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Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates

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Abstract

Among primate species there is pronounced variation in the relationship between social status and measures of stress physiology. An informal meta-analysis was designed to investigate the basis of this diversity across different primate societies. Species were included only if a substantial amount of published information was available regarding both social behavior and rank-related differences in stress physiology. Four Old World and three New World species met these criteria, including societies varying from small-group, singular cooperative breeders (common marmoset and cotton top tamarin) to large-troop, multi-male, multi-female polygynous mating systems (rhesus, cynomolgus, talapoin, squirrel monkeys, and olive baboon). A questionnaire was formulated to obtain information necessary to characterize the stress milieu for individuals in particular primate societies. We standardized cortisol values within each species by calculating the ratio of basal cortisol concentrations of subordinates to those of dominants in stable dominance hierarchies and expressing the ratio as a percentage (relative cortisol levels). The meta-analysis identified two variables that significantly predicted relative cortisol levels: subordinates exhibited higher relative cortisol levels when they (1) were subjected to higher rates of stressors, and (2) experienced decreased opportunities for social (including close kin) support. These findings have important implications for understanding the different physiological consequences of dominant and subordinate social status across primate societies and how social rank may differ in its behavioral and physiological manifestations among primate societies.

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Introduction

In mammals, including humans, challenges to homeostasis commonly evoke a series of endocrine and neural actions

known as the stress response. While not as stereotyped as once thought, the stress response typically involves release of catecholamines (norepinephrine and epinephrine) from

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the sympathetic nervous system and adrenal medulla, release of adrenocortical steroid hormones (glucocorticoids), and initiation of a variety of other endocrine responses, including suppression of hormones related to anabolism, growth, and reproduction (Orth and Kovacs, 1998; Sapolsky, 2000, 2002). Collectively, the stress response aids in adapting an individual to an acute stressor by stimulating hepatic glucose release and visceral lipolysis, enhancing delivery (via enhanced cardiovascular tone) of glucose, fatty acids, and triglycerides to skeletal muscle and brain, triaging processes nonessential to immediate survival (such as growth, digestion, reproduction, and tissue repair), and constraining inflammatory and immune responses. Despite these adaptive functions, it has long been recognized that chronic or prolonged activation of the stress response can have deleterious physiological effects, including the induction or worsening of hypertension, insulin-resistant (type II) diabetes, ulceration in the gastrointestinal tract, anovulation, impotence, osteoporosis, psychogenic dwarfism, and immunosuppression (Sapolsky, 2002).

Because of the pathological consequences of a prolonged stress response, much attention has focused on individual differences in patterns of secretion of stress response hormones. These can include differences in blood hormone levels prior to and during the stress response, the speed of physiological recovery of homeostasis after the stress response abates, or the ease with which different types of stressors differentially provoke separate components of the stress response. As examples of such differences, a number of psychiatric disorders and personality types have been associated with what can arguably be termed a maladaptive and overactive stress response. These include major depression (Holsboer, 1999), repressive personality (Brandtstadter et al., 1991), and Type A personality (Williams, 1989). Differential fetal programming (Seckl, 2001) and endocrine disruption of pre- and perinatal environments (Clarke et al., 1994) can result in further exaggeration of adult stress responses.

Another branch of psychoneuroendocrine research has focused on ways in which individual differences in the stress response can reflect differences in dominance status among social animals. In some species, subordination has been reported to be associated with a chronically overactive stress response (as assessed by hypersecretion of glucocorticoids or catecholamines, higher blood pressure, and greater incidences of stress-related pathologies). This pattern is thought to reflect the classical picture of dominance hierarchies as linear “pecking orders” in which resources are unevenly distributed, inequalities are maintained through aggression and intimidation, and subordinates are subject to the most severe resource limitations, the fewest opportunities for coping, and the greatest physical and social stressors (Albeck et al., 1997).

The relationship between social rank and patterns of the stress response is not consistent among primates in that there is no monolithic relationship between social status and

any aspect of stress physiology (Abbott et al., 1997; Clarke and Boinski, 1995; Sapolsky, 1993). This diversity appears to reflect, among other things, the extraordinary variety of primate social systems, which often constitute striking exceptions to hierarchical pecking orders (Dunbar, 1988; Strier, 1996; de Waal, 1989) and include complex, affiliative relationships that ameliorate responses to stressors, such as through reconciliation (de Waal, 1993, 2000), providing different forms of coping mechanisms to individuals (Bercovitch, 1991).

The purpose of the meta-analysis performed in this study is to identify the social variables that predict primate societies in which (1) subordinates have overactive stress responses, (2) subordinates have diminished stress responses, or (3) stress responses do not vary with social rank. More broadly, we are attempting to understand the social roles of individuals, in terms of their rank, sex, and species, and the relationship of such roles in different primate species to differences in the stress response.

Likely variables contributing to individual differences in the stress response

In order to identify primate societies that give rise to differing relationships between rank and physiology, it is important to first review factors that stimulate or ameliorate the stress response.

One factor is the frequency at which an individual is exposed to physical stressors. As such, it is important to consider rank-related differences in (1) availability of food and the effort needed to acquire it, (2) exposure to pathogens, (3) likelihood of being threatened by a predator, and (4) the incidence of aggressive challenge and injury.

Of at least equal importance is the rate at which an individual is exposed to psychological stressors. An extensive and elegant literature has demonstrated that psychological variables can stimulate the stress response outright and can dramatically modulate the response to physical stressors (Bakshi and Kalin, 2000; Levine et al., 1989; Lui et al., 1997; McEwen, 2001; Sapolsky et al., 2000). Broadly, for the same physical insult, individuals are far more likely to have a stress response and a stress-related disease if they lack a sense of control or lack predictive information about the timing, severity, or duration of the stressor. It thus becomes important to understand whether there are rank-related differences in the extent to which individuals (1) can control access to resources, (2) are subject to aggression, and (3) can establish stable and predictable social relations.

Finally, the response to physical or social stressors is considerably blunted by the availability of coping responses, such as social outlets for frustration or social support (Sapolsky, 2002). Thus, rank-related differences in the availability of social contact, social grooming, sexual behavior, and frustration displacement of aggression become as relevant as low rank and the degree of accompanying stressors.

Table 1
Primate species and sex included in both methods of statistical analyses, illustrating the social/mating system and group structure/physical environment for each

Species	Relative cortisol levels (%)	Social/mating system	Group structure/ physical environment
1. Common marmoset (<i>Callithrix jacchus</i>), female [New World]	45	Small groups, singular cooperative breeders ^a	Captive, mixed sex groups of 3–6 unrelated adults in cages 0.6 × 0.9 m × 1.8 m high ^b
2. Cotton top tamarin (<i>Saguinus oedipus</i>), female [New World]	80	Small groups, singular cooperative breeders ^a	Captive, families of parents and offspring in cages 0.8 × 1.5 m × 2.3 m high ^c
3. Cotton top tamarin (<i>S. oedipus</i>), male [New World]	82	Small groups, singular cooperative breeders ^a	Captive, families of parents and offspring in cages 0.8 × 1.5 m × 2.3 m high ^c
4. Squirrel monkey (<i>Saimiri scurieus</i>), female [New World]	98	Large groups, multi- male, multi-female, polygynous ^a	Captive, single or mixed sex groups of 3–4 un related adults in cages 1.0 × 1.0 m × 2.3 m high ^e
5. Rhesus monkey (<i>Macaca mulatta</i>), male [Old World]	99	Large groups, multi- male, multi-female, polygynous ^f	Captive, troops of ~150 related and unrelated rhesus in 0.3-ha outdoor enclosure, Sebana Seca Field Station, Puerto Rico ^g
6. Talapoin monkey (<i>Miopithecus talapoin</i>), female [Old World]	105	Large groups, but multi-male, multi- female only in the breeding season, polygynous ^d	Captive, mixed sex groups of 7–11 unrelated adults in cages 3.5 × 1.5 m × 1.7 m high ^h
7. Cynomolgus monkey (<i>Macaca fascicularis</i>), female [Old World]	127	Large groups, multi- male, multi-female, polygynous ^f	Captive, mixed sex groups of 5–7 unrelated adults in outdoor pens 1.7 × 3.3 m ⁱ
8. Squirrel monkey (<i>S. scurieus</i>), male [New World]	145	Large groups, multi- male, multi-female, polygynous ^d	Captive, single, or mixed sex groups of 3–4 un related adults in cages 1.0 × 1.0 m × 2.3 m high ^e
9. Olive baboon (<i>Papio anubis</i>), male [Old World]	147	Large groups, multi- male, multi-female, polygynous ⁱ	Free-ranging, troops of ~40–50 related and un related baboons, in Masai Mara National Reserve, Kenya ^k
10. Talapoin monkey (<i>M. talapoin</i>), female [Old World]	154	Large groups, but multi-male, multi- female only in the breeding season, polygynous ^d	Captive, mixed sex groups of 7–11 unrelated adults in cages 3.5 × 1.5 m × 1.7 m high ^h

Note. “Relative cortisol levels” indicate basal cortisol concentrations in the subordinates expressed as a percentage of basal cortisol concentrations in dominants. Data on olive baboons were derived from free living troops in East Africa, while all other data came from captive populations.

Relevant citations for social/mating system:

^a French, 1997,

^d Rowell and Dixson, 1975,

^f Caldecott, 1986,

ⁱ Smuts, 1986.

Relevant citations for group structure/physical environment:

^b Saltzman et al., 1998,

^c Snowdon et al., 1985,

^e Mendoza and Mason, 1991,

^g Bercovitch and Clarke, 1995,

^h Yodyingyud et al., 1985,

^j Kaplan et al., 1986,

^k Sapolsky, 1983.

Methods

Questionnaire

Based upon the known physical and psychological modulators of the stress response, the first and last authors formulated a questionnaire containing key questions that were designed to obtain information necessary to characterize the stress milieu for individuals in particular primate

societies. More broadly, we attempted to ask questions that would formalize the characteristics of subordinate and dominant individuals—what stressors and what sources of coping are available—for each primate species. We considered these questions only in the handful of monkey species for which substantial amounts of published data are available regarding both social behavior and rank-related differences in stress physiology (Table 1).

The most frequently studied physiological endpoint of

the stress response is the circulating or urinary concentration of cortisol. Cortisol is the predominant circulating glucocorticoid in primates and it became our variable of choice for consideration in the meta-analysis. We standardized cortisol values within each species by calculating the ratio of basal cortisol concentrations in subordinates to those in dominants in stable social groups and expressing the ratio as a percentage (relative cortisol levels; Table 1). Determination of relative cortisol levels eliminated between-species differences in circulating cortisol levels, particularly the ~10-fold difference in circulating levels between small-bodied, New World primates and Old World primates, including humans (Coe et al., 1992).

Cortisol concentrations, however, are also modulated by many behavioral and physiological variables in addition to the stress response, including physical activity (Girard and Garland, 2002), immune function (Hermus and Sweep, 1990), food intake or nutritional status (Ausman et al., 1989) and reproductive function (Kime et al., 1980; Saltzman et al., 1998). Consequently, we focused on circulating or urinary cortisol concentrations obtained under basal conditions (i.e., rapidly, from undisturbed animals) in studies in which the dominance hierarchy was stable (Table 1). Urinary cortisol concentrations reflect circulating concentrations of cortisol that are “free” or not bound to corticosteroid binding globulin (CBG), the glucocorticoid-specific circulating binding protein (Robinson et al., 1985; Yamamoto et al., 1977). New World primates, however, including squirrel monkeys, common marmosets, and cotton top tamarins in this study, have little or no circulating CBG, so that cortisol circulates unbound to a specific circulating binding protein or only loosely bound to albumin (Klosterman et al., 1986; Pugeat et al., 1984; Robinson et al., 1985). The apparent resistance to the extremely high basal levels of free cortisol in New World primates is not due to poor affinity of glucocorticoid receptors (GR) for glucocorticoids (Scammell et al., 2001). Instead, there is overexpression of an intracellular, cytosolic binding protein for glucocorticoids, FK-506 binding immunophilin (FKBP51; Reynolds et al., 1999), that specifically inhibits binding of glucocorticoids to GR (Denny et al., 2000; Scammell et al., 2001) and accounts for the absence of hypercortisolemic pathology. The degree of HPA activation in New World primates, nevertheless, appears similar to that in Old World primates, as exemplified by the utilization of New World primates as models for human HPA function, stress, and psychopathology (e.g., Cilia and Piper, 1997; Johnson et al., 1996).

For squirrel monkeys, rhesus monkeys, and cynomolgus monkeys, social rank was based on outcomes of contested resources or approach-avoidance interactions (Table 1). In marmosets, tamarins, talapoin, and olive baboons, ranking was based on the outcome of agonistic interactions, identifiable from submissive gestures, behaviors, vocalizations, and withdrawals, because outcomes of contested resources

have proven unreliable in these monkeys. All co-authors, except our statisticians (M.B. and T.G.), completed the questionnaire regarding stressors and sources of coping in primate species that we have studied in depth (Table 1). In all cases, these individuals are experts in the social behavior of their particular primate species and are often the primary generators of the relevant cortisol data used in this meta-analysis (Table 1). Individual co-authors filled out the questionnaire only for the species about which they are expert: female marmosets (D.H.A. and W.S.), male and female talapoin (E.B.K.), male rhesus (F.B.B.), female cynomolgus (C.A.S.), female and male squirrel monkeys (S.P.M.), female and male tamarin (C.T.S. and T.E.Z.), and male olive baboons (R.M.S.). All but the first and last authors were kept unaware of how the data were to be analyzed until they had returned the completed questionnaire.

Rationale for specific questions in the questionnaire

The six following contributing factors were identified as the factors most likely to be germane to the effects of rank on circulating or urinary cortisol concentrations. We subdivided each contributing factor into one or more specific questions (totaling 17) to obtain more detailed information about a particular contributing factor and its relationship to cortisol levels (Table 2). The questions are not mutually exclusive and there is clear overlap in some cases, e.g., Question 2F with Questions 2A–2E in Table 2, and adjustments were made for these potential redundancies (following receipt and analyses of the answers) in Results.

Contributing factor 1: What is it like to be a dominant individual in each primate society surveyed?

Question 1A: How much of a role does aggression play in the attainment of dominance? In some primate societies, dominance is attained through overt, dyadic aggression (baboons: Sapolsky, 1990; mandrills: Wickings and Dixon, 1992), while in others, it can involve the formation of coalitional alliances (macaques: Bercovitch, 1988; langurs: Sommer, 1988; chimpanzees: de Waal, 1982) combined with overt aggression, or can be inherited (common marmoset: Abbott, 1984; Lazaro-Perea et al., 2000; cotton top tamarin: Savage et al., 1997). These different scenarios seem likely to carry very different consequences for the qualities of the stressors encountered during attainment of high rank and individuals' responses to these stressors.

Question 1B: How much of a role does aggression play in the maintenance of dominance? In some societies, dominance is maintained through intimidation, psychological harassment, or alliances, rather than through direct, dyadic aggression (for reviews see Dunbar, 1988; Harcourt, 1987; de Waal, 1982). Again, each of these different situations is likely to have different consequences for responses to stressors encountered by a dominant individual.

Table 2

Numerical value answers to the questionnaire in relation to relative cortisol levels and to the coefficients generated from the correlations between the responses to a question and the relative cortisol levels

	Basal cortisol levels in subordinates (relative to dominant animals):										Correlation with Cortisol Values ^a
	45–82%		98–105%			127–154%					
	Fem mar	Fem tam	Male tam	Fem sqr	Male rhe	Fem tal	Fem cyn	Male sqr	Male bab	Male tal	
I. What is it like to be a dominant individual in this society?											
(1A) How much of a role does aggression play in the attainment of dominance?	3	0	0	3	2	2	1	0	3	2	–0.47
(1B) How much of a role does aggression play in the maintenance of dominance?	1	0	0	3	1	1	0	1	1	1	–0.39
(1C) How disproportionately does dominance carry physical and psychological rewards?	3	3	3	0	3	3	3	1	3	3	0.02
II. What is it like to be a subordinate individual in this society?											
(2A) How frequently are subordinates subject to stressors?	1	0	0	1	2	2	3	1	3	3	0.57 ^b
(2B) How available is social support for subordinates?	2	1	1	1	1	2	1	0	1	1	–0.82 ^b
(2C) Do subordinates have alternatives to overt competition?	1	2	2	1	1	2	1	1	1	2	0.08
(2D) How likely is a subordinate to be caught at such covert behaviors?	2	0	0	3	1	2	—	3	1	2	—
(2E) If caught, how likely is the animal to be aggressively punished?	1	—	—	0	2	2	2	0	2	3	—
(2F) Overall, how much should subordinate status be thought of as an undesirable state actively imposed by more dominant animals?	1	0	0	0	3	2	2	1	3	3	0.43
III. What are the typical routes by which ranks change?											
(3A) Do animals rise in the hierarchy through strenuous challenge of the status quo?	1	0	0	0	1	1	1	1	3	1	0.42
(3B) How labile is the dominance system?	1	1	1	3	1	1	0	1	2	1	–0.30
IV. What is the nature of revolutionary change in hierarchies?											
(4A) How often do such “revolutions” occur, in which there are rapid and dramatic changes throughout the hierarchy?	1	0	0	2	0	0	1	1	2	1	0.29
(4B) When such revolutions occur, do rates of aggression among dominant animals increase?	1	—	—	3	—	—	3	3	3	3	—
(4C) When such revolutions occur, do rates of aggression among subordinates increase?	0	—	—	2	—	—	1.5	3	0	0	—
(4D) When such revolutions occur, do rates at which subordinate animals suffer displaced aggression from dominant animals increase?	0	—	—	2	—	—	2	3	3	3	—
V. The role of kinship.											
(5A) How important is kinship in understanding interactions among these animals?	3	3	3	1	1	3	3	0	0	0	–0.61
VI. Non-agonistic factors relevant to the stress-response.											
(6A) Are there circumstances in which one has to invoke a physiological explanation, rather than a response to agonistic behavior, to make sense of the profile of a particular stress hormone?	2	2	2	0	1	0	0	0	0	0	–0.61

Note. “0” applies minimally or not at all in the particular species/sex; “1,” “2,” “3,” indicate mildly, moderately, and strongly relevant to the particular species/sex, respectively. “—” indicates no reliable data available. Species and designated number from Table 1: mar (common marmoset; 1), tam (cotton top tamarin; 2 and 3), sqr (squirrel monkey; 4 and 8), rhe (rhesus monkey; 5), tal (talapoin monkey; 6 and 10), cyn (cynomolgus monkey; 7), bab (olive baboon; 9).

^a Bivariate correlation based on phylogenetically independent contrasts.

^b Indicates final variables resulting from stepwise forward multiple regression analysis using phylogenetically independent contrasts, following the elimination of several variables, as described in the text.

Question 1C: How disproportionate are the physical and psychological rewards of dominance? Dominant individuals in different primate societies have very different degrees of control over resources [e.g., food; Harcourt, 1987 (various primate species)] or reproductive activity (common marmo-

sets: Abbott, 1987; cotton top tamarins: Ziegler et al., 1987; baboons: Sapolsky, 1992), and very different degrees of predictability of social situations and their control over them. Such differences will obviously translate into differences in the need for coping outlets in subordinates.

Contributing factor 2: What is it like to be a subordinate individual in each primate society surveyed?

Question 2A: How frequently are subordinates subject to stressors? The answers should reflect whether subordinates are disproportionately victims of aggression (particularly unpredictable, third-party, displacement aggression that elevates cortisol in recipients, e.g., baboons: Ray and Sapolsky, 1992; Sapolsky and Ray, 1989; Sapolsky et al., 1997; Virgin and Sapolsky, 1997), predatory attack, disruption of feeding, disruption of mating, and so on.

Question 2B: How available is social support for subordinates? Subordinate animals can have reduced access to grooming, social contact, or formation of alliances (baboons: Ray and Sapolsky, 1992; Sapolsky and Ray, 1989; Sapolsky et al., 1997; Virgin and Sapolsky, 1997; talapoin: Keverne et al., 1984).

Question 2C: Do subordinates have alternatives to overt competition? In some primate societies, subordinates can disperse to a different group (e.g., macaques: Saueremann et al., 2001), can safely and temporarily become peripheral to the group [Harcourt, 1987 (various primate species)], or can form intersexual alliances that result in covert matings in out-of-the-way places — often called “stolen copulations” (Digby, 1999; Lazaro-Perea, 2001; Smuts, 1986). These different scenarios may lead to quite different physiological consequences when stressors are encountered by subordinate individuals.

Question 2D: How likely is a subordinate to be caught at such covert behaviors?

Question 2E: If caught, how likely is the animal to be aggressively punished?

Question 2F: Overall, how much should subordinate status be thought of as an undesirable state actively imposed by more dominant animals? While this is typically the case in some primate systems, in others, subordinate status is a stable and compliant state. Question 2F represents a composite of Questions 2A–2E and seeks to clarify the general character of subordinate status in each primate society involved in this analysis.

Contributing factor 3: What are the typical routes by which ranks change?

Question 3A: Do animals rise in the hierarchy through strenuous challenge of the status quo? While this can be the case (e.g., male olive baboon; Sapolsky, 1993), dominance may instead be obtained by passively waiting one’s turn, or by inheriting a higher rank due to the death or departure of a more dominant individual (e.g., female common marmoset; Lazaro-Perea et al., 2000). These differing routes of ascension may present differing degrees of stressors.

Question 3B: How labile is the dominance system? The extent of dominance lability will translate into a measure of the likelihood of a subordinate animal moving out of the subordinate cohort. Primate systems differ dramatically both in the degree to which one or both sexes typically display hierarchies and in the plasticity of hierarchies (Dunbar, 1988; Strier, 1996).

Contributing factor 4: What is the nature of revolutionary change in hierarchies?

Question 4A: How often do such “revolutions” occur? In some primate societies, there are rapid changes in rank throughout the hierarchy that can be more dramatic than a mere shift to the adjacent rank. “Revolutions” can occur relatively frequently in labile systems, or can be nonexistent in “hereditary” hierarchies.

Question 4B: When revolutions occur, do rates of aggression among dominant animals increase?

Question 4C: When revolutions occur, do rates of aggression among subordinate animals increase?

Question 4D: When revolutions occur, do rates at which subordinate animals suffer displaced aggression from dominant animals increase? The frequency and stressfulness of such revolutions (as assessed in these questions) may have an impact on stress-sensitive physiology.

Contributing factor 5: What role does kinship play in attaining dominance?

Question 5A: How important is kinship in understanding interactions among these animals? This variable was included because of the potential buffering effects of kin against social stress. In some primate species (e.g., at least olive baboons and talapoin, rhesus, and cynomolgus monkeys in this study: Table 1) hierarchies of adults in one sex comprise unrelated individuals, if the individuals of that sex disperse over a sufficient distance (Pusey and Packer, 1987).

Contributing factor 6: Are there nonagonistic factors relevant to the stress response?

Many nonagonistic factors can affect the stress response in primates, including ovarian function (Saltzman et al., 1998, 2000; Smith and Norman, 1997). We will, however, only focus on physiological adaptations to subordinate status that can occur because subordinates in certain societies, such as those of cooperatively breeding species (Abbott et al., 1998), do not experience a high degree of harassment and HPA activation (Abbott et al., 1997; Saltzman et al., 1998).

Question 6A: Are there circumstances in which one has to invoke a physiological adaptation to subordinate status, rather than a response to agonistic behavior, to make sense

of the profile of a particular stress hormone? One striking example of this will be considered below in discussing hypocortisolism in subordinate female common marmosets (Abbott et al., 1997, 1998).

Data analysis

Four Old World and three New World species were included in the analyses, and because of the sometimes dramatic differences between the sexes within the same primate society, males and females were treated as separate data points. This generated a total of 10 observations from the literature (Table 1), including societies varying from small-group, singular cooperative breeders (common marmoset and cotton top tamarin) to large-troop, multi-male, multi-female polygynous mating systems (rhesus and cynomolgus monkeys, and olive baboon). The questionnaire comprised questions 1A–6A described above. Respondents (all authors, except M.B. and T.G.) answered on a scale of 0–3, in which the social state described in the particular question was not at all (0), mildly (1), moderately (2), or highly applicable (3) to the species and sex under consideration. Answers were correlated with only a single physiological parameter: relative basal cortisol levels. The latter were derived from basal cortisol concentrations (in blood or urine collected by the same methods and at the same time of day within a species) in subordinate animals of a particular species and sex that were expressed as a percentage of basal cortisol values in dominant animals of that species and sex. Answers to the questionnaire also provided a degree of standardization for between-species behavioral data analogous to that derived from using relative basal cortisol levels. Quantitative behavioral data per se were not used because of a lack of comparability between species, such as the different agonistic behaviors displayed by different species, the different behaviors actually scored in the various studies, and the different units of measure employed (e.g., frequency, duration, or scan).

This analytical design produced 17 predictor variables (questions 1A–6A in Table 2) with four possible answers for each, one response variable, and 10 observations. Data were first analyzed by multiple regression (through the origin) with phylogenetically independent contrasts (Felsenstein, 1985; Garland et al., 1992, 1999). These analyses take into account the general nonindependence of values for species, i.e., the general phenomenon that closely related species will tend to resemble each other for many aspects of their biology, including social systems and cortisol responses (Blomberg and Garland, 2002). The estimate of phylogenetic relationships was taken from Purvis (1995), as follows: (((*Callithrix*, *Saguinus*)*Saimiri*)(((*Macaca mulatta*, *Macaca fascicularis*)*Papio*)*Miopithecus*)). As the data set includes males and females within each of three species, sex was treated as a bifurcation in the analyses within each species concerned. Independent contrasts were computed with the PDTREE program (Garland et al., 1999), with

branch lengths set according to Pagel's (1992) arbitrary method. Thus, bifurcations within species had branch lengths of one unit, as did bifurcations between species, with the constraint that all tips of the tree were contemporaneous in height.

How to incorporate between-sex variation into a phylogenetically based statistical analysis has not been examined in the literature. Our approach to placement of the sexes and to setting of branch lengths assumes that the expected amount of between-sex variation is similar in magnitude to the amount of between-species variation. We checked the adequacy of this assumption by examining a diagnostic plot of the absolute values of the standardized contrasts in relative cortisol values against their standard deviations (square roots of sums of corrected branch lengths; Garland et al., 1992). This plot indicated no significant correlation ($r = -0.26$, $df = 7$, two-tailed $P = 0.50$) and demonstrated that the three between-sex contrasts were similar in magnitude to the five between-species contrasts. Thus, the branch lengths used seem to be statistically adequate.

Because there were only 10 observations and 17 predictor variables, it was appropriate to include no more than three predictors in any resulting regression equation, in order to reduce bias (Venebles and Ripley, 1999). Therefore, before performing multiple regression analyses, we eliminated several potential predictors, based on various criteria. Five variables (2D, 2E, 4B, 4C, and 4D) were excluded because of missing values. Four more were then excluded either because of their significant correlation with other variables (Table 2: 1B and 3B; correlated with 1A as $r = 0.86$ and $r = 0.78$, respectively; correlated with each other as $r = 0.90$) or because of their poor correlation (Table 2: 1C and 2C) with relative cortisol levels (Table 1). For completeness, however, we report all of the simple pairwise correlations between each independent variable and cortisol ratio (except for the five variables excluded because of missing data) in Table 2. The eight remaining variables (1A, 2A, 2B, 2F, 3A, 4A, 5A, and 6A) were subjected to multiple regression analyses with phylogenetically independent contrasts and a stepwise forward selection procedure (P to enter = 0.05, P to remove = 0.10).

Because of the clustered nature of the response variables, we also analyzed the data using a tree-based method (Hastie and Tibshirani, 1990; Venebles and Ripley, 1999). In this approach, there is a single response variable (e.g., relative basal cortisol levels) and an array of predictors (17 variables; questions 1A–6A in Table 2) that enable construction of a "tree" to serve as a decision/classification algorithm. This second round of statistical analysis is unrelated to the phylogenetic tree used with the independent contrasts in the first round of analysis. Rather, this tree-based method is a conventional statistical analysis that does not attempt to account for phylogenetic relationships or sex. The data points are, however, not entirely independent of one another; e.g., New World primates comprise three species, but two are represented twice in separate male and female data

points, and Old World primates comprise four species, but one is represented twice as separate male and female data points (Tables 1 and 2). While such lack of discrimination in the tree-based method might give the appearance of inflated degrees of freedom and probabilities of significance, the tree analysis focuses on the selection of the number of variables that provide the greatest amount of information, by forward selection at each branch of the tree (Fig. 2).

As with the phylogenetically based analysis, not all variables were submitted to the tree algorithm for analysis. This elimination of variables was derived independently from that performed prior to the phylogenetic analysis. Answers to Questions 1A, 1B, 1C, 2C, 2D, 3B, 4A, 4C, and 4D were omitted for having either very low correlations (by tree regression analysis) with the relative basal cortisol levels or missing values. Answers to Questions 2E and 2F were omitted for being highly correlated with those to 2A; answers to Questions 4B and 6A were similarly omitted for correlation with answers to 4D and 5A, respectively. Answers to the remaining questions (2A, 2B, 3A, and 5A) were carried through the tree regression analysis. These are four of the eight variables finally selected for the phylogenetically based analysis, above. The best-fit regression coefficients obtained by the tree analysis for these four questions are not shown in Table 2, as the tree analysis was performed as supplemental to the phylogenetic analysis, and provided independent partial confirmation of the validity of the findings by selecting four of the same variables and predicting similar results.

In the tree-based method, should the response variability be significantly attributable to answers from one question, this would form a decision tree with a single branch point. For example:

- (1) If the answer to Question 1A is $>X$, then this predicts relative cortisol levels = $Y1\%$ (branch 1).
- (2) If the answer to Question 1A, however, is $<X$, then this predicts relative cortisol levels = $Y2\%$ (branch 2).

In contrast, if the response variability is entirely attributable to answers from two questions (e.g., Questions 2A and 2B), this would form a decision tree with two layers of branch points:

- (1) If the answer to Question 2A is $>X$, then relative cortisol levels are $>Y\%$ (branch 1). Given this outcome, if the answer to Question 2B is $>Z$, then relative cortisol levels = $Y11\%$ (branch 1.1), while if the answer to Question 2B is $<Z$, then relative cortisol levels = $Y12\%$ (branch 1.2).
- (2) If the answer to Question 2A, however, is $<X$, then relative cortisol levels are $<Y\%$ (branch 2). Given this outcome, if the answer to Question 2B is $>W$,

then relative cortisol levels = $Y21\%$ (branch 2.1), while if the answer to Question 2B is $<W$, then relative cortisol levels = $Y22\%$ (branch 2.2).

The tree-based analysis incorporates the minimal number of decision branch points that yield the maximal predictability of response variance (i.e., construction of a decision tree predicting relative cortisol levels from answers to questions in Table 2 that maximizes the variance explained by the model, e.g., Fig. 2). Branch points are determined as the points that most effectively minimize within-branch variation while providing the greatest possible separation between branches (Hastie and Tibshirani, 1990; Venebles and Ripley, 1999).

Results

Basal cortisol concentrations of subordinate individuals in stable dominance hierarchies, as compared to those of their dominant counterparts, show considerable variability among primate species, with relative cortisol levels ranging from 45% (subordinates lower than dominants) to 154% (subordinates higher than dominants; Table 1). Species in which cortisol concentrations in subordinates are lower than those of dominants (relative cortisol levels = 45–82%) include female common marmosets (Abbott et al., 1997, 1998; Saltzman et al., 1994, 1996, 1998) and female and male cotton top tamarins (Ginther et al., 2001; Ziegler et al., 1995). Those in which cortisol levels are approximately equal in dominants and subordinates (relative cortisol levels = 95–105%) include female squirrel monkeys (Saltzman et al., 1991; Vogt et al., 1980), male rhesus monkeys (Bercoitch and Clarke, 1995; Suomi et al., 1989), and female talapoin (Keverne et al., 1984; Yodyingyud et al., 1985), and those in which cortisol levels are greater in subordinates than in dominants (relative cortisol levels = 127–154%) include female cynomolgus monkeys (Shively et al., 1997; Shively, 1998), male squirrel monkeys (Coe et al., 1979; Manogue et al., 1975; Steklis et al., 1986; Vogt et al., 1980), male olive baboons (Sapolsky, 1982, 1990; Sapolsky et al., 1997), and male talapoin (Eberhart et al., 1983, 1985; Keverne et al., 1984; Yodyingyud et al., 1985).

This diversity in relative cortisol levels is not random: it can be explained by the different social environments experienced by individuals in their different societies. For example, adult male olive baboons (in which basal cortisol concentrations in subordinates are nearly 50% higher than in dominants) experience an overtly aggressive society in which violent action is key to attaining dominance, and threat and intimidation are necessary to maintain it (references given in Table 1). In comparison, at the other end of the social spectrum, female common marmosets (in which basal cortisol concentrations in subordinates are approximately 50% lower than those in dominants) experience a

relatively nonaggressive society in which the attainment of dominance mostly depends on rare instances of aggression at times of vacated dominant positions and the maintenance of dominance requires little threat or intimidation (French, 1997; Lazero-Perea et al., 2000). Social structure within a primate species may not be completely uniform across all habitats occupied (Dunbar, 1988), but the descriptions and references provided in Table 1 are typical for the species considered.

Answers generated by the questionnaire allowed us to examine the relationship between (a) the quality of life for dominant and subordinate animals and (b) the relative basal cortisol level. Answers to the questionnaire are summarized in Table 2. For each question, phylogenetically independent contrast analysis was performed on the numeric values of the answers to the questionnaire (Table 2) and on the relative basal cortisol value (Table 1). The resulting correlation coefficients are shown in Table 2. The multiple regression analysis produced two significantly predictive questions, 2A (partial regression slope = 20.1, $P = 0.010$) and 2B (partial regression slope = -40.5 , $P < 0.001$; residual standard error: 8.77 on 2 and 7 degrees of freedom; multiple $R^2 = 0.88$). For illustrative purposes, the relationship between the answers to these two questions and relative basal cortisol values are shown in Figs. 1a and 1b (produced from graphing answers to Questions 2A, “How frequently are subordinates subject to stressors?” and 2B “How available is social support for subordinates?”, respectively, against relative basal cortisol values). Thus, across the primate species studied (Table 1), subordinate individuals have increasingly higher relative basal cortisol levels as: (a) subordinates are subject to more frequent stressors (Question 2A; Fig. 1a), and (b) subordinate animals have fewer available sources of social support (Question 2B; Fig. 1b).

The nonphylogenetic, tree-based method found that answers to the same two questions (2A and 2B, Table 2), together with answers to Question 5A, generated a highly predictive decision tree for relative cortisol values (overall $P < 0.001$; Fig. 2). Clearly the degree to which subordinates experience stressors and the amount of available social support both play important roles in determining relative cortisol levels. The tree-based analysis also suggests that increased relatedness among group members may ameliorate relative cortisol levels.

At the top of the decision tree (Fig. 2), independent of any other question, if the answer to Question 5A is “0” (male talapoin monkeys, male olive baboons, and male squirrel monkeys), the tree analysis predicts a relative cortisol value of 149%. If the answer is greater than “0,” then answers to Question 2A (Table 2) provide the next significant ($P < 0.001$) predictor for the remaining species and sexes (Fig. 2), and so on. The tree analysis thus indicates that the degree to which subordinates are related to dominant animals provides a clear distinction between those individuals with high relative cortisol levels (male talapoin

monkeys, male olive baboons, and male squirrel monkeys; Table 1) and all others included in this study (Fig. 2). Those that exhibit the minimum rating for kinship (or relatedness) exhibit the greatest relative cortisol levels. Interestingly, all the data points in this first branch of the tree analysis are from males. For the species and sex in Table 2 that do not exhibit the minimum rating for kinship, the degree to which subordinates are subject to stressors provides the next significant branching point in the tree analysis (Fig. 2).

Subordinates that experience the highest (“3”) or second-highest (“2”) ratings (Table 2) for being subject to stressors are predicted to have relative cortisol levels of 127% (e.g., female cynomolgus, female talapoin, and male rhesus monkeys Table 1), respectively. Subordinates that are rated as experiencing few or no stressors (“0” or “1” on Question 2A; Table 2) are distinguished only by the answers to Question 2B (Fig. 2). Those that have a higher rating for social support of “2” (none rated “3”; Table 2) are predicted to have relative cortisol levels of 45% (e.g., female common marmosets; Fig. 2). Those that have little (“1”) or no (“0”) social support (e.g., female cotton top tamarin, female squirrel monkey, male cotton top tamarin, and male rhesus monkeys; Table 2) are only finally distinguished at this stage by answers to Question 2A regarding the degree of exposure to stressors (Fig. 2). Those that rate as “0” for this question are predicted to have relative cortisol levels of 81% (e.g., male and female cotton top tamarins; Table 2), while those that rate greater than “0” are predicted to have relative cortisol levels of 98% (e.g., female squirrel and male rhesus monkeys; Fig. 2). Interestingly, subordinate male and female cotton top tamarins have a very similar relationship between their relative cortisol levels and the low levels of social support and stressors experienced, suggesting a lack of sex difference in this regard in cotton top tamarins. The majority of outcomes from the tree-based analysis, nevertheless, suggest that the more subordinates are subjected to stressors, the greater their relative cortisol levels become. The relative cortisol level is diminished, however, when social support is available (Fig. 2).

Discussion

In some species, social subordination is associated with a more pathologic, hypercortisolemic profile than in dominant animals (e.g., Blanchard et al., 1993; Fuchs and Flugge, 2002). There is no consistent relationship, however, between social rank and stress response among primates (Abbott et al., 1997; Sapolsky, 1993). Results from the present study suggest that the different relationships between social rank and stress response among primate species may be explained by crucial differences in social behavior and organization between primate societies. Our meta-analysis of selected primate species examines how the same social rank can involve very different *qualities* of life in different primate societies. Most broadly, we find that basal hypercor-

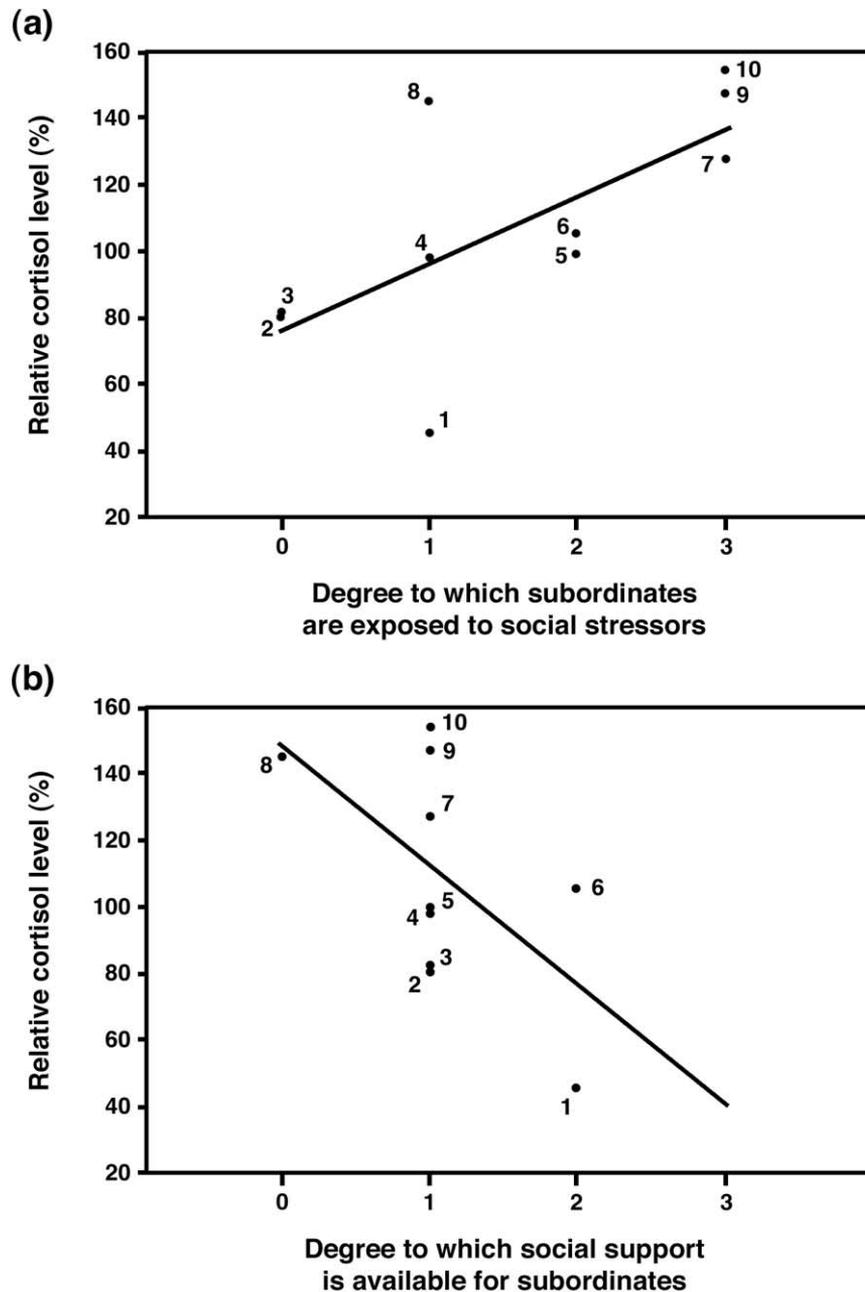


Fig. 1. Demonstration of (a) the positive relationship (partial regression slope = 20.1, $P = 0.010$; as derived from phylogenetically independent contrast analysis) between relative cortisol levels and the degree to which subordinate animals are exposed to social stressors (estimated as values: 0–3, Question 2A; Table 2), and (b) the negative relationship (partial regression slope = -40.5 , $P = 0.001$; as derived from phylogenetically independent contrast analysis) between relative cortisol levels and the degree to which social support is available to subordinates (estimated as values: 0–3, Question 2B; Table 2). The relative cortisol values for individual species and sex are numbered as shown in Table 1.

tisolism occurs among subordinate animals only in species in which subordinate status carries the highest rates of physical and/or psychological stressors, in which subordinates have fewer available sources of social support, and in which subordinates are minimally related to other members of their social group. In other words, a life filled with frequent stressors, little social support, and few kin produces frequent incidences of adrenocortical activation.

Answers to questions that were predictive of relative cortisol levels

Using two different analytical approaches (phylogenetic independent contrasts and tree-based analysis), we consistently identified two variables that, together, are significantly predictive of cortisol levels in subordinate animals relative to those found in dominants across the primate

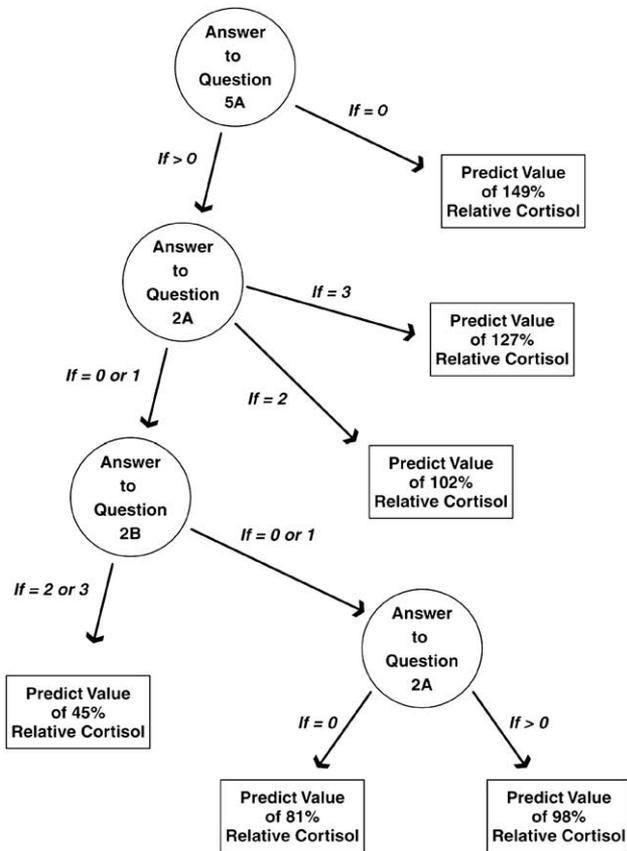


Fig. 2. The decision tree produced by tree-based statistical analyses of answers to Questions 2A, 2B, 3A, and 5A (Table 2; see text for rationale behind exclusion of variables). In this approach, there is a single response variable (relative basal cortisol levels) and an array of predictors (Questions 2A, 2B, 3A, and 5A; Table 2) that enabled construction of the decision tree to serve as a decision/classification algorithm. The answers to Questions 5A, 2A, and 2B provide the key branch points that predict relative cortisol levels in such a way as to maximize the variance explained by this tree compared to any other answer combination (see text).

species studied. As a first variable, higher relative cortisol concentrations are found among subordinate animals, as they are subject to higher rates of stressors (Question 2A). This is logical, given the ability of both physical and social/psychological stressors to stimulate cortisol secretion (Sapolsky, 2000, 2002). In such cases of exposure of subordinates to high rates of stressors, even basal cortisol levels are elevated in subordinates because an ostensive “basal” state involves a certain degree of ongoing stress (Blanchard et al., 1993). In addition, such relative basal hypercortisolism can reflect a change in the setpoint in the neuroendocrine regulation of the adrenocortical axis. Repeated elevations of glucocorticoid concentrations into the range seen for major stressors can lead to downregulation of corticosteroid receptors in brain regions that mediate glucocorticoid negative feedback (Sapolsky et al., 1984). The result of such receptor downregulation is impaired negative feedback sensitivity at the level of the brain, resulting in diminished neuroendocrine restraint on the adrenocortical axis and el-

evated basal glucocorticoid levels. Evidence for such feedback resistance has been observed among subordinate primates in species with high rates of stressors, such as subordinate male olive baboons (Sapolsky, 1990). In this regard, there is evidence in the tree analysis that subordinate male talapoin and cynomolgus monkeys, as well as subordinate male olive baboons, experience particularly elevated ratings for both displacement aggression and relative cortisol levels and thus may all be at risk for developing feedback resistance to glucocorticoids.

Second, we observed higher relative cortisol concentrations as subordinates experienced decreased opportunities for social support (Question 2B). An extensive literature demonstrates that having an outlet available for frustration decreases the glucocorticoid response to various stressors (Levine et al., 1989; Sapolsky et al., 2000). For example, allowing rats access to a running wheel decreases the magnitude of the glucocorticoid response to shock (Levine et al., 1989). Social outlets can be particularly efficacious at reducing the stress response; among primates, these include social grooming (e.g., dominants grooming subordinate female common marmosets: Lazero-Perea et al., in press), social contact, and, as noted, engagement in displacement aggression (Ray and Sapolsky, 1992; Sapolsky and Ray, 1989; Sapolsky et al., 1997; Virgin and Sapolsky, 1997). Thus, it is logical that among species in which subordinates lack ready access to such coping outlets, subordinate animals are more likely to exhibit hypercortisolism.

In addition to the two variables identified by the phylogenetic independent contrast analyses, the tree-based analysis indicated a further variable that played a predictive role, namely the degree of kinship (Question 5A: although not included in the multiple regression, this was also among the three most predictive variables based on pairwise correlations determined by phylogenetically based analysis; Table 2). Higher relative cortisol levels in subordinates were associated with societies in which behavioral interactions were unlikely to involve close kin. This variable was at the first branch point in the tree analysis (Fig. 2). This implies that regardless of the answers to Questions 2A and 2B, high relative cortisol levels may be predicted among subordinates if they do not have the opportunities to interact with close kin. It is reasonable that this variable should play a predictive role, insofar as the degree of kinship (Question 5A) was among the three most predictive variables (Table 2). Kin selection is an important component of natural selection theory (Hamilton, 1964) and a key variable in understanding social dynamics in primate societies (e.g., Gouzoules and Gouzoules, 1987): degrees of aggression and of cooperation co-vary as a function of degree of relatedness. Having kin available is likely to ameliorate stress in at least two broad ways. First, close relatives are particularly likely to supply coalitional support, thereby decreasing the rate at which social stressors are generated. Second, close relatives are a readily available means of coping outlets such as social grooming. These points are perhaps best

appreciated when contrasting the highly kin-based lives of female marmosets with the very different, non-kin-based lives of male baboons and male talapoin (Table 1). In this regard, males were identified as being significantly at risk for hypercortisolism in non-kin situations, suggesting that infrequent behavioral interactions with close kin may have greater implications for long-term changes in the male HPA axis than is found in females.

Interestingly, in the highly kin-based societies of marmosets and tamarins, in which subordinate females have the poorest fecundity and the highest incidence of anovulation of the primate species considered in this paper (Abbott et al., 1997; Ziegler et al., 1990), physiological factors other than the stress response may influence the cortisol levels found in subordinates. Subordinate female marmosets and tamarins exhibit lower basal cortisol concentrations than dominant females, with female marmosets exhibiting the more pronounced diminution (Table 1). Impaired ovarian function in subordinate female common marmosets, at least, contributes to a state of hypoestrogenism, and the latter has been associated with a reduction in circulating cortisol levels in females of several primate species (common marmoset: Abbott et al., 1997; Saltzman et al., 1998; squirrel monkey: Coe et al., 1986; rhesus monkey: Smith and Norman, 1987). In female marmosets, at least, social subordination also results in a further degree of hypocortisolism that cannot be mimicked by experimentally induced hypoestrogenic states (e.g., ovariectomy: Abbott et al., 1997; Saltzman et al., 1998; unpublished data). The low cortisol levels in subordinates are also not due to reduced circulating levels of adrenocorticotropin (Abbott et al., 1998; Johnson et al., 1996; Saltzman et al., in review), but are, instead, at least partly due to reduced adrenocortical responsiveness to adrenocorticotropin (Saltzman et al., 2000). Such hypocortisolism may be considered as a beneficial adaptation to a hypoestrogenic, nonbreeding adult state (Abbott et al., 1998), rather than as an impaired or dysfunctional stress response, and may aid in protecting subordinate female marmosets from typical pathophysiological consequences of low estrogen, such as osteoporosis (Colman et al., 1997).

Answers to questions that were not predictive of relative cortisol levels

It is of interest to consider briefly the answers to the remaining questions that did not contribute to the final regression equation or tree analysis. First, it is not surprising that the degree of competition for attainment of dominance among high-ranking individuals fails to predict relative cortisol levels (Question 1A). Such competition typically not only generates stressors for those participants, but translates into increased rates of displacement stressors for subordinates as well (Sapolsky, 1993). In Question 1B, aggression played a minimal role in maintaining dominance in most of the species considered (Table 2), thereby distorting any correlational anal-

ysis. In Question 1C, the rewards of dominance were too uniform across species to reflect societal variation (Table 2). Apparently, among the primate species studied, the experiences of dominant animals are fairly consistent across the different societies. Thus, the variation in relative cortisol levels found in this study (Table 1; Fig. 1) may be due to differences in the quality of life parameters for subordinate animals and not for dominants. As there were few between-species differences in the answers to Questions 2C–2F related to the quality of life for subordinates, alternatives to competition with dominants (Question 2C; Table 2) appear to represent only a minor factor in the social life of subordinate primates in many of the species studied.

The next two questions examined the ways in which ranks shift within hierarchies that are generally stable. One was concerned with whether a rise in the hierarchy arose from strenuous efforts on the part of the individual, or occurred as a less stressful default (Question 3A). The lack of predictability of this variable is understandable as extreme likely stressfulness of rank transition is only found in male baboons (Table 2). The other question concerned the frequency with which ranks change (Question 3B). This was only minimally predictive, possibly because there was little variability in the answers to this question for the primate species studied.

A number of questions concerned periods of hierarchical instability (Contributing Factor 4; Table 2). Hypercortisolism among subordinate animals tended to be predicted when such hierarchical instabilities involved high rates of aggression among dominant animals (Question 4B; Table 2). This, however, appeared to be merely a surrogate marker for Question 4D, insofar as high rates of aggression among dominant animals readily translate into the more salient measure, subsequent displacement of aggression onto subordinates. Data regarding the frequency of hierarchical revolutions (Question 4A) and the extent of aggression among subordinates at such times (Question 4C) did not have sufficient variability to predict relative cortisol values. It is reasonable that these variables should play a predictive role, insofar as hierarchical instability can generate severe physical and psychological stressors for subordinates, as well as greatly curtail their access to coping outlets (Sapolsky, 1993). Moreover, displacement represents a source of coping for the dominant individual, which is likely to reduce cortisol levels in dominants (Levine *et al.*, 1989). Such revolutions were relatively uncommon among these species (Question 4A; Table 2), but their occurrence and outcome, as well as frequency, may reflect the nature of the data used in this meta-analysis. We focused on stable social groups, and thus potentially minimized the likelihood of revolutionary change. Most of our data were also obtained from social groups maintained in captivity (Table 1). Management practices employed to maintain stable captive groups may therefore further minimize the likelihood of revolutionary change in the hierarchy. However, the increased population density

found in captive versus free-living primate social groups may encourage increased levels of interindividual aggression, depending on sex and species (Judge and de Waal, 1997). It remains to be determined whether social groups in captivity consistently exhibit different rates of revolutionary change in their social hierarchy than groups living in the wild.

Conclusion

We have identified two social variables in primate societies (Questions 2A and 2B; Table 2) that consistently predict whether subordinate or dominant animals exhibit elevated basal cortisol levels (hypercortisolism). Our findings have important implications for understanding the different physiological consequences of low social rank in different primate societies:

- (1) “Rank” is not uniform in its social meaning across different primate species, and some investigators have questioned the utility of the rank concept in some cases (Rowell, 1966). Insofar as rank is not a consistent construct, the physiological correlates of rank follow suit. This is likely to extend beyond comparisons among primate species, as in the present study, to (a) between a variety of nonprimate species, and (b) between different populations within the same species.
- (2) These studies were carried out on populations of primates living in captivity (and thus, well-fed and under veterinary care) or in a particularly benign ecosystem in the wild (in this case, the Serengeti and including only male olive baboons; Table 1). As such, the individuals assessed in all study populations were probably subject to few or no stressors attributable to hunger, illness, or predation, and probably had particularly high densities of potentially stressful social interactions, given their close proximities. Thus, much as with many present-day human societies, the physiology of stress in our study populations of nonhuman primates can mostly be understood in the context of social and psychological stressors generated between conspecifics within their social environment.
- (3) The extent to which social stress has physiological or pathophysiological consequences is not merely a function of the frequency or severity with which an individual is exposed to stressors. This represents only half the equation. Of equal importance is the availability and efficacy of coping responses (and possibly close kin) to offset the physiological impact of social stressors, indicating that subordination leads to not one, but a variety of social consequences across the different primate societies. Our comparative meta-analysis of selected nonhuman primate

species identified components significantly involved in both of these aspects of the stress response.

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