

Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*)

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In humans, bereavement is associated with an increase in glucocorticoid (GC) levels, though this increase can be mitigated by social support. We examined faecal GC levels and grooming behaviour of free-ranging female baboons to determine whether similar effects were also evident in a non-human species. Females who lost a close relative experienced a significant increase in GC levels in the weeks following their relative's death compared with the weeks before, whereas control females showed no such increase. Despite the fact that females concentrate much of their grooming on close kin, females who lost a close female relative did not experience a decrease in grooming rate and number of grooming partners; instead, both grooming rate and number of grooming partners increased after a relative's death. While the death of a close relative was clearly stressful over the short term, females appeared to compensate for this loss by broadening and strengthening their grooming networks. Perhaps as a result, females' GC levels soon returned to baseline. Even in the presence of familiar troop-mates and other relatives, females experienced a stress response when they lost specific companions, and they apparently sought to alleviate it by broadening and strengthening their social relationships.

Keywords: bereavement; predation; grooming; glucocorticoids; stress; baboon

1. INTRODUCTION

It was not long before we came to realize that the life of the baboon is in fact one continual nightmare of anxiety.

Eugene Marais (1939), from his 1907 study
My Friends the Baboons

Although Marais hypothesized that baboons' 'nightmare of anxiety' was directly attributable to predation, little is known about the long-term effects of frequent predation pressure on stress in non-human primates. The body's immediate response to an acute stressful event like predation is to elevate levels of circulating glucocorticoids (GCs), which serve to mobilize energy reserves and curtail non-essential metabolic processes (Sapolsky 2004). While adaptive over the short term, this 'flight or fight' response is physiologically costly when sustained over extended time periods. Because predator attacks are traumatic, unpredictable and uncontrollable, they could potentially cause chronic anxiety among individuals who witness such events. The impact of predation might be particularly

strong in individuals who lose a close relative or companion.

In humans, bereavement and feelings of loneliness are associated with increased cortisol production, declines in immune responses and, in some cases, increased morbidity and mortality (e.g. Irwin *et al.* 1987; Cacioppo *et al.* 2000; McCleery *et al.* 2000; reviewed in Segerstrom & Miller 2004). These effects, however, can be mitigated by social support (Thorsteinsson & James 1999). Social support appears to be particularly important for women's mental health (Taylor *et al.* 2000; Kendler *et al.* 2005).

Social support also appears to be important for the health and reproduction of non-human primates. In captivity, female macaques (*Macaca* spp.) 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, 1996). In natural groups of anubis and yellow baboons (*Papio hamadryas anubis* and *Papio hamadryas cynocephalus*), socially integrated males have lower basal GC levels than more isolated males (Sapolsky *et al.* 1997), and more socially integrated females raise infants more successfully (Silk *et al.* 2003).

Female chacma baboons (*Papio hamadryas ursinus*) in the Okavango Delta of Botswana experience significant increases in GC levels as a result of male immigration,

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infanticide and rank instability (Beehner *et al.* 2005; Engh *et al.* in press). As a rule, females mount GC responses to these stressors only when their own lives, the lives of their offspring, or their social ranks are at direct risk. Here we examine the effects of predation, focusing on a far more subtle risk to females' reproductive success—the loss of close kin. Female baboons retain close bonds with matrilineal kin throughout their lives, and often bias their grooming towards these individuals (Silk *et al.* 1999). Moreover, there is some evidence that females that are more socially integrated experience higher infant survival (Silk *et al.* 2003). The loss of a close female relative might, therefore, be expected to increase measures of social isolation and lead to an increase in GC levels.

Predation by leopards and lions is the primary cause of mortality among juvenile and adult baboons in the Okavango (Busse 1980; Cheney *et al.* 2004). Predators are known or suspected to be responsible for up to 96% of adult female deaths (Cheney *et al.* 2004). Here we assess the effects of predation on female GC levels. We first examine whether females' GC levels rose in response to predation and varied according to the severity of predation events. We then compare the stress response shown by females who lost a close relative to that shown by unaffected females and consider the behavioural responses and coping mechanisms of these affected individuals.

2. MATERIAL AND METHODS

(a) Study site and subjects

The bulk of the study was conducted over a 16-month period (May, 2003–August, 2004) in the Moremi Game Reserve, located in the Okavango Delta of Botswana. The habitat consists of seasonal floodplains interspersed with slightly elevated wooded 'islands' (for a description, see Bulger & Hamilton 1987; Cheney *et al.* 2004). At the time of this study, the group contained approximately 70 individuals, including an average of nine adult males and 22 adult females. The group has been observed since 1978, and all animals are fully habituated to human observers on foot. Maternal relatedness for all natal animals is known. Close kin included mothers, offspring and maternal siblings.

Like many other species of Old World monkeys, female baboons in this population form linear dominance hierarchies that usually remain stable over long periods of time (Silk *et al.* 1999; Bergman *et al.* 2003; Cheney *et al.* 2004). Daughters acquire ranks similar to those of their mothers, and members of the same matriline typically hold adjacent ranks. Females remain in their natal groups throughout their lives, whereas males usually emigrate to neighbouring groups at sexual maturity.

(b) Confirmed and suspected predation

Between May, 2003 and August, 2004, there were 26 adult or juvenile deaths. Three animals (12%) disappeared after becoming ill, while the remaining 23 disappeared healthy and were presumed or confirmed to have been killed by predators. Ten animals (two adult males, five adult females, three juveniles) were *confirmed* victims of predation. In these cases, we either witnessed the predator's attack or found the corpse of a baboon cached in a tree, a sign of leopard predation. One other adult male died as a result of an apparent snake bite. Six animals (three males, two females, one juvenile) disappeared under circumstances where

predation was strongly *suspected*. These circumstances included alarm calls and the sighting of predators or predator tracks in close proximity to the baboons at the time of the individual's disappearance (for further details, see Cheney *et al.* 2004). Finally, six animals (two males, one female, three juveniles) were classified as having *disappeared healthy*. These animals disappeared after having been seen, apparently healthy, within the previous 24 h (Cheney *et al.* 2004). Two adult males were included in this category because after disappearing they were never seen again in adjacent groups (most males who emigrate from the study group are located again in other groups; Cheney *et al.* 2004).

Of the 23 animals who were confirmed or suspected to have died from predation, 12 (52%) were known or suspected to have been killed by lions and four (17%) by leopards. Most if not all of the remaining animals were probably also victims of lion or leopard attacks, although hyenas and crocodiles also prey on baboons at this site (Cheney *et al.* 2004).

(c) Hormone collection and analysis

We collected a total of 630 faecal samples for hormone analysis from 21 females. All females more than 6 years of age at the beginning of the study were sampled. On average, we collected one sample from each female every 13.99 (± 0.61 s.e.) days for a total of 30.00 (± 1.89 s.e.) samples/female. No female was sampled twice before a faecal sample had been obtained from all other females. Hormones were extracted from faeces in the field using methods described by Beehner & Whitten (2004; see also Beehner *et al.* 2005) and analysed in the laboratory of Dr Patricia Whitten (Emory University). All samples were assayed for GC metabolites using a corticosterone RIA kit (ICN Diagnostics Division) previously validated for use in baboons (Beehner & Whitten 2004). Inter-assay coefficients of variation were $12.16 \pm 1.03\%$ (high control, $N=9$) and $8.82 \pm 3.36\%$ (low control, $N=9$). The intra-assay coefficient of variation for a subset of 35 samples was $5.97 \pm 6.81\%$. Based on Wasser *et al.*'s (2000) estimate, we assumed a 24 h delay between social and demographic events and faecal samples reflecting hormonal changes resulting from these events.

Faecal samples were classified as positive for *predation* in the four weeks after one or more juveniles or adults was preyed upon or disappeared healthy. In some of the analyses described below, we supplement our data with 54 faecal samples gathered from eight females in the same group between August–October 2002 using identical methods for collection and extraction (Beehner *et al.* 2005).

(d) Behavioural data

We collected 10 min focal samples on all females throughout the study period. During each focal, we recorded all social interactions, including aggression and grooming. Aggression included vocal and visual threats, as well as physical attacks. Grooming bouts were timed. We used the Shannon–Weaver index to measure grooming diversity (Cheney 1992; Henzi *et al.* 1997; Silk *et al.* 1999). The index was calculated as $H = -\sum P \ln(P)$, where P is the proportion of grooming that a female gives to each partner. The index was standardized by dividing it by the maximum value possible $H_{\max} = \ln(N-1)$, where N was the number of females 3 years or older residing in the group.

In some analyses, data on grooming were supplemented by additional behavioural data gathered in 2002 on 18 females in the same social group.

(e) Statistical analysis

We used general linear mixed models (GLMM) to assess the influence of characteristics of predation on GC levels. Because we sampled the same individuals repeatedly, we included individual identity as a random factor in our GLMMs, with first-order autocorrelation as a covariance structure. Seasonality was not included in our analyses because there were no seasonal effects on GC levels in either males or females (J. C. Beehner, unpublished data). We used restricted maximum likelihood methods for model estimation and Satterthwaite's *F* tests to gauge fixed effects. All analyses were performed in SPSS 12.0 (SPSS Inc.) unless otherwise noted.

Analyses of the consequences of losing close relatives were conducted using non-parametric tests to control for the effects of small sample size. All tests were two-tailed, with adjusted *p*-values listed in the text. We used QVALUE (v.1.0) to correct for multiple testing (Storey 2002). QVALUE calculates a minimum false discovery rate (FDR), controlling the proportion of true null hypotheses that are rejected. Controlling for FDR among multiple tests is a more equitable compromise between type I and type II errors than is a Bonferroni correction. Because it is not as strict as traditional family-wise corrections, FDR retains more statistical power, which is especially important when sample sizes are small (Storey & Tibshirani 2001; Nakagawa 2004). We set the FDR at 0.05, and the π_0 value, obtained through the program's smoother function, was 0.4762.

3. RESULTS**(a) Predation events and GC levels**

We first examined whether females' GC levels were higher in months when individuals were *confirmed* victims of predation and months when healthy animals disappeared for unconfirmed reasons (*suspected* predation and *disappear healthy*); we found no difference (GLMM: $F_{1,293}=0.452$, $p=0.290$). We, therefore, combined all three types of disappearances into a single category (termed *predation* for ease of discussion) in our overall GLMM.

GC levels were significantly higher in the four weeks following a predation event than when there was no such event (GLMM: $F_{1,610}=6.966$, $p=0.021$; see Engh *et al.* in press for more details). GC levels in months when individuals were confirmed or suspected to have been killed by lions did not differ from those in months when individuals were confirmed or suspected to have been killed by leopards (GLMM: $F_{1,200}=2.139$, $p=0.140$).

Lions always attacked in coalitions of three or more, causing the baboons to panic and scatter in different directions. The resulting subgroups often remained 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 (GLMM: $F_{1,133}=17.474$, $p=0.004$).

(b) The loss of a close relative and GC levels

Predation appeared to be especially stressful for females whose close relatives were killed. To examine how a relative's death affected a female's GC levels, we matched each of the 22 females who lost a close relative (*affected* females) with an unaffected control female in the same reproductive state from whom we had obtained faecal

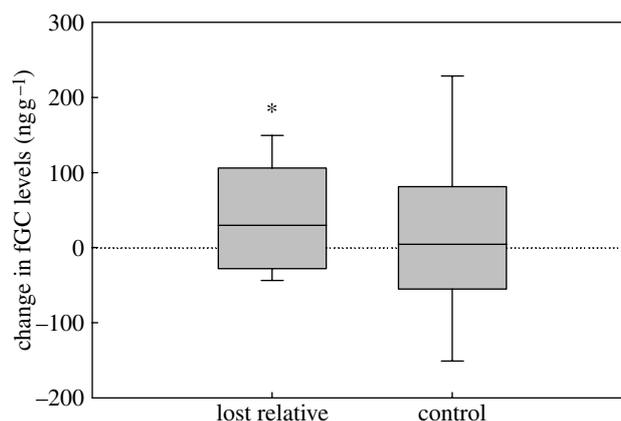


Figure 1. Change in fGC levels of 22 females who lost a close relative (i.e. mother, maternal sibling, offspring) to observed or suspected predation, compared to matched controls whose relatives did not die. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. An asterisk denotes a significant difference.

samples at the same time (18 affected and control females from the 2003–2004 study, and four affected and control females from the 2002 study). 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 (Wilcoxon signed-ranks test: $Z=-2.678$, $n=22$, $p=0.018$). By comparison, the GC levels of control females showed no similar increase ($Z=-0.438$, $n=22$, $p=0.354$; figure 1). This analysis included females who lost a juvenile offspring to predation. Results were similar, however, when we restricted the analysis to the 10 females who lost an adult female relative (affected females: $Z=-2.293$, $n=10$, $p=0.039$; control females: $Z=-1.070$, $n=10$, $p=0.219$).

Although females who lost a close relative to predation experienced a significant increase in GC levels, this effect was only transient. When we compared females' GC levels in the month before their relative's death with their levels in the *second* month following their relative's death, we found no significant difference ($Z=-0.227$, $n=15$, $p=0.410$); faecal samples during the second month were not available for seven females, either because their relative disappeared towards the end of the study or because they were drawn from the 2002 study, when faecal samples were collected for only four months).

The relatively transient effect of a relative's death on females' stress levels may have occurred in part because bereaved females attempted to cope with their loss by extending their social network. Because females concentrate much of their grooming on close kin (Silk *et al.* 1999), females who lost a close female relative might have been expected to experience a decrease in grooming diversity, number of grooming partners and grooming rate. However, the opposite occurred.

There were 14 females for whom we had grooming data during the three months before and the three months after a close adult female relative's death (five females from the 2003–2004 study, and eight from the 2002 study). We used the Shannon–Weaver diversity index to calculate how evenly each affected female's grooming interactions were distributed among all potential female partners over the

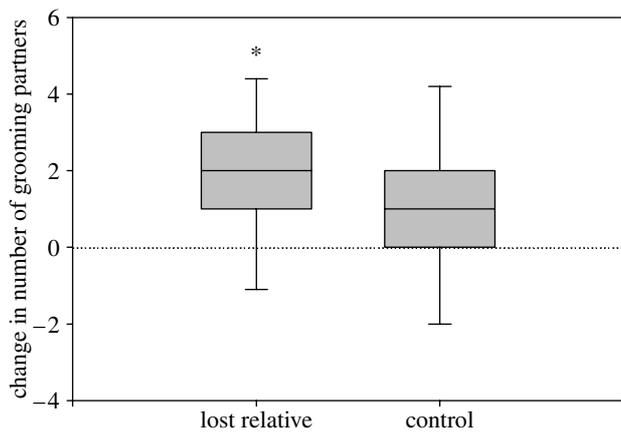


Figure 2. Change in number of grooming partners of 14 females from the three months before to the three months after the loss of a close female relative, compared to matched controls. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. An asterisk denotes a significant difference.

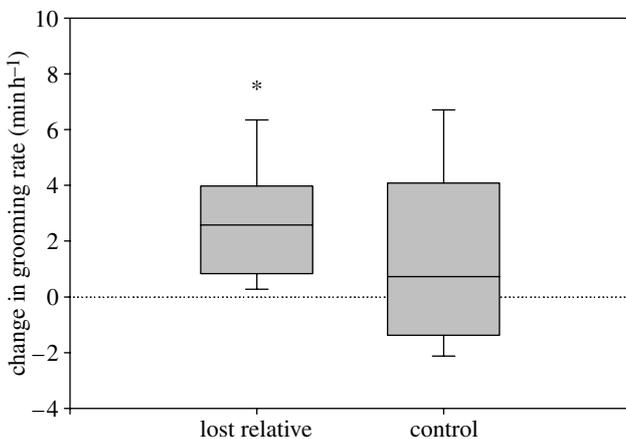


Figure 3. Change in the grooming rates of 14 females from the three months before to the three months after the loss of a close female relative, compared to matched controls. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. An asterisk denotes a significant difference.

age of 3 years during each time period, and compared their indices to those of 14 control females in the same reproductive state. There was a significant increase in grooming diversity following a close relative's death (Wilcoxon signed-ranks test: $Z = -2.981$, $n = 14$, two ties, $p = 0.010$). Affected females also groomed significantly more individuals. On average, each female groomed $1.86 (\pm 0.29 \text{ s.e.})$ females before her relative died, and $3.79 (\pm 0.65 \text{ s.e.})$ after ($Z = -2.540$, $n = 14$, one tie, $p = 0.021$; figure 2). Finally, there was a significant increase in the rate at which affected females groomed other females in the months after a close relative's death ($Z = -2.731$, $n = 14$, $p = 0.016$; figure 3). In contrast, control females experienced no significant increase in grooming diversity (Wilcoxon signed-ranks test: $Z = -0.804$, $n = 14$, one tie, $p = 0.275$), number of grooming partners ($Z = -1.489$, $n = 14$, three ties, $p = 0.134$; figure 2), or grooming rate ($Z = -1.161$, $n = 14$, $p = 0.204$; figure 3).

While the death of a close relative and grooming partner was clearly stressful over the short term, females appeared to compensate for this loss by increasing their grooming diversity, the number of their grooming partners, and the rate at which they groomed other females. Perhaps as a result, their GC levels soon returned to baseline.

We would have liked to assess how grooming diversity and rate changed in the week or two immediately following a close relative's death, but our behavioural data were insufficient to accurately measure those variables over such short periods. Four of the nine females for whom we had both grooming and GC data had more than one female grooming partner before their relatives died, but that did not appear to buffer them from the stress of losing a grooming partner. On average, their GC levels rose by $70.61 \text{ ng g}^{-1} (\pm 24.91 \text{ s.e.})$ in the month after their relative's death. The GC levels of the five females with only a single female grooming partner rose an average of $50.04 \text{ ng g}^{-1} (\pm 54.90 \text{ s.e.})$ over the same time period.

4. DISCUSSION

The results of this study support Marais' intuition that predation is a major source of stress for baboons. Females' stress levels were significantly higher in months when individuals were either known or suspected to have been killed by predators, and attacks that caused the group to be widely separated for longer periods of time were significantly more stressful than attacks that did not.

GC measures were especially high in females who lost a close relative. Among humans, social isolation, loneliness and bereavement are associated with increased GC levels (e.g. Irwin *et al.* 1987; Thorsteinsson & James 1999; McCleery *et al.* 2000; Tuner-Cobb *et al.* 2000; Rosal *et al.* 2004; Steptoe *et al.* 2004; reviewed in Segerstrom & Miller 2004). Baboons appeared to experience similar physiological responses to loss. Even among bereaved females, however, the increase in GCs was only evident in the month immediately following their relative's disappearance; by the second month, females' GC levels had returned to baseline. During this time, their grooming diversity, number of grooming partners and rate of grooming other females increased, suggesting that female baboons compensated for the loss of a grooming partner by broadening and strengthening their grooming networks.

It is impossible to determine whether the increase in GCs following the loss of a relative is a result of seeing a baboon killed, losing a close companion or both. Two factors, however, suggest that the loss of a close companion may be the more important. First, predator attacks were witnessed by many adult females, but only females who lost a close relative showed significant increases in GC levels. Second, because female baboons restricted most of their grooming to a small number of individuals, the loss of a close grooming partner had the potential to produce a marked increase in social isolation. Perhaps in response, females who lost a close companion—but not others—appeared to make deliberate attempts to establish new social bonds.

From a 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. It is well established that the stress response in both animals and humans can be mitigated by social contact and affiliation (Sapolsky *et al.* 1997; reviewed by Carter 1998; Panksepp 1998; Aureli *et al.* 1999). The pituitary hormone oxytocin, which can be released by physical contact (Uvnas-Moberg 1997), appears to play an important role in affiliation-mediated stress reduction, and its effect is particularly pronounced in females (reviewed by Taylor *et al.* 2000). Oxytocin both inhibits the release of GCs and promotes affiliative behaviour, including not only maternal behaviour but also an increased tendency to associate with other females (Carter 1998; Taylor *et al.* 2000).

To date, most studies of the relationship between stress and social isolation in animals have been conducted under artificial conditions on infants separated from their mothers, monogamous rodents separated from their mates, or group-living animals deprived of all social companions (reviewed by Carter 1998; Panksepp 1998). In contrast, in the current study wild baboons that lost close companions were not separated from their social group and could still interact with other relatives and companions. Even in the presence of familiar troop-mates, females experienced a stress response when they lost specific companions, and they apparently sought to alleviate it by broadening and strengthening their social relationships.

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