

Advances in
THE STUDY OF BEHAVIOR

VOLUME 39



Advances in THE STUDY OF BEHAVIOR

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Preface

Advances in the Study of Behavior has made "contributions to the development of cooperation and communication among scientists in the field" of animal behavior since 1965. The present volume continues to reflect the diversity of approaches that animal behaviorists use and the array of problems they address. The volume includes studies on social behavior (Cheney and Seyfarth, Schino and Aureli, Topál *et al.*), reciprocal altruism (Schino and Aureli), social learning (Galef), mate choice and conflict (Schlupp), and alternative mating tactics (Radwan). The trend in animal behavior toward more integrative and multidisciplinary studies is reflected in studies on the effect of stress on social behavior (Cheney and Seyfarth), the mechanisms of reciprocal altruism (Schino and Aureli), and both proximate and ultimate approaches to alternative mating tactics (Radwan). The studies in this volume include both laboratory and field research on a wide diversity of species including primates (papers by Cheney and Seyfarth, Schino and Aureli), dogs (Topál *et al.*), rats (Galef), fish (Schlupp), and mites (Radwan). The volume also reflects a continuing interest in applying our understanding of animal behavior to human behavior (Cheney and Seyfarth, Topál *et al.*). By highlighting particularly well-developed and original research programs, this volume continues to stimulate new, exciting advances in animal behavior.

With this volume, we welcome Dr. Leigh Simmons to our team of editors. His eclectic research interests and experience as an editor make him a particularly valuable addition. I remain the executive editor, and Tim Roper, Marc Naguib, Kathy Wynne-Edwards, and John Mitani continue as editors. Together we hope to maintain the intellectual diversity that has characterized this series since the beginning.

H. JANE BROCKMANN

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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 kills 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 km², fording or swimming from one wooded island to another at the height of the flood