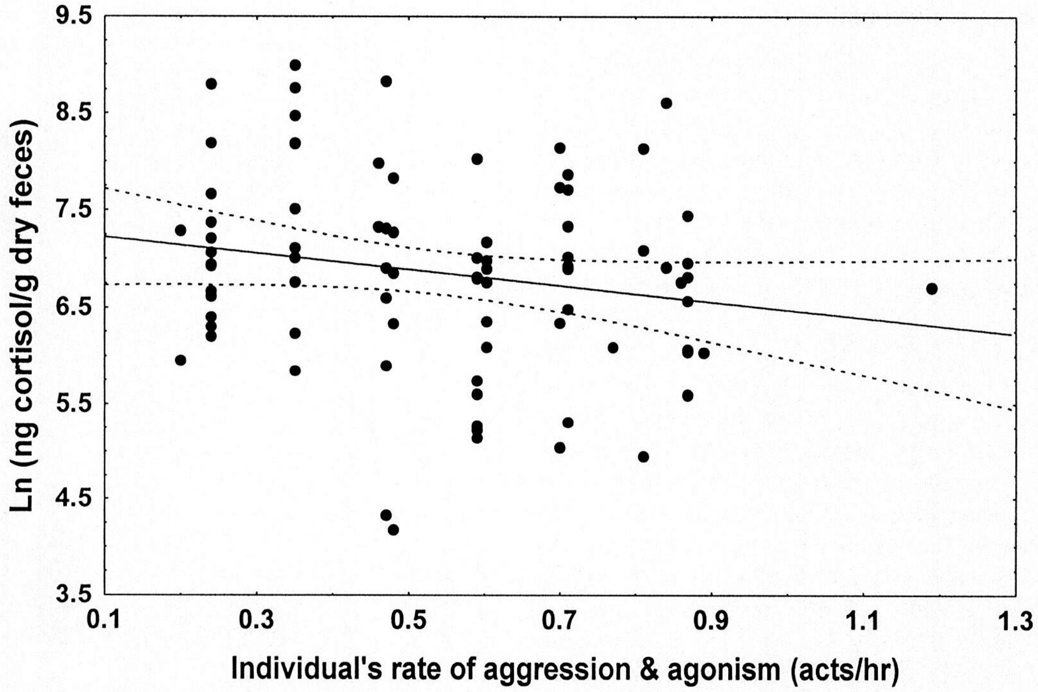


FIG. 6.—The relationship between basal glucocorticoid levels and rates of aggressive and agonistic behavior in wolves (simple regression with 95% confidence limits).

drive this relationship are not yet clear. It will be difficult to identify the behavioral driving forces in some cases, because the answers probably depend on knowing what an animal is thinking, rather than what it is doing.

For example, Sapolsky (1990) suggests that certain behavioral traits or "personalities" are associated with elevated GCs in baboons, regardless of the rank of the individual that has these traits. This conclusion is well supported by data from baboons (Sapolsky 1990; Sapolsky and Ray 1989). I have not tested this hypothesis directly for these 3 social carnivores, but it seems unlikely to hold, simply because relationships between age, rank, and GC levels are strong. Consequently, one would expect a relationship between personality and GC levels only if personality changes with age in a predictable manner. Under this scenario, it would be difficult to distinguish between the effect of personality and the effect of age itself.

Finally, objectively measuring and interpreting personality traits that appear to affect GC levels present serious problems. To illustrate, GC levels were higher in baboons with a poor "ability to behaviorally differentiate between winning and losing a fight" and in baboons with a poor "ability to behaviorally differentiate between a threatening interaction [versus] the neutral presence of a rival male" (Sapolsky 1990:873). To evaluate these aspects of personality requires the ability to understand the social interactions of another species well enough that we can determine when an individual is making a mistake in its interpretation of the behavior of a conspecific. This is a high standard, particularly if the species differs substantially from humans in its sensory capabilities (for example, a canid might use its well-developed sense of smell to determine that an individual is not likely to fight, even when its overt behavior is apparently threatening to human eyes). If basal GC levels do indeed relate to personality more closely than they relate to rank, it will be intriguing to see if the behavioral traits associated with stress responses are consistent among species.

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