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# Stress and Coping Mechanisms in Female Primates

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## I. INTRODUCTION

Like pornography, stress is difficult to define but instantly recognizable. Everyone has felt stress, but not everyone suffers from chronic stress. Although our body's response to stress helps us to cope with physical and psychological challenges over the short term, over the long term it prevents us from dealing with the same challenges. A trigger for the stress response might be a physiological challenge, such as cold weather or a glucose imbalance, or an easily identifiable event, such as a traumatic incident or the death of a close companion. Other sources of stress, however, are more amorphous and difficult to specify.

In humans, two classes of causal agents interact to promote stress (defined below): physical agents, like smoking, excess alcohol, or a diet high in cholesterol, and psychological agents, like a catastrophic event, a death in the family, loneliness, or tension at work. Stress can also arise from subtle factors related to a lack of predictability, control, and support in daily life (e.g., Marmot, 2004). Bereavement, loneliness, and lack of social support are especially potent stressors that can compromise the immune system, lead to cardiovascular disease, and increase the risk of mortality (e.g., Cacioppo et al., 2000; Irwin et al., 1987; McCleery et al., 2000; reviewed in Segerstrom and Miller, 2004).

To what extent, however, are these causes of stress unique to humans? Humans have a wider variety of social relationships than other animals, our societies are much more stratified, our dependence on others for our material well-being is much greater, and our daily lives are much more multifaceted and complex. Furthermore, our ability to attribute thoughts, beliefs, and motives both to ourselves and others—our “theory of mind” (Premack and Woodruff, 1978)—drives us to dwell on our misfortunes and

misconstrue and obsess about our relationships with others. We can perceive feelings of loneliness even when we are surrounded by others and feel loss of control even when we have dependable shelter and sustenance. It is very unlikely that any animal is capable of the same sort of introspection and mental state attribution that humans engage in routinely (reviewed by Cheney and Seyfarth, 2007; Tomasello et al., 2005). Similarly, it is well known that stress and feelings of loneliness in humans can be mitigated by friendship and social support (Rosal et al., 2004; Steptoe et al., 2004; Thorsteinsson and James, 1999). Such support seems to be particularly important for women's mental health (Kendler et al., 2005; Taylor et al., 2000). However, the empathy of friends does not require that the friends too be afflicted with feelings of grief or loneliness. Our ability to provide support and empathy is independent of our current emotional state. It is by no means clear whether animals—even apes—can empathize with others or recognize others' grief (Cheney and Seyfarth, 2007; Silk, 2007). As a result, the causes and amelioration of stress in humans may differ in subtle but fundamental ways from those in other species.

Like humans, animals suffer from stress when they are socially isolated or subjected to uncontrollable or unpredictable traumatic events. For example, monogamous rodents show physiological signs of stress when they are separated from their mates (reviewed by Carter, 1998; see below). Similarly, rats and dogs that are subjected to intermittent shocks experience more stress if they are unable to control the rate at which they receive shocks, or if they are unable to predict when shocks will be delivered (Sapolsky, 2002; Seligman, 1975; Weiss, 1970). Under natural conditions, however, animals are seldom subjected to social isolation or stressors such as shocks, so the ecological validity of these observations is unclear. Indeed, until the advent of Robert Sapolsky's pioneering research (e.g., Sapolsky, 1993a, 1998) on stress in wild male baboons (*Papio hamadryas anubis*), almost nothing was known about the causes and alleviation of stress in wild animals. And although there have now been numerous studies of stress and coping mechanisms in wild male nonhuman primates, female nonhuman primates have received very little attention (Adkins-Regan, 2005; Reeder and Kramer, 2005).

Here, we review the causes and alleviation of stress in wild female monkeys, focusing in particular on baboons. We should note at the outset that there have been surprisingly few studies of stress in female primates generally and wild female primates specifically, which is why our review is not as comprehensive as we would like it to be. In particular, nothing is known about the causes and amelioration of stress in female apes. Nonetheless, we believe that a review of stress in wild female primates is timely, in part because wild populations of primates offer a better model for human

stress than captive ones. First, females in natural populations of monkeys typically live in large social groups that consist of both kin and nonkin, maintaining relationships that are both cooperative and competitive. These societies create a context for both increased social stress and opportunities for its alleviation. Second, females living under natural conditions are confronted with a variety of environmental stressors and traumatic events that not only present a challenge to reproduction and survival but also have the potential to damage an individual's social relationships. For example, a female baboon who sees a lion kill a close relative experiences not just a physiological but also a psychological stressor: her social network has now been damaged. Although some captive colonies approach wild groups in their size and social complexity, studies of stress in female monkeys have typically been conducted on individuals living either in newly established and unstable groups or in isolation from their companions—contexts that are highly stressful and very artificial.

We argue that many of the causes of stress in female monkeys—and its alleviation—are fundamentally social. Stress is influenced by events that threaten a female's survival and reproductive success, including in particular predation and the immigration of a potentially infanticidal male. Like humans, female monkeys rely on a stable social network to cope with stress. The presence of kin or close companions *per se* does not alleviate stress; rather it is the strength of a female's social bonds with a small number of specific companions. Females whose grooming networks are focused on a few individuals show lower levels of stress than females whose grooming networks are diffuse and relatively unselective. Females experience significant increases in stress when this network is damaged by the death of a close grooming partner, and they take active steps to seek out and identify new partners. The causes and amelioration of stress in female monkeys appear to be subtle and complex. It is the nature and quality of a female's social relationships, rather than sociality alone, that allows a female to cope with and manage stress.

## II. THE STRESS RESPONSE

When the brain perceives a stressor, the hypothalamus responds by releasing corticotropin-releasing hormone, which in turn stimulates the adrenal gland to release glucocorticoids (GCs). GCs are secreted primarily by the adrenal glands within minutes following the onset of a physical or psychological stressor (reviewed by Adkins-Regan, 2005; McEwen and Wingfield, 2003; Nelson, 2000; Sapolsky, 1998, 2002). GCs increase the availability of glucose in the bloodstream by promoting glucose production

and curtailing glucose uptake and storage (Nelson, 2000). Energy is mobilized, memory is sharpened, and immediately nonessential but energetically expensive functions like digestion, repair, growth, and reproduction are temporarily shut down. An increase in circulating GCs (cortisol and corticosterone in birds and mammals) is just one part of a cascade of neurological, hormonal, and immunological responses that characterize the “stress response” of the hypothalamic–pituitary–adrenal (HPA) axis.

Elevated GC levels enhance survival by mobilizing a suite of physiological and behavioral responses. The benefits of these behaviors may persist even when GC levels remain elevated over several weeks. For example, many species of birds and mammals show persistently elevated GC levels during winter and other periods of food scarcity, when environmental conditions demand an increase in metabolic rate (reviewed by Nelson et al., 2002). Similarly, although wild European rabbits (*Oryctolagus cuniculus*) that have temporarily been kept captive for several weeks experience both elevated GC levels and deterioration in body condition, they nevertheless survive at high rates after release (Cabezas et al., 2007).

However, although these anabolic processes are an essential and adaptive response to short-term challenges, they can be detrimental if sustained over long periods of time. Because elevated GC levels increase the immediate availability of energy from storage sites, increase cardiovascular activity, and suppress physiological activities that are not required for immediate survival, a chronic stress response can have harmful consequences, including loss of muscle mass, hypertension, immune and/or reproductive suppression, and even death (McEwen and Wingfield, 2003; Munck et al., 1984; Pride, 2005b; Sapolsky, 2002; Sapolsky et al., 2000). This is true of both physiological and psychological stressors. For example, social isolation and anxiety increase vulnerability to infections. Equally important, elevated GC levels over prolonged periods reduce the sensitivity of the HPA stress response to new challenges. Thus, chronic stress impedes the ability to mount future stress responses. For example, one function of GCs is to increase appetitive and food-seeking behavior—adaptive responses when food resources are scarce. Chronically elevated GCs, however, impede the ability of insulin to promote glucose uptake, leading to the accumulation of fat, obesity, and atherosclerotic plaques. Subordinate captive female rhesus macaques (*Macaca mulatta*) with chronically elevated GC levels show an increased preference for fatty, high calorie foods, in part perhaps because high calorie foods activate dopamine reward pathways (Wilson et al., 2008). Brain activity shows a similarly paradoxical reaction to stress. Emotionally salient events, facilitated by the sympathetic nervous system and the release of epinephrine, activate the hippocampus and the amygdala, aiding in the formation of memories that may prove useful in future dangerous or important

encounters. Chronic stress, however, can result in neuronal atrophy and death, particularly in the hippocampus, impairing declarative, contextual, and spatial memory (McEwen and Wingfield, 2003).

As many have pointed out, however, stress is a vague, “ethereal concept” (Nelson et al., 2002) that often implicitly incorporates both the stressor and the stress response, each of which feeds back upon the other (e.g., Levine, 2005; Levine and Ursin, 1991; McEwen and Wingfield, 2003; Sapolsky, 2002). In its popular usage “stress” suggests a chronic, maladaptive challenge to homeostasis, even though the stress response is highly adaptive over the short term. Moreover, while there are obvious detrimental physiological and cognitive consequences of chronic stress, there is no definitive threshold for “bad,” as opposed to “good,” stress. It may be possible to determine when an individual’s GC levels are above baseline, but it is far more difficult to define when an individual is “highly stressed,” except after physiological damage has resulted. Finally, although it is relatively easy to identify the causal effects of a traumatic event on an individual’s stress response, it is much more difficult to trace the more subtle causes and consequences of an individual’s social status, support network, and daily social interactions on her “stress” hormones.

For many of these reasons, McEwen and Wingfield (2003; see also Goymann and Wingfield, 2004) have introduced the concept of “allostasis,” which they define as “maintaining stability (homeostasis) through change.” Whereas homeostasis refers to the systems that are essential for survival and reproduction, allostasis is the process that maintains those systems in balance, allowing individuals to adjust to social and environmental challenges. According to this reasoning all energetic challenges, including low temperatures, food deprivation, social isolation, and frightening events that activate the sympathetic nervous system prompt the secretion of GCs, which help to mobilize the energy required to restore homeostasis. And because restoring homeostasis requires more energy than maintaining it, exposure to stressors increases energetic demands. Functions that are energetically costly, like the reproductive and immune systems, are temporarily suppressed.

“Allostatic load” is the cumulative cost to the body as the individual attempts to adjust her physiology and behavior both to temporary events and to more permanent states, like social subordination (Goymann and Wingfield, 2004; McEwen and Wingfield, 2003). Over the short term, an increase in allostatic load is adaptive, because it helps the organism to cope with unpredictable events and results in behaviors that ultimately help to reduce GC levels. If, however, allostatic load increases dramatically, or if short-term responses to the increase fail to return the individual to homeostasis, chronically high levels of GCs may trigger a response that results in damage to organs essential for survival and reproduction.

McEwen and Wingfield argue that the concept of allostasis is useful because it combines the energetic demands of survival and reproduction with those associated with social and environmental challenges into a continuum. "Stress" now refers to those environmental, social, and psychological factors that disturb homeostasis, increase allostatic load (whether adaptive or not), and elicit both physiological and behavioral responses (McEwen and Wingfield, 2003; Nelson et al., 2002). Phrased somewhat differently, a stressor can be thought of as "any event that causes an individual to increase energy consumption above baseline." (Nelson et al., 2002: 157). Because GC levels are expected to rise as allostatic load increases, they can be used to assess allostatic load.

Throughout this chapter, we use the term "stress" as McEwen and Wingfield does, to refer to an increase in allostatic load, as indicated by an increase in GC levels. A stressor is an event or condition that increases GC levels. We use the term "coping mechanism" to refer to behaviors that occur after an increase in GC levels, and that are correlated with a subsequent reduction in GC levels.

### III. STRESS AND SOCIAL ATTACHMENT

In both animals and humans, stressful experiences—including not only pregnancy and birth but also conflict, war, and other traumatic events—often precede and motivate the formation of close social bonds (reviewed by Bartz and Hollander, 2006; Carter, 1998; Panskepp, 1998; Tops et al., 2007). Some degree of stress may even be essential for the formation of strong emotional attachments (reviewed by Simpson and Rholes, 1994). The link between stress and social attachment occurs in part because stress prompts the release of the peptide oxytocin, a hormone that motivates attachment, trust, and pair-bonding behavior.

Oxytocin interacts with GCs bidirectionally: separation, loss, and other stressful psychological events initially act to reduce oxytocin levels and increase GC levels. The increase in GCs, in turn, prompts the release of oxytocin, which increases attachment-seeking behavior, ultimately effecting a decrease in GC levels and HPA axis activity. In humans, administration of cortisol increases plasma oxytocin levels (Tops et al., 2007). This effect appears to be particularly strong in women (Taylor et al., 2000).

Much of the research concerned with the relationship among GC levels, oxytocin, social attachment, and social isolation in animals has been conducted on rodents. In rodents generally, oxytocin promotes social affiliation and parental behavior and is essential for social recognition (reviewed by

Bartz and Hollander, 2006; Carter, 1998; DeVries et al., 2003; Lim and Young, 2006; Panskepp, 1998; Tamashiro et al., 2005; Uvnas-Moberg, 1997; Von Holst, 1998).

Rodents' stress responses to social contact and isolation vary according to the social environment in which they have evolved. For example, the wounds of socially monogamous mice (*Peromyscus californicus* and *P. eremicus*) heal more rapidly when they are pair-housed than when they are socially isolated (DeVries et al., 2007; Glasper and DeVries, 2005). In contrast, social contact does not facilitate healing in the closely related *P. leucopus*, a polygynous species that does not form pair bonds. Similarly, in an experiment conducted on three social and one solitary species of African mole rats (*Heterocephalus* spp.), only members of the solitary species showed a lack of social tolerance and an increase in GC levels when introduced to an unfamiliar conspecific (Ganem and Bennett, 2004).

In the monogamous prairie vole, separation from a social partner of the opposite sex causes an increase in GC levels in both males and females, while reunification results in a decrease. This effect holds only for familiar partners; GC levels remain elevated if the separated voles are placed with an unfamiliar animal (reviewed by Carter, 1998). Interestingly, in previously unpaired individuals, stressful experiences and the administration of corticosterone stimulate the formation of pair bonds in males but not in females, who are more motivated to develop preferences for other females (Carter, 1998; Tops et al., 2007). These differences in social attachment may again reflect adaptive responses to differences in each sex's grouping and dispersal patterns (Carter, 1998). Although prairie voles are monogamous, males typically disperse at sexual maturity and do not mate with members of their natal group. Females, in contrast, may produce litters in their natal nest and retain bonds with matrilineal kin throughout their lives. The importance of kin or other close female companions to successful reproduction is also seen in wild European rabbits, where females who have litter mates in their current social group are more affiliative and begin to breed at younger ages, apparently as a result of reduced stress (Rodel et al., 2008).

Most species of nonhuman primates are group-living; social isolation is rare and an artifact of captive experiments. When isolated from familiar companions, monkeys show all of the classic behavioral and physiological symptoms of depression, particularly if they were previously housed in a social group. For example, monogamous titi monkeys (*Callicebus moloch*) that have been separated from their partners experience a sharp increase in GCs (Mendoza and Mason, 1986). Similarly, marmosets (*Callithrix* spp.) and tamarins (*Saguinus* spp.) of both sexes show elevated GC levels when temporarily placed in isolation; GC levels return to baseline when they



are reunited with their partners (Ginther et al., 2001; Johnson et al., 1996; Smith and French, 1997; Smith et al., 1998). The presence of a social partner also helps to dampen the stress response in novel physical environments (French and Schaffner, 2000). Finally, female rhesus macaques that are socially isolated or placed into a novel group exhibit elevated stress responses; this increase is dampened, however, by the presence of a preferred grooming partner (Gust et al., 1994). Even the threat of isolation from offspring or familiar companions can be sufficient to trigger a stress response. Lactating female rhesus macaques that were captured and held overnight in an individual cage with their infants had significantly higher plasma GC levels than similarly treated nonlactating females (Maestripieri et al., 2008). The heightened stress response of lactating females may have reflected their perception of risk to their infants.

#### IV. OKAVANGO BABOONS

Much of the data described in this review are derived from a long-term study of one group of free-ranging chacma baboons (*Papio hamadryas ursinus*) living in the Okavango Delta of Botswana. Like many other species of Old World monkeys, including in particular the macaques (*Macaca* spp.), female baboons remain in their natal groups throughout their lives, maintaining close bonds with their matrilineal female kin (Cheney and Seyfarth, 2007). Females assume dominance ranks similar to their mothers and usually retain their relative ranks throughout their lives. The result is a conservative matrilineal dominance hierarchy in which all the members of one matriline outrank or are outranked by all the members of another (Cheney et al., 2004; Samuels et al., 1987; Silk, 2002; Silk et al., 1999). Although there is often a positive correlation between female rank and reproductive success, this correlation rarely reaches significance (reviewed by Cheney et al., 2004; Silk, 2002), and all females produce offspring. Close bonds are manifested primarily through grooming. In contrast, male Old World monkeys typically emigrate from their natal groups at sexual maturity and form comparatively unstable dominance hierarchies based largely on fighting ability.

The Okavango Delta has a wider diversity of plant and tree species than other African woodland savannahs, and a high density of predators, including leopards (*Panthera pardus*), lions (*Panthera leo*), crocodiles (*Crocodilus niloticus*), and spotted hyenas (*Crocuta crocuta*). The area is seasonally flooded, and the baboons forage over an area of roughly 4 km<sup>2</sup>, fording or swimming from one wooded island to another at the height of the flood

(Cheney et al., 2004; Hamilton et al., 1976). During the period of study (1992–2007), group size ranged from approximately 70 to 85 individuals, including 19–26 adult females (>6 years), 3–12 adult males, and their offspring. The ages and matrilineal relatedness of all animals were known, and all individuals were fully habituated to humans on foot.

Behavioral samples on all adult females were conducted daily, using focal animal sampling (Altmann, 1974). In addition, weekly fecal samples were obtained from each adult female on a systematic basis (see, e.g., Beehner and Whitten, 2004; Beehner et al., 2005; Crockford et al., 2008; Engh et al., 2006b for details). There is a delay of 1–3 days between hormone secretion and detection in fecal steroids (Beehner and Whitten, 2004; Heistermann et al., 1993; Wasser et al., 2000; Ziegler et al., 1996); diet can also reduce or slow down steroid excretion. In contrast to hormones derived from blood or saliva, therefore, fecal hormones do not reflect physiological responses to specific single events, but rather “cumulative” hormone production over several days. Unless otherwise noted, all of the hormonal data on wild animals discussed below were derived from fecal samples.

## V. REPRODUCTIVE AND SEASONAL INFLUENCES

Studies of stress in nonhuman primates have tended to focus on males rather than females in part because of the confounding influences of reproductive state. Female mammals tend to have higher baseline GC levels than males, and a more robust stress response (Reeder and Kramer, 2005). Moreover, as in humans, basal GC levels in nonhuman primates increase steadily during pregnancy and decline rapidly postpartum (reviewed by Bowman et al., 2001; for baboons, see Altmann et al., 2004; Beehner et al., 2005, 2006; Crockford et al., 2008; Ramirez et al., 2004; Weingrill et al., 2004). As a result, all analyses of physiological and psychological stress in female primates and other animals must first control for reproductive state.

Elevation of the HPA axis during pregnancy may function in part to help females cope with the metabolic demands of gestation. Given the role of elevated GC levels in attachment formation, they may also prepare females to bond with their infants. Indeed, several studies of baboons have suggested that females with higher prepartum GC levels subsequently show higher levels of affiliative behavior toward their infants (Bardi et al., 2004; Nguyen et al., 2008; Ramirez et al., unpublished data). In contrast, higher postpartum GC levels can be associated with higher levels of infant rejection (Bardi et al., 2004; Ramirez et al., 2004).

GC levels are also strongly influenced by ecological variables. Numerous studies of birds and mammals have shown that GC levels are elevated during the winter, during times of food or water scarcity, and during periods of elevated metabolic and energetic demands (reviewed by, e.g., Nelson et al., 2002; Romero, 2002; Wingfield and Ramenofsky, 1999).

In ring-tailed lemurs (*Lemur catta*), females' mean GC levels are highest during months of low rainfall and fruit availability (Pride, 2005c). Elevated GC levels are associated with low daily food intake and high rates of aggressive intergroup encounters, but not with intragroup aggression or antipredator alarm calls (Pride, 2005a). Moreover, individuals in smaller groups tend to have higher GC levels than those in larger groups (Pride, 2005c). This association suggests that the acquisition and defense of food against other groups represent significant challenges to female survival, and that larger groups may have an advantage over smaller groups. Given the hypothesized importance of intergroup competition and resource defense to female reproductive success in nonhuman primates (Cheney, 1992; Isbell, 1991; Wrangham, 1980), it is unfortunate that no other studies have investigated the relationship between female GC levels and intergroup aggression.

Chacma baboons living at high latitudes in the Cape Peninsula of South Africa have elevated GC levels during the winter months, when they experience colder temperatures and shorter resting periods, both of which may increase metabolic rates (Weingrill et al., 2004). GC levels among gelada baboons (*Theropithecus gelada*) are similarly affected by cold temperatures (Beehner and McCann, 2008). In Amboseli, Kenya, an area of highly seasonal rainfall, female yellow baboons (*P.h. cynocephalus*) tend to exhibit higher GC levels during the dry season than during the wet season (Gesquiere et al., 2008; see also Sapolsky, 1986). Furthermore, GC levels are higher in hotter months and in months when females spend more time foraging than resting.

In contrast, in the Okavango Delta of Botswana seasonal effects on females' GC levels are less noticeable, at least in relatively normal years (Beehner et al., 2005; Crockford et al., 2008). This probably occurs because females in the Okavango have ready access to water throughout the year, as well as much greater diversity of tree and other plant species than do baboons in most other areas of Africa (Beehner et al., 2005; Cheney et al., 2004). GC levels do appear to rise in years when the annual flood arrives earlier than normal, before the fruits of the marula (*Sclerocarya birrea*) and jackalberry (*Diospyros mespiliformis*) trees have ripened (Cheney and Seyfarth, unpublished data). Even these increases, however, are overshadowed by the much greater increase in GC levels during periods of social instability (see below).

## VI. DOMINANCE RANK

When considering the relationship between GC levels and dominance rank in female mammals, it is useful to distinguish between species with high and low reproductive skew. In species with high reproductive skew, only one female usually breeds, while other females, who are often the offspring or siblings of the dominant breeding female, act as helpers. These cooperatively breeding species include meerkats (*Suricatta suricatta*), wolves (*Canis lupus*), wild dogs (*Lycaon pictus*), and, among the primates, tamarins and marmosets. Tamarins and marmosets live in small family groups composed of a breeding pair and varying numbers of adult helpers who are usually closely related to the breeding pair (Goldizen, 1987).

By contrast, in species with low reproductive skew all females breed, and there is little if any reproductive suppression. Although females may form a dominance hierarchy in which high-ranking females enjoy some reproductive advantages, there is usually no significant correlation between rank and reproductive success. Such species include spotted hyenas, lions, rabbits, and most species of nonhuman primates, including baboons and macaques (see above).

### A. SPECIES WITH HIGH REPRODUCTIVE SKEW

In cooperatively breeding species with high reproductive skew, the single dominant breeding female often has significantly higher GC levels than the nonbreeding helpers (wolves: Sand and Creel, 2004; wild dogs: Creel, 2001; meerkats: Carlson et al., 2004; dwarf mongoose, *Helogale parvula*: Creel, 2005; reviewed by Creel, 2001; but see Hacklander et al., 2003 for a reverse effect in marmots, *Marmota marmota*). Some studies of tamarins and marmosets have also documented higher GC levels in dominant breeding females than in nonreproductive subordinates (common marmosets: Abbott et al., 1997; Saltzman et al., 1994, 1996, 1998; cotton-top tamarins (*S. oedipus*): Ziegler et al., 1995), although this pattern is not always found (common marmosets (*C. jacchus*): Sousa et al., 2005; Ziegler and Sousa, 2002; golden lion tamarins (*Leontopithecus rosalia*): Bales et al., 2005).

It appears, therefore, that reproductive suppression in helpers is not stress-related (Carlson et al., 2004; Creel, 2001). Indeed, a notable characteristic of subordinate females in all of these species is that they are usually closely related to the dominant breeding female. Although dominant females often kill any infants produced by subordinate females (e.g., Creel and Creel, 2002; Saltzman et al., 2008; Sousa et al., 2005), subordinate females receive generally low rates of aggression and enjoy high levels of social support from kin. This support may mitigate any stress

that might otherwise result from subordination (Abbott et al., 2003). Conversely, high GC levels in the dominant breeding female probably reflect the metabolic demands of breeding rather than any costs associated with the maintenance of dominance. Dominant female wolves, for example, are not more aggressive than subordinate females (Sand and Creel, 2004).

## B. SPECIES WITH LOW REPRODUCTIVE SKEW

There have been comparatively few studies of rank-related stress in nonprimate mammals with low reproductive skew. Goymann et al. (2001) found that lower-ranking nonlactating female hyenas had higher GC levels during months when their groups' territories were stable. During unstable periods, however, when females were forced to travel outside their groups' territorial boundaries to hunt, all females exhibited elevated GC levels. In contrast, Dloniak et al. (2006) reported no relationship between rank and GC concentrations in pregnant spotted hyenas living in the northern portion of the Serengeti ecosystem in Kenya. Instead, GC concentrations appeared to be more strongly influenced by instability in the female dominance hierarchy, with females exhibiting higher levels during period of rank instability (Van Meter et al., 2009).

The degree to which female monkeys exhibit rank-related stress seems to depend largely on whether subordinates are able to avoid aggression and derive support from kin and other companions. Under constrained captive conditions, and especially when living in unstable or newly formed groups, subordinate females often exhibit high levels of stress. When female long-tailed macaques (*M. fascicularis*) were randomly housed in groups of four individuals, females who acquired subordinate ranks developed many of the classic signs of physiological and behavioral depression, including hunched posture, low levels of activity, disturbed menstrual cycles, weight loss, higher heart rates, and increased mortality (Shively, 1998; Shively et al., 2005). The frequency of depression in subordinate females was higher than that in individually housed females. Similarly, female pig-tailed macaques (*M. nemestrina*) in a newly formed group exhibited higher GC levels and a significant decrease in T-helper cells than females housed in individual cages, despite the fact that their dominance hierarchy was established without serious fighting or wounding (Gust et al., 1996). Females who received a greater frequency of grooming showed a smaller decrease in T-helper cells, suggesting that social support played a role in mitigating the effects of social instability.

Other studies of female long-tailed (Stavisky et al., 2001) and rhesus macaques (Gust et al., 1993) living in newly established captive groups have failed to document a relationship between social subordination and

elevated GC levels. In fact, in one comparison subordinate females had higher GC levels in an established group than in a newly formed one (Gust et al., 1993). This might have occurred because females in the newly established group reconciled with each other after aggression at high rates. However, it might also have been due to the fact that ranks in the newly formed group were unstable and difficult for human observers to determine.

Although there have been comparatively few studies of rank-related stress in wild female monkeys, current evidence suggests that low-ranking females do not typically exhibit high GC levels (long-tailed macaques: van Schaik et al., 1991; baboons: Nguyen et al., 2008; Weingrill et al., 2004, reviewed by Abbott et al., 2003; Sapolsky, 2005). Analyses of GC levels among females in the Okavango baboon population over three different time periods have also revealed no evidence of rank-related stress (Beehner et al., 2005; Crockford et al., 2008; Engh et al., 2006b). These observations are perhaps not surprising. Although high-ranking female baboon and macaques have priority of access to food, the correlation between rank and reproductive success is typically only weakly positive, and low-ranking females are as likely as high-ranking females to have close relatives available for social support. While high-ranking females can redirect aggression onto more targets than low-ranking females, the level of harassment they impose upon low-ranking females is moderate, and low-ranking females do not typically receive aggression at significantly higher rates than other females (Abbott et al., 2003; Cheney and Seyfarth, unpublished data; Walters and Seyfarth, 1987).

Despite the lack of evidence for chronically elevated GC concentrations in free-ranging subordinate female baboons, low-ranking individuals may nonetheless sometimes be subjected to nutritional and social stressors that exert other subtle physiological effects. In the Okavango baboon population, for example, the GC levels of all females rose dramatically during the week after a potentially infanticidal male immigrated into their group (Wittig et al., 2008). However, subordinate females maintained this increase for a longer period of time than dominant females, with the GC levels of high-ranking females beginning to decrease at least 1 week earlier than those of low-ranking females. This may have occurred because higher-ranking females were able to exert greater control over the timing and nature of their social interactions, allowing them to experience less stress during periods of instability. Whether there is any fitness advantage to being able to reduce GC levels more rapidly, however, remains to be determined.

Similarly, in one study of adolescent male baboons in Amboseli, Kenya, the sons of subordinate mothers were found to have significantly higher GC levels than the sons of dominant mothers (Onyango et al., 2008), even though subordinate females in this population do not generally appear to

have elevated GCs themselves (Nguyen et al., 2008). This effect persisted beyond the age when males become larger than females, extending even beyond maternal death. These results suggest potential long-term organizational effects of maternal dominance status on offspring HPA axis, possibly related to nutritional stress, aggression, or lack of social support (Onyango et al., 2008).

Further complicating matters, dominant females living in multifemale groups of ring-tailed lemurs sometimes exhibit higher GC levels than subordinate females (Cavigelli, 1999; Cavigelli et al., 2003; but see Pride, 2005a,c). Dominant female ring-tailed lemurs tend to be more aggressive than lower-ranking females, and they are also more active participants in intergroup encounters (Cavigelli, 1999; Pride, 2005a,c). These observations suggest that occasional high GC levels in dominant females may result from high-energy expenditure during aggressive interactions and intergroup defense rather than from any inherent attribute of rank.

Taken together, these studies suggest that there is no simple correlation between dominance rank and GC levels in female primates. Although stress and depression can be induced in low-ranking females under confined, unstable captive conditions (e.g., Shively et al., 2005), under more natural conditions low-ranking females receive comparatively little aggression and show little evidence of rank-related stress or reproductive suppression (Cheney et al., 2004; Silk, 2002). Moreover, because the female dominance hierarchy remains stable for years at a time, females' stress responses are by definition usually unaffected by female rank instability.

This is not to say, however, that females' ranks are always immutable. Although upheavals in the female dominance hierarchy in species such as macaques and baboons are very rare, they do occasionally occur (Samuels et al., 1987; Silk, 2002). One such event occurred in the Okavango baboon group in 2003, when the members of a lower-ranking matriline initiated two attempts to overthrow a higher-ranking matriline (Engh et al., 2006b). The first period of upheaval, which lasted a week, was ultimately unsuccessful and resulted in the retention of all females' previous ranks. A second, successful challenge targeted a large, noncohesive, middle-ranking matriline composed of several sisters and aunts and only one mother-daughter pair. Eventually, three females from this matriline fell to the bottom of the dominance hierarchy. During these periods of instability, the targeted females received significantly higher rates of aggression than other females, and their GC levels also rose significantly. Interestingly, however, those females whose ranks eventually rose also experienced a significant increase in GC levels. In contrast, the GC levels of females at the top of the dominance hierarchy, whose ranks were not at risk, showed little change (Engh et al., 2006b).

These results are somewhat similar to those obtained in studies of female hyenas (Van Meter et al., 2009) and male baboons. In free-ranging groups of baboons, low-ranking males tend to have higher basal GC levels than high-ranking males when the dominance hierarchy is stable. When a dominant immigrant male enters the group and challenges the reproductive control enjoyed by high-ranking males, however, GC levels of high-ranking males are higher than those of low-ranking males (Bergman et al., 2005; Sapolsky, 1990, 1992, 1993a,b, 2005; Sapolsky et al., 1997). Thus, the loss of control and predictability associated with rank instability appear to be more stressful than low rank *per se*.

## VII. BEHAVIORAL CORRELATES OF GC LEVELS DURING PERIODS OF SOCIAL STABILITY

In addition to the seasonal and nutritional effects previously described, elevated GC levels in female primates appear to be correlated primarily with the loss of a close companion and events that directly jeopardize their survival and reproduction (see below). During periods of social and ecological stability, females' GC levels are generally low. This is true even of subordinates, as long as they have social support and opportunities to avoid the aggression of dominants.

We were able to examine females' GC levels in the Okavango baboon population during one-eight-month long period of social stability in 2004, when there was no male immigration and relatively few cases of predation (Crockford et al., 2008; see below). All females' GC levels were significantly lower than during a subsequent, more eventful period precipitated by the immigration of a dominant male (Fig. 1). Nonetheless, there was still some variation in females' GC levels, even after controlling for reproductive state. This variation was correlated with subtle behavioral attributes that varied between individuals and within individuals across time.

Interestingly, we could detect no relationship between females' GC levels and the number of close female kin (Crockford et al., 2008). This is perhaps not surprising. Although female baboons maintain their grooming relationships with a few close relatives (Silk et al., 1999, 2006a,b, 2009), when kin are not available they form stable grooming partnerships with nonrelatives. This may mitigate any detrimental effects on stress or GC levels associated with the lack of close kin.

The primary factors influencing females' GC levels during this stable period appeared to be related to the control and predictability that they were able to exert over their social interactions. Not surprisingly, pregnant and cycling females who received higher rates of aggression from other



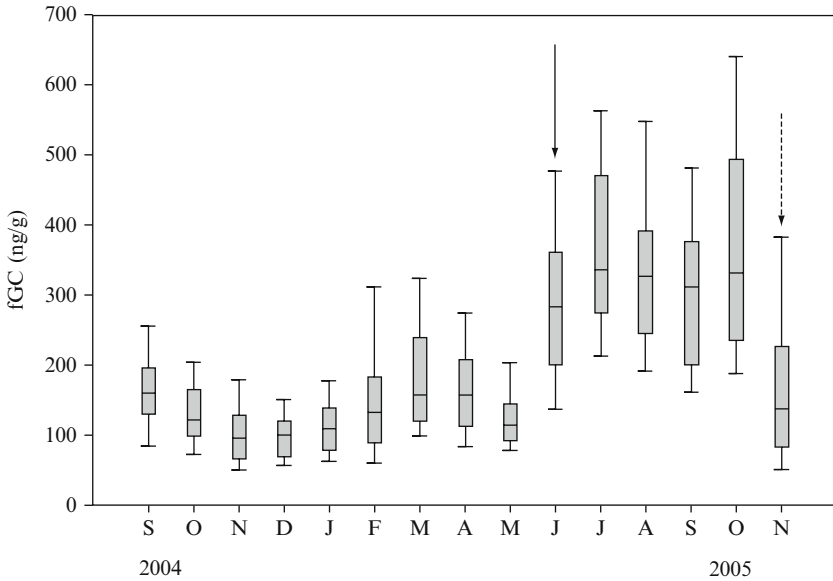


FIG. 1. The average monthly distribution of glucocorticoid levels (fGC) in 18 adult females between September 2004 and November 2005. The period from 15 October 2004 to 30 May 2005 was a period of relative social stability, when there were no changes in the alpha male position, no male immigration, no observed infanticidal attempts, no confirmed predation, and few disappearances. On 1 June (the week highlighted by the solid arrow), a new male immigrated into the group, and all females' GC levels increased significantly. The subsequent 5 months were marked by additional male immigration, instability in the male dominance hierarchy, infanticide, and the disappearance of several adult females. In the first week of November (highlighted by the dashed arrow), the male dominance hierarchy stabilized, and females' GC levels decreased significantly. Boxes show interquartile range with the median depicted by the internal line; whiskers indicate 95% confidence intervals.

females had higher GC levels than females who received lower rates of aggression. Conversely, pregnant and cycling females who received grunts at a high frequency from approaching dominant females had lower GC levels than those who received grunts at a lower frequency. Furthermore, pregnant females had lower GC levels in months when they received grunts at a higher than average frequency. Grunts are signals of benign intent and are reliably associated with a low probability of aggression (Cheney et al., 1995b; Silk et al., 1996). Grunts also function to reconcile opponents after aggression (Cheney and Seyfarth, 1997; Cheney et al., 1995b; Wittig et al., 2007a). Thus, grunts may mitigate the stress associated with aggression in part because they permit females to assess and predict the behavior of higher-ranking animals.

Lactating females' GC levels, however, showed the opposite pattern. This was probably a consequence of the intense attention that mothers with young infants receive from others. Infants are highly attractive to female baboons, and the mothers of young infants receive high rates of ostensibly friendly, but unsolicited, interactions from higher-ranking females (Altmann, 1980; Seyfarth, 1976; Silk et al., 2003a). These interactions are almost invariably accompanied by grunts. Because females with young infants seldom initiate these interactions and have little control over them, the close association between grunts and infant handling may weaken the otherwise placatory effects of grunts as signals of benign intent.

The relation between GC levels and females' level of control over their social interactions was most apparent, however, in their grooming relationships. Grooming appears to be the primary coping strategy adopted by female monkeys to reduce stress (Aureli et al., 1999; Boccia et al., 1989; Gust et al., 1993; Shutt et al., 2007). Little is known, however, about how and why grooming might function to alleviate stress. It is not clear, for example, whether social contact alone is sufficient to reduce stress, as opposed to social contact with a few select companions.

The grooming interactions of female baboons, like those of females in other monkey species, are highly differentiated. Although a female may groom with all other females in her group during the course of a year, most of her grooming is concentrated among a few predictable partners who are usually, but not always, close female kin (Silk et al., 2006a,b, 2009). These focused grooming interactions appear to be adaptive, because females who maintain the strongest bonds with other females experience higher offspring survival and longevity (Silk et al., 2003b, 2009).

Indeed, regardless of the number of close female kin they had, females in all reproductive states had lower GC levels in months when they concentrated their grooming among a few consistent partners than in months when their grooming was less focused and more equally distributed among partners (Fig. 2; Crockford et al., 2008). We used the Shannon–Wiener diversity index (Wilson and Bossert, 1971) to measure the diversity of a female's grooming partners. This index is a measure not of grooming network size but of grooming partner skew. For example, an individual who grooms with a large number of other females but restricts most of her grooming to one to two preferred partners will have a low grooming diversity index. Conversely, an individual who grooms with a large number of other females but distributes her grooming evenly among all her partners will have a high grooming diversity index. These results suggest that females may experience increased GC levels when their

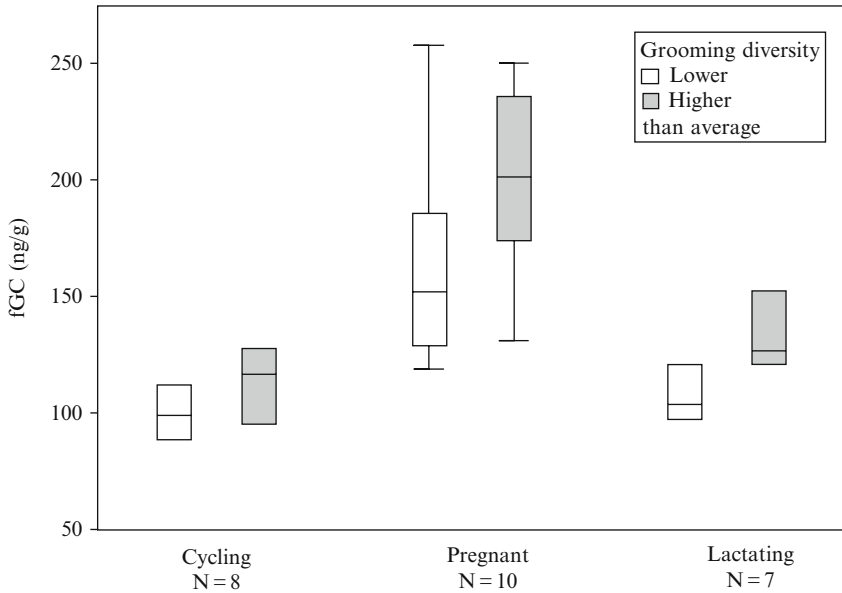


FIG. 2. Within-individual comparisons of females' GC levels between months when they had a higher diversity of grooming partners than average and months when they had a lower diversity of grooming partners than average. Females are separated by reproductive state. Females had significantly higher GC levels in months when they had a higher diversity of grooming partners than average. Legend as in Fig. 1.

grooming networks become less stable and discriminating. There was no correlation between GC levels and absolute grooming time, time spent grooming, or time spent being groomed.

For cycling females, the correlation between higher GC levels and an increased grooming diversity index was also associated with higher rates of aggression received and lower frequencies of grunting by approaching dominant females. Cycling females who are involved in sexual consortships are often the targets of aggression from adult females. It seems possible that they may attempt to mitigate this aggression by actively grooming potential aggressors. Indeed, cycling females' grooming was more diverse and less focused in months when they groomed more individuals than groomed them.

In contrast to cycling females, lactating females' grooming networks were more diverse in months when they were groomed by more partners than they groomed, indicating that the increase in their grooming diversity was

unsolicited. The lack of control that lactating females were able to exert over their grooming partners, in combination with the attention given to their infants, may have contributed to their increased GC levels. In support of this argument, Shutt et al. (2007) found that GC levels in pregnant female Barbary macaques (*M. sylvanus*) were lower in individuals who groomed others at higher rates than they were groomed, and who groomed more partners than groomed them.

Taken together, the results suggest a complex relationship between GC levels, active as opposed to passive grooming initiations, and grooming network size. Unstable, diffuse grooming networks are associated with higher GC levels. Although these results do not distinguish between the cause and effect of this association, it seems probable that GC levels increase when the expansion of a female's grooming network is unsolicited and initiated by others. A diffuse grooming network may provide less support than a more focused and selective one because it is less controllable and predictable. On the other hand, active expansion of a grooming network by females who are receiving increased aggression may function as a mechanism to mitigate stress by reducing the likelihood of aggression.

Numerous studies have shown that loss of control and unstable social bonds can increase stress in animals and humans, even in the absence of any specific traumatic event (see Section I; see also Carter, 1998; Marmot, 2004; Panskepp, 1998; Sapolsky, 2004). Although GC levels in female baboons are most strongly influenced by events that directly affect their reproductive success (see below), these more subtle social factors also exert an effect. GC levels may be lower if a female is able to predict the intentions of other group members—for example, if dominant females grunt to her to signal their intent—and if she is able to express some preference over the timing and identities of her grooming partners. A focused grooming network may function to lower GC levels in part because it provides females with a dependable and controllable number of social partners. In short, it may be better to have a few good friends than many acquaintances.

If these conjectures are valid, we would predict that, during periods of social or environmental instability, females who have more focused grooming relationships should experience less stress than those whose grooming relationships are diffuse and distributed more evenly among a wide variety of partners. Furthermore, females should attempt to alleviate stress by restricting their grooming interactions to a few preferred partners.

### VIII. TRAUMATIC EVENTS AND GC LEVELS

As with humans, the greatest stressors affecting female primates are unpredictable, traumatic events over which they have little control. As we have discussed, rank instability appears to be more stressful than subordination itself. Events that threaten a female's survival or the survival of her infant are even more stressful.

#### A. MALE IMMIGRATION

The immigration of a dominant, potentially infanticidal male is a potent stressor for female baboons. The disruption caused by the immigration of a male who quickly rises to the most dominant (or alpha) position is typically reflected by a sharp elevation of GCs in both males and females (Alberts et al., 1992; Beehner et al., 2005; Engh et al., 2006b; Sapolsky, 1993a,b; Wittig et al., 2008). In some cases, this elevation is associated with increased aggression against females. Following the immigration of a highly aggressive male into one group of yellow baboons in Kenya, Pereira (1983) reported an increase in serious injuries for both males and females, an elevated rate of fetal loss, and one infant death. In a subsequent period, another male immigration event was similarly associated with significantly higher rates of aggression, marked elevations in GCs, and an increase in fetal loss (Alberts et al., 1992). These observations suggest that the arrival of an unfamiliar and aggressive male may result in early termination of pregnancy in baboons. While slightly elevated GCs are necessary to maintain a pregnancy, chronically elevated GCs exert an inhibitory effect on the female reproductive system (Bronson, 1989).

Frequently, however, the immigration of an aggressive dominant male does not result in increased attacks on females, and the event appears to function more as a source of psychological than physical stress. For example, female mantled howler monkeys (*Alouatta palliata*) experience a significant rise in GC levels when a new male enters their group (Cristobal-Azkarate et al., 2007). This elevation appears to be associated primarily with the potential risk of infanticide and the social instability resulting from increased aggression among males, because female howlers do not aggressively defend their group against incursion by immigrant males, nor are they frequently attacked by immigrant males.

Among the Okavango baboons, the arrival of a high-ranking immigrant male has a particularly disruptive impact on lactating, and to a lesser extent pregnant females, because such males often commit infanticide (Bulger and Hamilton, 1987; Busse and Hamilton, 1981; Collins et al., 1984; Palombit et al., 2000; Tarara, 1987). Male mating activity in the Okavango

population is strongly correlated with dominance rank, and the alpha male monopolizes most mating (Bulger, 1993). However, turnover in the alpha rank position is also high, and a male typically maintains alpha status for less than a year (Hamilton and Bulger, 1990; Palombi et al., 2000). Infanticide appears to be a sexually selected strategy that accelerates the return to fertility in lactating females, permitting the infanticidal male to mate with as many females as possible during his short tenure in the alpha position (see reviews in Ebensperger, 1998; Hausfater and Hrdy, 1984; van Schaik and Janson, 2000). In the Okavango, infanticide is the single most important cause of infant mortality (Cheney et al., 2004).

Examination of Okavango females' GC levels during two different time periods showed that lactating females experienced significant increases following the immigration of a dominant male, while cycling females showed no increase. Pregnant females' responses were more variable, and fell in between those of cycling and lactating females (Beehner et al., 2005; Engh et al., 2006b). Not surprisingly, lactating females' GC levels showed an even greater increase when an immigrant male began to commit infanticide (Engh et al., 2006b).

In another period, however, male immigration was associated with an immediate and dramatic increase in GC levels among females in all reproductive states, although lactating females showed the greatest increase (Fig. 1; Wittig et al., 2008). This heightened response may have occurred because the immigration event coincided with a period of frequent and aggressive encounters with other groups and the sudden death of the group's resident alpha male. The initial week of upheaval was followed by 5 months of additional immigrations and instability in the upper levels of the male dominance hierarchy. Most females' GC levels remained elevated for the next 20 weeks, until after one of the immigrant males finally established himself firmly in the alpha position (see also Beehner et al., 2005 for similar results).

Females' stress responses appeared to be specifically related to the threat of infanticide rather than to any increase in aggression associated with instability in the male dominance hierarchy, because females did not receive higher rates of aggression from males or other females during these periods (Beehner et al., 2005; Engh et al., 2006b). Furthermore, females' GC levels did not increase when a natal male, who posed little threat of infanticide, rose to the alpha position (Beehner et al., 2005). Indeed, the specificity of females' stress response can be compared with that of adult males in the same group during the same time periods. In contrast to females, the GC concentrations of males were significantly elevated during all periods of instability in the male dominance hierarchy, whether caused by the rise in dominance of a natal male or an immigrant (Bergman et al., 2005). Male-male rates of aggression showed a similar pattern, with

elevated levels during all periods of male rank instability. Unlike females, males appeared to be responding to any instability in the upper ranks of the male hierarchy, not just to the arrival of an unfamiliar male, a result that has also been documented in other baboon populations (Sapolsky, 1993b).

In some respects, it seems surprising that lactating females' GC levels should return to baseline within several months after the immigration of a real or potentially infanticidal male, because females are at risk of infanticide until they resume sexual cycling, usually a year or more after their infant's birth. There appear to be a number of reasons for females' failure to maintain elevated GC levels throughout the period when their infants are at risk. First, because most infanticide occurs in the 3 or 4 months after the male's immigration and ascent to the alpha position, the threat of infanticide diminishes with time (Cheney and Seyfarth, unpublished data). Second, it may simply be too costly for females to maintain an elevated stress response for more than several months, particularly as the risk of infanticide declines. Third, although baboons seem to be able to anticipate the threat of infanticide over the short term, they may not have the cognitive capacity to recognize that a male remains a threat until they have resumed sexual cycling. We explore some of these questions in more detail below.

## B. PREDATION AND THE LOSS OF KIN

In his 1905 study of baboons living in South Africa, Eugene Marais observed "It was not long before we came to realize that the life of the baboon is in fact one continual nightmare of anxiety" (Marais, 1939). The reason was predation. Predation is a ubiquitous, pervasive, and chronic threat to wild primates, and is presumed to have exerted strong selective pressure on the evolution of sociality (Kappeler and van Schaik, 2002; Sterck et al., 1997; van Schaik, 1983). Unfortunately, however, there are few extant populations of primates where predation still occurs at any significant rate (reviewed by Busse, 1982; Cheney and Wrangham, 1987; Cowlshaw, 1994), and few studies have examined the effects of predation on stress.

There is no consistent relationship between predation risk and GC levels in animals. Indeed, animals confronted with high rates of predation often exhibit low basal GC levels despite showing high levels of antipredator behavior. For example, in California ground squirrels (*Spermophilus beldingi*), animals living in areas of high predation risk exhibit more vigilance behavior but lower GC levels than animals living in areas of low predation risk (Mateo, 2007). Similarly, bank voles (*Clethrionomys glareolus*) that are experimentally exposed to weasel odor decrease their foraging efforts but show no increase in GC levels (Ylönen et al., 2006). There is also no relation between GC levels and rates of alarm calling in ring-tailed lemurs (Cavigelli, 1999; Pride, 2005a).

The lack of a positive relation between predation risk and GC levels, though perhaps counterintuitive at first glance, is doubtless adaptive, as chronically elevated GC levels would prevent individuals from mounting an acute stress response when actually attacked.

The Okavango baboons are some of the few primates still exposed to high rates of predation; they are preyed upon by lions, leopards, and to a lesser extent crocodiles, spotted hyenas, and other carnivores (Busse, 1982; Cheney et al., 2004). Predation is estimated to account for over 95% of adult female deaths. In 2002, 25% of the group's 28 females disappeared as a result of confirmed or suspected predation (Cheney et al., 2004). Eighteen months later, another 26% of the adult females disappeared over a 12-month period. Bulger and Hamilton (1987) report a similarly high proportion of deaths among adult females due to predation in 1984.

Not surprisingly, predator attacks are highly stressful for adult female baboons. Females' GC levels were significantly higher in the 4 weeks following a predation event than in weeks when there had been no predation (Engh et al., 2006a). Predation was particularly stressful when it caused group members to become separated. Lions often attack in coalitions of three or more, causing baboons to panic and scatter in different directions. The resulting subgroups often remain separated for several days before reuniting. GC levels were significantly higher in months when lion attacks resulted in the group's separation for several days compared to months when lion attacks did not separate the group.

Predation was especially stressful for females whose close relatives were killed. Females who lost a close relative experienced a significant increase in GC levels in the month following their relative's death compared with the month before. By comparison, the GC levels of control females matched for reproductive state showed no similar increase (Fig. 3; Engh et al., 2006a). The rise in GC levels among females who lost a close relative to predation was, however, transient. By the second month following the predation event, these females' GC levels had returned to baseline. The relatively transient effect of a relative's death on females' stress levels may have occurred in part because "bereaved" females seemed to attempt to cope with their loss by extending their social network and identifying new grooming partners (see below).

## IX. STRESS ALLEVIATION AND SOCIAL BONDS

Sapolsky's studies of stress in male baboons revealed a number of behavioral strategies that appeared to enable some individuals to cope with the vicissitudes of life better than others. These included grooming



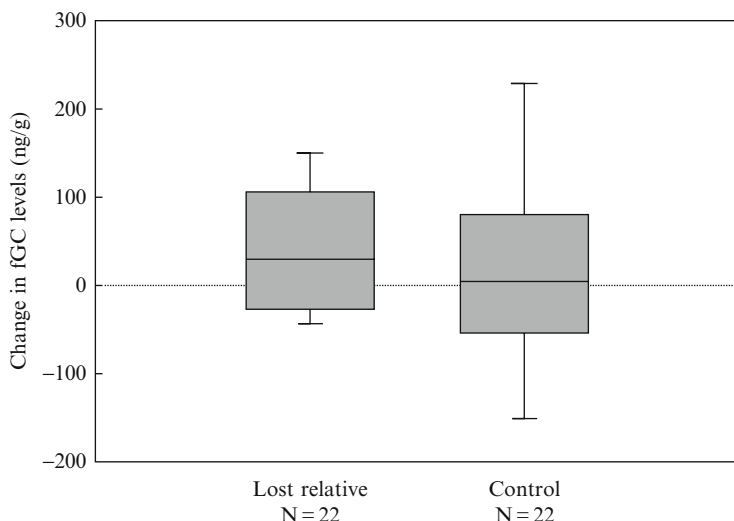


FIG. 3. Changes in GC levels of 22 females who lost a close relative (mother, maternal sibling, or offspring) to observed or suspected predation from the month before to the month after the predation event, compared with 22 control females who did not lose a close relative. Females who lost a close relative to predation experienced a significant rise. Legend as in Fig. 1.

relationships with females, the ability to distinguish between threatening and neutral interactions, the ability to recognize whether they had won or lost an aggressive interaction, and the tendency to redirect aggression onto a previously uninvolved third party when attacked (Ray and Sapolsky, 1992; Sapolsky and Ray, 1989; Virgin and Sapolsky, 1997). Thus, males who coped best had social support, social control, and were better able to predict the outcome of their interactions (Sapolsky, 1998). Most importantly, these coping strategies appeared to translate into higher reproductive success, because males who manifested these traits had lower GC levels and retained their high ranks for longer durations. Similar coping strategies can be found in females.

Although GCs extracted from feces provide a measure of the effects of an individual's social relationships on stress over days and weeks, they do not permit any evaluation of the immediate effects of specific behaviors on GC levels. Recent advances in techniques that permit the noninvasive assessment of GCs from saliva and urine, however, are beginning to make such short-term evaluations feasible, at least in captive animals. These studies suggest that specific behaviors can help to alleviate stress even

within very short time periods. For example, saliva samples taken from common marmosets just after they had mobbed and alarm called at a snake model revealed that alarm calling resulted in a significant decrease in GC levels. In fact, there was a significant positive correlation between the number of alarm calls produced and the magnitude of the decrease in GC concentrations (Cross and Rogers, 2006). At a proximate level, alarm calls may help to reduce stress because they reduce the risk of predation. They may also provide the vocalizer with some control over the predator encounter.

In other contexts, too, vocalizations may serve to reduce stress over the immediate term. Marmosets that were temporarily isolated from their long-term mate showed a significant increase in urinary GCs. However, isolated marmosets who heard their mate's signature vocalization showed a significantly lower increase than individuals who heard an unfamiliar individual's vocalization or no vocalization (Rukstalis and French, 2005). Simply hearing the vocalization of a close companion, therefore, may exert a calming influence.

As we have discussed, the immigration of a potentially infanticidal dominant male is highly stressful to female baboons, particularly when they are lactating. In an apparent response to the threat of infanticide, lactating females in the Okavango Delta often form close, affiliative relationships, or "friendships," with specific adult males (Palombit et al., 1997, 2000, 2001; Weingrill, 2000). These males are always long-term residents of the group who are the infants' real or potential fathers (Moscovice et al., 2009). Observational and experimental data indicate that male friends are more likely than other males to aid females under attack, especially when the aggressor is a potentially infanticidal alpha male (Palombit et al., 1997, 2000).

Analyses conducted over two different time periods have shown that lactating females who have a male friend when an immigrant male enters the group have significantly lower GC concentrations than females without a male friend. Although GC levels rose significantly in lactating females without friends, GC levels in females with friends showed little change (Fig. 4; Beehner et al., 2005; Engh et al., 2006b). Females in the Okavango take a more active role than males in the formation and maintenance of friendships, and females with friends experience fewer attacks by potentially infanticidal males (Palombit et al., 1997, 2000). The comparatively lower stress levels manifested by lactating females with friends support the hypothesis that females recognize the risk posed by potentially infanticidal immigrants and actively attempt to compensate for this risk by forming friendships with long-term resident males.

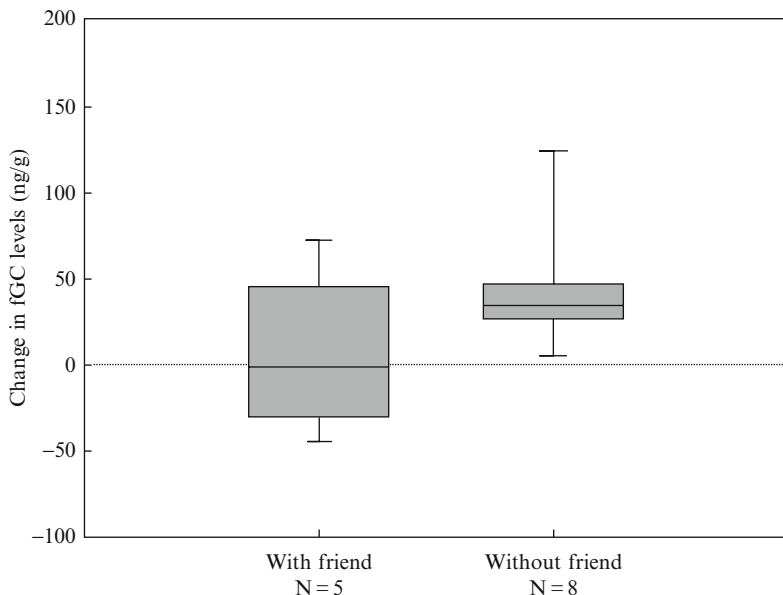


FIG. 4. Changes in GC levels in females with and without a male friend during a period of infant attacks. Females without a male friend experienced a significant rise. Legend as in Fig. 1.

Baboons are a highly sexually dimorphic species, and although females actively defend their own and their relatives' infants against infanticidal attacks, if the infanticidal male is determined and relentless their efforts are usually fruitless. It is therefore interesting that female baboons also responded to the threat of infanticide by consolidating their relationships with other females. Because these relationships are relatively ineffective in preventing infanticide, their function may be primarily psychological.

As we have discussed, female baboons appear to have lower GC levels in months when their grooming networks are more focused. These observations led us to predict that, when confronted with an acute stressor like the immigration of a potentially infanticidal male, females with more focused grooming relationships would experience less stress than those whose grooming relationships were diffuse. We also predicted that grooming would function as a coping mechanism to alleviate stress, leading all females to reduce their grooming diversity and restrict their grooming interactions to a few preferred partners.

As we have mentioned, an 8-month period of relative social stability for the Okavango baboons ended abruptly when the resident alpha male died suddenly and a potentially infanticidal male immigrated into the group. Strikingly, all females reduced their grooming diversity in the weeks following the onset of the unstable period, to focus more strongly on a few preferred partners (Fig. 5). For most females, these partners were close kin. Two sorts of data suggest that this more focused pattern of grooming acted to reduce stress. First, for both females at high and low risk of infanticide, the change in grooming patterns preceded and was correlated with a decrease in GC levels 1 week later. Second, cycling and pregnant females whose grooming networks had been more focused during the previous stable period experienced a smaller increase in GC levels in the week after the onset of the unstable period (Fig. 6; Wittig et al., 2008).

Several studies have suggested that grooming functions in part to decrease stress and anxiety (e.g., Aureli et al., 1999; Boccia et al., 1989; Shutt et al., 2007). The Okavango baboon data suggest more specifically

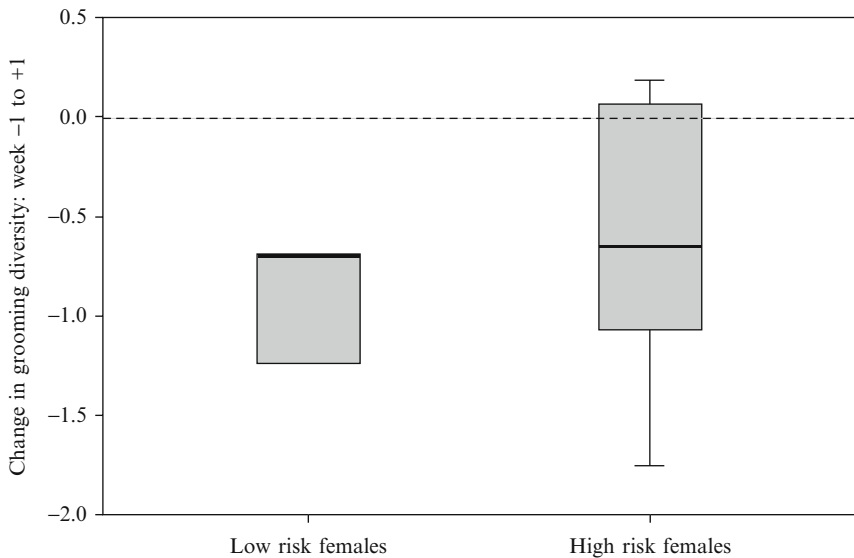


FIG. 5. Changes in the diversity of females' grooming partners from the week before the male immigration event to the week after his immigration. Females at "low risk" of infanticide were either cycling or in the early stages of pregnancy; females at "high risk" of infanticide were either lactating or in the last trimester of pregnancy. Females in both categories significantly decreased the diversity of their grooming partners in the week after the male's arrival. Legend as in Fig. 1.

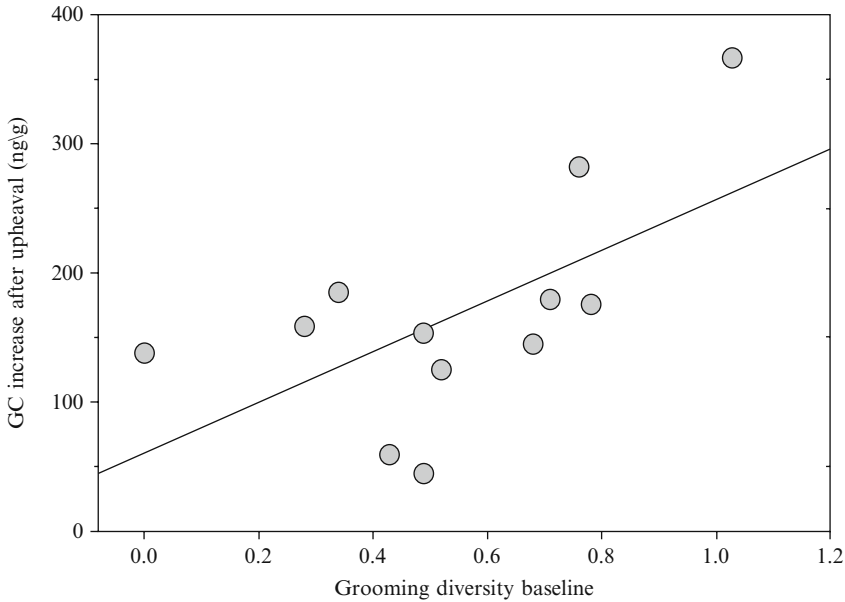


FIG. 6. The correlation between cycling and pregnant females' grooming diversity before the male immigration event and the increase in their GC levels in the following week (increase =  $\text{GC levels}_{\text{week 1}} - \text{GC levels}_{\text{week 1}}$ ). Females who had a lower diversity of grooming partners experienced a smaller increase than females with a higher diversity of grooming partners.

that a concentrated grooming network focused on a few predictable partners is more important than grooming direction or grooming rate in reducing stress. During periods of social stability, female baboons had lower GC levels when their grooming network was more restricted (Crockford et al., 2008). During periods of instability, all females—regardless of their immediate risk—contracted their grooming network even further, and females whose grooming network had been more focused experienced smaller increases in GC levels (Wittig et al., 2008).

## X. COPING WITH A DAMAGED SUPPORT SYSTEM

If a predictable, stable, and focused grooming network helps baboons to cope with stress, what do female baboons do when this network is damaged by the death of a close grooming partner? The loss of a close relative and grooming partner is highly stressful to female baboons, and “bereaved” females experience a significant rise in GC levels. This rise, however, is

transient; by the second month after their relative's death, GC levels have returned to baseline. Apparently, stress is transitory because females attempt to cope with their loss by seeking out social contact.

Because females concentrate much of their grooming on close kin (Silk et al., 1999), females who lose a close female relative might be expected to experience a decrease in grooming diversity, number of grooming partners, and grooming rate. However, the opposite seems to occur. In one analysis of 14 females who lost a close adult female relative to predation, all females increased the number of female grooming partners in the 3 months following this loss, while 14 control females matched for reproductive state showed no similar increase (Fig. 7; Engh et al., 2006a). These control females had also witnessed the predation events, but they had not lost a preferred grooming partner and their social networks remained intact. Females who had lost a close relative also increased their grooming rates and the diversity of their grooming partners, while control females did not.

From a proximate, physiological standpoint, it is not surprising that females initiated bond formation with other females after the loss of a companion, and that this increase in social contact had a stress-reducing effect. As we

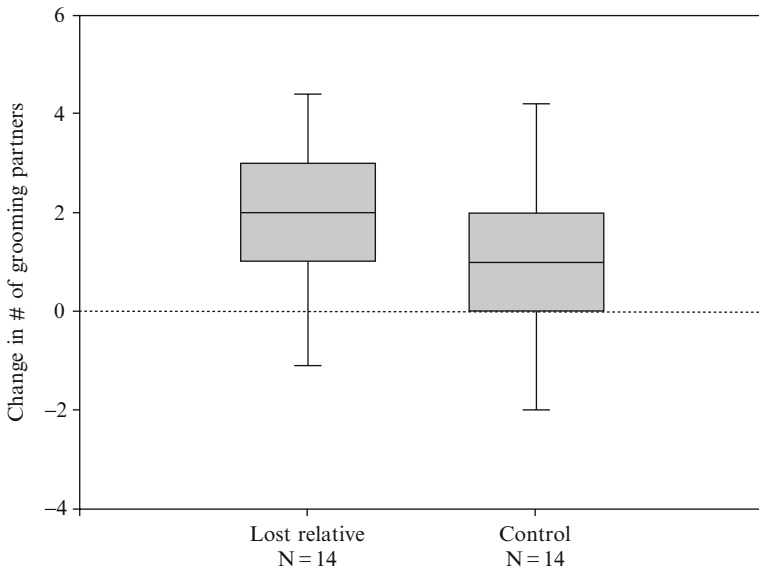


FIG. 7. Change in number of grooming partners of 14 females from the 3 months before to the 3 months after the loss of a close female relative, compared to matched controls. Females who lost a close female relative groomed significantly more females in the months after the loss. Legend as in Fig. 1.

have discussed, the stress response in both animals and humans can be mitigated by social contact and affiliation (Sapolsky et al., 1997; reviewed by Carter, 1998; Panskepp, 1998; see Section I). Increases in GC levels prompt the release of oxytocin, which motivates the urge for social bonding and physical contact (Uvnas-Moberg, 1997). Oxytocin both inhibits the release of GCs and promotes affiliative behavior, including not only maternal behavior but also an increased tendency to associate with other females (Carter, 1998; Taylor et al., 2000). From a functional perspective, this behavior may be adaptive because it enables females to identify and establish new social relationships. It may also provide females with the opportunity to bring some measure of control and predictability into their disrupted lives.

## XI. COPING MECHANISMS IN MONKEYS AND HUMANS: SIMILARITIES

Stress in female monkeys appears to be driven primarily by real and anticipated threats to fitness: their own and their offspring's survival, unpredictable and uncontrollable events, and the loss of a close relative or companion. The stress associated with all of these events can be alleviated by the presence of close social companions. When captive female macaques are socially isolated or placed into a novel group, they experience increased stress. This stress can be dampened considerably, however, by the presence of a preferred grooming partner (Gust et al., 1994). Similarly, in the Okavango, female baboons with undamaged social networks appear to turn to their male friends and their closest female partners for support during periods of instability, in particular following the immigration of a potentially infanticidal male. Their grooming networks become correspondingly more focused and less diffuse.

These results complement those obtained in studies of humans. Women show a greater desire than men to seek social contact during times of stress, and they are also more likely to turn to smaller support groups (Taylor et al., 2000). In both sexes, the number of "core" individuals on whom people rely for support during times of crisis (3–5 individuals) tends to be significantly smaller than their circle of mutual friends (12–20) or regular acquaintances (30–50) (Dunbar and Spoor, 1995; Hill and Dunbar, 2003; Zhou et al., 2005). In the elderly, strong social networks enhance survival (Giles et al., 2005), and when humans perceive future social opportunities to be limited or at risk—either as they age or when they become ill—they tend to contract their social networks and become more selective in their social relationships (Carstensen, 1992, 1995).

One of the most potent stressors in both humans and other animals is the loss of a close companion. In humans, bereavement and feelings of loneliness are associated with increased GC production, decline in immune responses, and, in some cases, increased mortality (see Section I for references). These effects, however, can be mitigated by social support (Thorsteinsson and James, 1999). Social support seems to be particularly important for women's mental health (Kendler et al., 2005; Taylor et al., 2000). The same is true of female monkeys. Similarly, when female baboons in the Okavango Delta lose a close relative to predation, they attempt to compensate for this loss by temporarily expanding their grooming network and increasing the number of grooming partners.

The data on "bereavement" in baboons are especially interesting because most previous studies of stress and social isolation in animals have been conducted on individuals deprived of all social companions. In contrast, the Okavango baboons who lost a close companion were more akin to humans experiencing loss, because they were not separated from their social group and could still interact with other relatives and companions. Even in the presence of familiar group mates and relatives, however, these females experienced a stress response to the disappearance of a specific individual. They apparently sought to alleviate it by broadening and strengthening their social relationships. Similar behavior occurs in the Amboseli baboon population, where females who lose a close relative seek to establish relationships with more distant kin, and those who lack even distant kin seek to establish relationships with unrelated females (Silk et al., 2006a,b).

## XII. COPING MECHANISMS IN MONKEYS AND HUMANS: DIFFERENCES

In addition to experiencing increased stress as a result of grief and anxiety in their own lives, humans often show stress in response to grief or anxiety in the lives of others. Health-care workers who attend to sick or traumatized patients often experience "compassion fatigue" and elevated stress profiles (Figley, 1995). Baboons have many opportunities to experience vicarious stress. There is little evidence, however, that they do so, even when their own fitness is affected. The reason for this may be related to their apparent inability to understand the beliefs, knowledge, and emotions of others.

As we have seen, both human and nonhuman species show physiological responses to the loss of close companions—what in humans we label as the emotion of grief. In a variety of animals ranging from rodents to primates, social isolation and separation from a close companion produce a stress



response. Baboons experience the same kinds of physiological responses when they lose a preferred companion, even when they have other kin or close companions with whom they can still interact.

Grief, however, is an egocentric emotion, like fear; it does not require the attribution of mental states to others. It is certainly possible to feel grief or a sense of loss without recognizing that others might feel the same way. In contrast, empathy requires that an individual be able to recognize emotions like grief or fear in others even when she is not experiencing these emotions herself. It demands that she deliberately imagines herself in another individual's position while still dissociating her own mental states from her companions. In humans, the recognition of emotions like pain, disgust, and shame in others activates many of the same areas of the brain as those activated when we experience or imagine ourselves experiencing the same emotions. Other areas of the brain, including in particular the right inferior parietal cortex and the prefrontal cortex, allow us to detach our own emotions and knowledge from others (Decety and Jackson, 2004, 2006). Thus, although we use much of the same neural architecture to understand our own and others' mental states, we are nonetheless able to maintain a degree of separation between them. The same does not seem to be true of nonhuman primates, even of chimpanzees (Cheney and Seyfarth, 2007; Silk, 2007; Tomasello and Moll, 2009; Tomasello et al., 2005).

Chimpanzees are often described as showing compassion; in the wild, they have been reported to build nests and bring food to an injured relative (Goodall, 1986). But there is considerable disagreement about whether chimpanzees experience empathy for the anxiety, fear, or grief of others. Most examples are anecdotal (e.g., Preston and de Waal, 2002) and subject to a variety of interpretations. And for each anecdote that seems to demonstrate empathy there are several counterexamples. In fact, two experimental studies designed explicitly to test whether chimpanzees show concern and regard for others concluded that they do not (Jensen et al., 2006; Silk et al., 2005). In this respect, it is particularly unfortunate that there have been almost no studies of the causes and amelioration of stress in wild apes.

Baboons' apparent inability to feel empathy may prevent them from being able to understand the plight of others. For example, when most of the group's juveniles were separated from all of the adults for several days during a period of high flood in the Okavango, adult females showed no evidence of recognizing their offspring's dilemma. Despite being able to hear their offspring's agitation and distress on the adjacent island, none of the females showed any behavioral reactions to the calls, nor did they show elevated stress responses during the days of the separation (Cheney and Seyfarth, 2007). One explanation for their apparent lack of empathy is that

they were incapable of recognizing that their offspring's fear of making a long and dangerous water crossing was greater than their own. Alternatively, it remains possible that the females' lack of concern simply reflected their knowledge, that their offsprings were in no immediate danger, and that they could easily return to them if necessary.

Similarly, when a potentially infanticidal male immigrates into a group of baboons, GC levels in cycling females are often unaffected. This is perhaps not surprising, because the offsprings of cycling females are not in danger. In many cases, though, these cycling females have daughters, mothers, or sisters who are lactating at the time and whose infants are at considerable risk. Because these infants are close relatives, their deaths would reduce the cycling females' own overall fitness. Although it could be argued that it is maladaptive for female baboons to respond to every indirect threat to their fitness, the relative lack of a stress response to the anxiety of a close relative is puzzling.

In sum, female baboons show stress responses primarily to events that directly affect themselves; the loss of a close relative, an infanticidal threat to their own infant, and rank instability that threatens their own dominance position. The indirect impact of a threat to their inclusive fitness, however, appears to be less important.

### XIII. THE ADAPTIVE VALUE OF SOCIAL BONDS, SOCIAL KNOWLEDGE, AND THE STRESS RESPONSE

The stress response is adaptive over the short term in large part because it is self-correcting: it induces individuals to take active measures to alleviate it. But because it is harmful if maintained over long periods of time, the stress response is also selective and egocentric. Confronted with an array of potential stressors, female baboons exhibit elevated GCs primarily in response to those events that directly affect their own survival and reproduction. In the Okavango, a female's lifetime reproductive success is determined primarily by longevity (which depends largely on predation) and infant survival (which depends largely on infanticide). A female's rank is relatively unimportant in determining her reproductive success, though it may play a crucial role in years of drought or poor floods. Perhaps as a result, females exhibit a stress response primarily to predation and the threat of infanticide, and, to a lesser extent, rank instability. Conversely, females do not show a stress response to several events that do not directly affect them, even though they cause a general uproar in the group at large: instability in the ranks of natal and other resident males; the immigration of

a potentially infanticidal male when the female does not have a vulnerable infant; and instability in the female dominance hierarchy if the female's own status is unaffected.

Baboons' stress responses also demonstrate that even environmental challenges like predation are inextricably linked with social ones. To survive and reproduce, baboons must not just avoid predation and find sufficient food to support themselves and their infants; they must also create, manage, and maintain the social relationships that buffer and support them in these endeavors. Marais (1939) may have been overstating matters when he described the life of a baboon as "one continual nightmare of anxiety." But however purple his prose, one thing is clear: in baboons, as in humans, many causes of stress—and its alleviation—are fundamentally social.

Although baboons lack a full-blown theory of mind, they have a rich and nuanced understanding of other individuals' social relationships. They recognize other individuals' relative dominance ranks and kinship relations, and they integrate this knowledge to recognize that the female dominance hierarchy is composed of a hierarchy of matrilineal families (Bergman et al., 2003; Cheney and Seyfarth, 1999; Cheney et al., 1995a). Their knowledge of other individuals' social relationships enables them to recognize that a "reconciliatory" grunt given by a close relative of a recent opponent can function as a proxy for direct reconciliation with the opponent herself (Wittig et al., 2007a). Conversely, it allows them to recognize that a threat grunt given by an opponent's close relative functions as an aggressive alliance (Wittig et al., 2007b). Knowledge of other individuals' social relationships may also permit baboons to identify new social partners when their social networks are damaged or threatened. Our data on Okavango baboons' stress responses suggest that females who have control over their social interactions and whose social relationships are focused and predictable experience the least stress. Ultimately, these focused social networks may also influence a female's reproductive success, because there is some evidence that females who maintain strong bonds with other females experience higher offspring survival and longevity (Silk et al., 2003b, 2009). It remains for future research to determine whether other populations of baboons and other species of monkeys show similar responses to real and perceived threats to fitness.

Reproductive success, at least in female baboons, appears to be related less to crude individual attributes like dominance rank or the number of close kin than to subtle behavioral attributes linked to the ability to create, manage, and sustain close social relationships. There appears to be a causal relationship between social skills, the stability of a female's

social network, and reproductive success. It is as yet unclear whether some females, or some types of personalities, are better able than others to navigate this complex social world.

Finally, the data on wild female baboons also suggest that the causes of stress in humans, as well as its alleviation, are evolutionarily ancient and emerged long before language and a theory of mind. Like humans, baboons find a diffuse social network and the lack of a few reliable friends stressful. And, as for humans, the quality and strength of social bonds are much more important for female baboons than their number. Thus, the skills that allow individuals to identify and nurture friendships appear to have been under strong selective pressure for many millions of years.

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