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Behavioural Processes

Associations between spatial position, stress and anxiety in forest baboons *Papio anubis*

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ABSTRACT

Spatial position within a group affects the value of group-living benefits such as reduced predation risk and improved foraging. The threat of predation, poor nutrition or increased competition from conspecifics can all cause stress. In many species, central positions are known to be more beneficial than peripheral positions in terms of reduced predation, vigilance and foraging. In this study, we examine whether spatial position within a group is associated with stress and anxiety in a troop of olive baboons (*Papio anubis*). We predicted that the benefits of occupying central positions would be reflected by a reduction in stress and anxiety for animals who spent the most time in the centre of the group. The study subjects appeared to compete actively for the centre of the group. Physiological stress measures (faecal glucocorticoid concentrations) were positively correlated with time spent in central positions. Time spent in central positions was positively correlated with proximity but negatively correlated with vigilance behaviours (alarm barks). Vigilance rates were positively correlated with measures of anxiety (self-scratch frequency). It is suggested that individuals experience chronic stress due to proximity to conspecifics in central positions, whilst perceived predation risk causes anxiety, with perceived predation risk experienced more by individuals on the periphery.

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1. Introduction

A number of factors may influence the amount of stress that is experienced by animals; either short or long-term. Long-term stress in particular may have a range of deleterious effects on health (Sapolsky et al., 2000) and; all things being equal we might predict that animals should seek to minimize stress as much as possible. However; there are a variety of reasons why we might still expect to find that some individuals experience more stress than others. For example; trade-offs between the costs of carrying out stressful activities and the benefits of engaging in them might lead to stressful behaviours being ultimately beneficial (e.g. competing with conspecifics may be stressful but might result in gains of food or mating opportunities). In other situations some individuals may be able to compete to gain access to limited resources that allow them to experience less danger and thus less stress e.g. to sleep or feed in a safer area than others. In social animals; social interactions; dominance rank; access to resources and spatial position within a group may all affect the way in which stress levels differ between individuals. Here; we investigate some of the correlates of this variation in a group of olive baboons.

Group living provides individuals several benefits, including reduced predation risk through increased sum vigilance and dilution effects (Bertram, 1978), and improved foraging success through wider foraging ranges and enhanced detection of food sources (Pulliam, 1973). These benefits are inter-related, as reduced predation risk, for an individual, results in less time spent being vigilant and more time foraging (Caro, 2005). Spatial position within a group influences the value of these group-living benefits for an individual. Peripheral individuals are more exposed to predation than those in the centre (Bertram, 1978), whilst in mobile groups, exposure to predation can vary at the front, back or side of the group depending on predator location or tactics (Bumann et al., 1997; Hirsch and Morrell, 2011). Across animal taxa, peripheral individuals have been shown to spend more time being vigilant than those placed centrally, for example in Brown-headed cowbirds (*Molothrus ater*, Fernández-Juricic et al., 2011), Przewalski's gazelle (*Procapra przewalskii*, Shi et al., 2011), impala (*Aepyceros melampus*; Blanchard et al., 2008) and brown capuchin monkeys (*Cebus apella*, Janson, 1990).

Given the probability that peripheral individuals are more at risk from predation it is perhaps unsurprising that a number of studies have suggested that animals will compete for more

central positions within a group. The 'desirability' of a central position may be indicated by aggression being linked to competition for central positions and/or a link between dominance rank and time in the centre of the group, for example within groups of common eider, where female aggression is positively correlated with centrality (*Somateria mollissima*; Öst et al., 2007), chacma baboons (*Papio cynocephalus ursinus*; Ron et al., 1996) and olive baboons (*Papio anubis*; Barton, 1993), where higher ranking females occupy more central positions. As noted by Barton (1993), the reasons for the relationship between dominance and central positions are not always easy to understand – for example they may be because dominant individuals are more 'attractive' social partners or because larger matrilines are both clumped together and contain more dominant individuals. However, if such relationships occur mainly during feeding (as found by Barton's 1993) this is more likely to suggest a preference for centrality when vigilance has a greater cost (as feeding and vigilance are mutually exclusive).

Front positions may also have advantages. Individuals placed at the front of the group benefit from early detection of or arrival at food sources. This "early arrival" or "finders-keepers" tactic has been observed in low-ranking Japanese macaques (*Macaca fuscata*; Bélisle and Chapais, 2001), tufted capuchin monkeys (*Cebus apella nigritus*; Di Bitetti and Janson, 2001), vervet monkeys (*Cercopithecus aethiops*; Gerald, 2002) and long-tailed macaques (*Macaca fascularis*; Dubuc and Chapais, 2007). The nature of food resources will influence the relative advantage or disadvantage of spatial position in terms of foraging: concentrated and slowly depleting food resources can be monopolised by dominant central individuals, whilst abundant, smaller foods can be quickly consumed by peripheral individuals (Hirsch, 2007).

Therefore, there are complex trade-offs for individuals in terms of the relative benefits and costs of spatial positions within a group. Broadly, peripheral positions have foraging advantages but higher predation risk, whilst central positions may be safer in terms of predation, they may expose individuals to aggression or negative social interactions with conspecifics. In this study we investigate whether the amount of anxiety and stress, shown by behaviour and physiology respectively, is linked to spatial position within a group of olive baboons and if so, which positions are more anxiety-inducing or stressful.

Investigating stress and the causes of stress in free-ranging animals has become possible in recent years with the advent of non-invasive sampling of urine or faeces. Stress response in many mammals is mediated by the hypothalamic–pituitary–adrenal axis (HPA), a complex set of feedback interactions between the hypothalamus, pituitary and adrenal glands (Herman et al., 2003). Activation of the HPA axis ultimately results in the production of glucocorticoids, such as cortisol. These hormones stimulate the release of glucose and thus allow the adaptive redirection of both energy and behaviour (Sapolsky et al., 2000). Metabolised glucocorticoids are eventually excreted in either urine or faeces, presenting the opportunity to monitor the stress state of an animal non-invasively (Hodges and Heistermann, 2003).

Strong correlations between an individual's blood cortisol levels and glucocorticoid metabolite levels have been found in faecal or urine samples, suggesting non-invasive sampling provides an authentic reflection of pre-metabolism stress levels (Barton et al., 1993; Whitten et al., 1998). Faecal glucocorticoid levels have been used to examine stress responses across animal taxa, including in birds (Wasser et al., 1997), reptiles (Kalliokoski et al., 2012), felids (Fanson and Wielebnowski, 2013) canids (van Kesteren et al., 2012), cervids (Creel et al., 2002) and in several primate studies (Tiefenbacher et al., 2000; Higham et al., 2009; Muehlenbein et al., 2012). These studies typically have examined stress response to human disturbance (e.g. Kalliokoski et al., 2012) or mating competition (e.g. van Kesteren et al., 2012). Here, we examine for the first time the relationship between spatial position within a group and physiological stress levels.

Self-directed (SDB) or displacement behaviours, such as self-scratching, self-grooming, yawning and body-shaking are commonly used as behavioural measures of anxiety in primates (Maestripieri et al., 1992). Some of these behaviours may also have a hygienic function, but raised frequencies have been found in a range of primate species under conditions likely to be stress-inducing (e.g. long-tailed macaques (Aureli and van Schaik, 1991; Das et al., 1998), chimpanzees (*Pan troglodytes*; Kutsukake, 2003), white-faced capuchins (*Cebus capucinus*, Manson and Perry, 2000) and humans (Mohiyeddini et al., 2013)). Correlations between SDB rates and physiological measures of stress are not consistent (Higham et al., 2009). SDBs likely represent a short-term coping strategy (anxiousness), and should be considered as separate to long-term or chronic stress response (Higham et al., 2009).

In this study we use both behavioural and non-invasive endocrinological methods to examine, respectively, the anxiety and stress associations with the spatial positions of adult and sub-adult members of a troop of olive baboons. We also examine the relationships between time spent in spatial positions and foraging, vigilance, grooming and aggression rates in order to evaluate factors that may influence anxiety and stress in different spatial positions within the group.

2. Methods

2.1. Subjects

Data were collected between March and May 2009 within the Gashaka Gumti National Park (GGNP), Nigeria. Research was conducted at the Gashaka field site (300 m, 07°21′N-011°30′E), based in Gashaka village near the farmlands on the banks of the river Gam Gam (Warren, 2003). The study group was the Gamgam troop, which during the study period (9th March-4th May 2009) consisted of 20 individuals: five adult females (aged between 9 and 17+ years old, Warren, 2003), two sub-adult males (both aged 8 years), a single adult male (age 12+ years), nine juveniles (aged between 1 and 4 years old) and 3 infants (<1 year old). This study focused on the adults and sub-adults of the troop.

2.2. Data collection

Subjects were each observed in one daily 30 min focal sample over 56 days, giving a mean of 17.4 (±SD3.0) h of behavioural data per subject. During focal observations, behaviour was recorded continuously noting both point (event) and state (duration) behaviours (Altmann, 1974). Behavioural anxiety indicators were recorded as point events: self-directed behaviours, self-scratches and yawns were included in this category (Maestripieri et al., 1992; Castles et al., 1999). Yawns were too infrequent and found to be too difficult to distinguish as SDBs as opposed to threats or normal yawns, so were subsequently removed from analyses. Spatial competition events, i.e. spatial supplants and retreats, were defined as displacements which had no immediate foraging benefit, and increased or reduced a subject's centrality relative to the rest of the group; these were recorded as point events. The frequency and direction of aggression (threats, displacements, and physical aggression) were also recorded as point events. Other point events recorded were vigilance (individual looks specifically away from current activity in searching manner) and alarm barks. All occurrences and durations of state behaviours included: foraging (searching for and feeding on food items), grooming (individuals brushing and picking through conspecific's hair; direction of

Distance (m)	Weighting factor ([1/area* π]*100)
≤1	w1 (100.0)
1-≤5	w2 (4.0)
5-≤10	w3 (1.0)
10-≤15	w4 (0.4)
>15	w5 (0)

Proximity =
(n1*w1)+(n2*w2)+(n3*w3)+(n4*w4)+(n5*w5)

Where: n = the no. of individuals at distance
w = weighting factor at distance

Fig. 1. Process of calculating proximity indices for subjects at the start and end of focal samples. Proximity method has been adopted from Perry (1997) and Stahl and Kaumanns (2003).

grooming also recorded), resting (individual inactive) and moving (sustained locomotion for more than 5 m).

At the start and end of each focal sample, the proximity of group members around the focal subject was recorded. The number of individuals was recorded at five distances: 0–1 m; +1–5 m; +5–10 m; +10–15 m; and >15 m. The presence of infants was not recorded; three females were lactating and had infants during the study period. These data were then used to calculate proximity indices applying a weighting factor (see Fig. 1) for each subject per focal (a mean of the proximity index at the start and end of the focal). The index weights closer proximity more heavily, with a high proximity index indicating the individual was observed in close proximity with several other individuals.

After each focal sample, a scan sample of all study subjects was taken, recording group spread, general activity and spatial position in relation to the rest of the troop. Seven different positions within the group were coded indicating a subject's position in terms of central or peripheral, and directionally, i.e. front, back or side (Fig. 2). Group spread was estimated as an area calculation, based on the estimated distance between the foremost and rearmost monkey (positions 1 and 4 in Fig. 2), multiplied by the estimated distance between the most peripheral monkeys on the side edges of the group (positions 2 and 3 in Fig. 2). The centre of the group was determined from group spread estimates at the start of the scan, facilitating the subsequent categorisation of individual spatial positions.
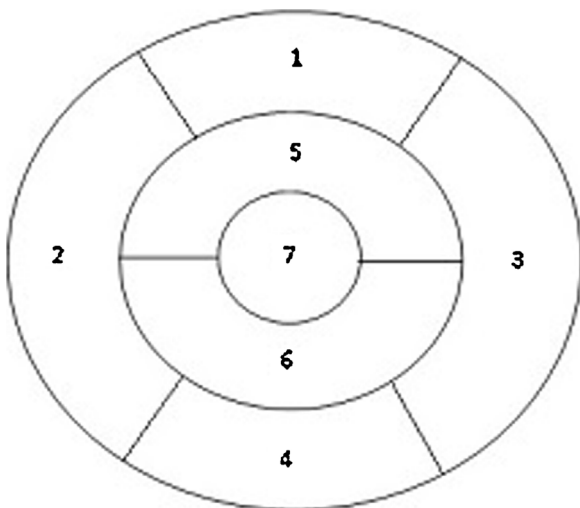

Fig. 2. Spatial positions recorded during scan samples, the front of the group is situated at position 1, the rear at position 4. The front of the group was determined by the direction the majority of the group was moving during the scan observation. Positions 1, 4, 2, and 3 were determined by individuals at the extremes of the majority group spread. Estimations of the centre (7) of the group then enabled observers to approximate positions 5 and 6. Diagram and methodology adapted from Hall and Fedigan (1997).

2.3. Faecal sample collection and hormone analysis

Opportunistic faecal samples were collected for all subjects following Hodges and Heistermann (2003). Faeces were first homogenized (typically with a nearby stick or stone) and a thumbnail-sized sample portioned into a 30 ml Azlon tube (Azlon 7BWH0030 N, Azlon, Stone, Staffordshire, UK) containing 10 ml of 95% ethanol. Results of a previous study demonstrated that time of day does not affect faecal glucocorticoid (fGC) levels for the study population (Higham et al., 2009).

In total 139 samples were collected during the study period; 8 samples were subsequently removed from the data set due to low dry faecal weight (any samples below 0.1 g were discarded) or with very low levels of fGCs (any samples requiring dilutions greater than 1/40 for analysis) as these samples fell outside the linear dilution range. Following these removals, 131 samples remained viable for study, a mean of 16.4 faecal samples per subject (±SD 3.3).

Samples were transported back to the University of Roehampton under DEFRA licence number AHZ/2537/2009/1. Double extraction (Ziegler et al., 2000) was used to extract the hormone from faecal samples into 99.5% methanol. Higham et al. (2009) reported the efficacy of the extraction procedure as $97.5 \pm 2.9\%$, determined by the recovery of tritiated estradiol for the same population and procedures used here.

Faecal glucocorticoid levels were measured using an enzyme immunoassay previously validated for use in baboons in an ACTH challenge test (Daspre, A., Heistermann, M., Rosetta, L., Lee, P.C., personal communication, 2007). Faecal extracts were analysed for 5b-androstane-3a, 11b-diol-17-one cortisol metabolites (3a,11b-dihydroxy-CM).

Intra- and inter-assay coefficients of variation for the measurement of high and low quality controls were 4.93% and 9.48% (high), and 6.34% and 13.90% (low), respectively, within accepted conventional limits.

2.4. Data analysis

Dominance was analysed using the dyadic aggressive interactions observed between study subjects during focal, scan and *ad libitum* sampling. For an observed aggressive interaction, the identities of the aggressor and victim were noted. The frequency of these interactions among the study subjects was calculated, as well as their composition, i.e. how often one study subject was an aggressor/victim to another subject. These data were compiled as a matrix and subsequently analysed using Matman software (version 1.3.2) to test for a significant linear dominance hierarchy amongst the study subjects (de Vries et al., 1993).

To analyse spatial position, positions 1–4 were combined into an "Outer" category and 5–7 to an "Inner" category. The ratios of scans found in the "Inner" compared to the "Outer" category were calculated, hereafter the "Inner Ratios", with a higher inner ratio indicating more time spent in central positions.

Proximity indices, fGC concentrations and the frequencies of self-scratches, spatial competition events and aggressions were log transformed to meet the requirements for parametric analyses.

Comparisons of mean by rank and sex were performed using analysis of variance (ANOVA) and covariance for mean proximity indices; mean inner ratios; mean fGC concentrations; mean times spent moving, resting, grooming, foraging and vigilance; mean frequencies of spatial competition events, self-scratches and alarm barks.

To analyse how time spent in the coded spatial positions predicted behaviour and physiological measures of stress, multiple regressions were performed controlling for rank, sex and group spread where appropriate.

All statistical analyses were performed using SPSS version 17.0.1.

3. Results

Controlling for rank, sex and group spread, mean inner ratios were significantly positively correlated with mean fGC concentrations ($r^2 = 0.44$, $F(3,7) = 6.42$, $p = 0.04$) (Fig. 3a), i.e. more time spent in central areas was associated with higher fGC concentrations. Controlling for rank, sex and group spread, the relationship between mean self-scratch frequencies and mean inner ratios was insignificant ($r^2 = 0.26$, $F(3,7) = 1.85$, $p = 0.28$). An insignificant negative correlation was found between mean self-scratch frequencies and mean fGC concentrations ($r^2 = 0.381$, $p = 0.35$; $n = 8$).

Controlling for rank, sex and group spread, mean proximity indices and mean inner ratios were significantly positively correlated ($r^2 = 0.42$, $F(1,7) = 6.08$, $p = 0.05$). Controlling for rank, sex and group spread, mean spatial supplant frequencies and mean inner ratios were significantly positively correlated ($r^2 = 0.62$, $F(1,7) = 12.41$, $p = 0.01$). Controlling for rank, sex and group spread, mean alarm bark frequencies and mean inner ratios were significantly negatively correlated ($r^2 = 0.62$, $F(1,7) = 12.41$, $p = 0.01$) (Fig. 3b).

Multiple regressions controlling for rank, sex and group spread found insignificant relationships between mean inner ratios and mean aggression received ($r^2 = 0.49$, $F(3,7) = 1.28$, $p = 0.40$) and given ($r^2 = 0.26$, $F(3,7) = 0.47$, $p = 0.72$), foraging ($r^2 = 0.17$, $F(3,7) = 0.26$, $p = 0.85$), grooming given ($r^2 = 0.17$, $F(3,7) = 0.26$, $p = 0.85$) and received ($r^2 = 0.06$, $F(3,7) = 1.16$, $p = 0.43$) and vigilance ($r^2 = 0.51$, $F(3,7) = 0.89$, $p = 0.52$).

Controlling for rank, sex and group spread, mean vigilance rates were positively correlated with mean self-scratch frequency ($r^2 = 0.71$, $F(3,7) = 6.68$, $p = 0.05$). Controlling for rank, sex and group spread, mean self-scratch frequency did not correlate significantly with any other behavioural activity. Controlling for rank, sex and group spread, mean fGCs did not correlate significantly with any behavioural activity.

A significant linear hierarchy was found in the adult females based on 103 interactions ($h = 0.95$; $p = 0.03$; $n = 103$). A significant linear hierarchy was not found when the males and females were examined together, nor among males alone. This appears to be the result of relatively few observations of subadult males interacting with other individuals. For the purposes of analysis, the males were grouped into one rank and analysed as being one rank higher than the lowest/highest female respectively.

Significant variation between ranks was found for inner ratios ($F(5,178) = 4.02$, $p < 0.001$), proximity indices scores ($F(5,230) = 7.828$, $p < 0.001$) and duration moving ($F(5,217) = 3.92$, $p < 0.001$). Insignificant variation was seen between ranks for all other measures of behaviour or fGC concentrations. Significant variation between sexes was found for the frequency of aggression received ($F(1,32) = 5.673$, $p = 0.02$), with males receiving significantly more aggression.

4. Discussion

This study presents novel evidence of the impact of spatial position in terms of stress. Analyses revealed time spent in more central positions was positively correlated with mean fGC concentrations (a measure of stress state) for the baboons. In order to explain higher stress levels being associated with time spent in central positions, the relationship between central positions and proximity to conspecifics, aggression, foraging and vigilance were examined.

Proximity indices were higher in central positions compared to the periphery. Increased proximity to conspecifics has previously been found to increase anxiety in baboons (Castles et al., 1999) and other primate species (Aureli et al., 1999; Manson and Perry, 2000). Here, although centrality was associated with higher proximity indices, neither fGC concentrations nor SDB frequency were correlated with proximity indices. It has been suggested that proximity alone does not induce anxiety or stress; more important are the levels of association an individual has with the conspecifics it is in proximity with (Ellis et al., 2011; McDougall, 2011; Di Sorrentino et al., 2012). The methods used in this baboon study are insufficient to carry out such analyses and future research examining the relationship between stress, anxiety and proximity could make use of tools such as social network analysis to understand which individuals experience anxiety or stress when in proximity with specific conspecifics (Croft et al., 2008).
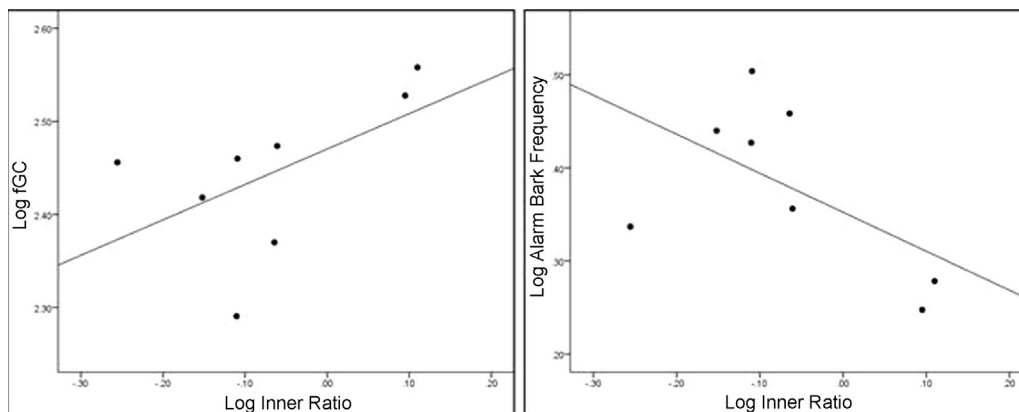
Fig. 3. Regressions of (a) log mean fGC ($r^2 = 0.44$, $F(3,7) = 6.42$, $p = 0.04$) and (b) log alarm bark frequency ($r^2 = 0.62$, $F(1,7) = 12.41$, $p = 0.01$) by log inner ratio. Inner ratios were determined by the proportion of scans that an animal was observed in inner (positions 5–7 in Fig. 2) to outer (positions 1–4 in Fig. 2) spatial positions. Higher ratios thus represent a greater amount of time spent in central positions.

This study found limited evidence among a group of olive baboons for spatial competition and patterns of stress for central positions. Spatial competition was evidenced by the positive correlation between the frequency of spatial displacements and the time that individuals were observed in central positions. Supplants play a key role in the establishment and maintenance of dominance hierarchies in primate groups (Walter, 1980; Borries et al., 1991; Koenig, 2000; Robbins et al., 2005). In baboons, these interactions have been shown to impact on the foraging success of individuals, with low ranking individuals often displaced from high value resources by dominant individuals (Shopland, 1987; Gil-Burmann et al., 1998; Barton, 1993). Here, we specifically examined supplants and displacements which appeared to increase an individual's centrality relative to the rest of the group, i.e. with no apparent foraging benefit (increasing access to food). The positive correlation between spatial competition event frequency and a central position within the group supports previous evidence for competition among baboons for central positions (Ron et al., 1996). There was no relationship found between spatial position and overall aggression and displacement rates.

Whilst there was no relationship found between spatial position and vigilance rates, a significant negative correlation between alarm barks and time spent in central positions was found. This finding shows some evidence of increased vigilance activity with time spent in peripheral positions. Although predation risks are relatively low in Gashaka, the group does experience attacks from local farmers (Ross et al., 2011) and either this or innate predator avoidance tactics may be an important factor driving competition for central spatial positions. Mean self-scratch frequencies were positively correlated with mean vigilance rates, however, there was no relationship between any measure of vigilance and fGC. These results indicate that social pressures (proximity and spatial competition) in the centre of a group may be chronic stressors for the monkeys, whilst perceived predation risk (which is higher on the periphery of the group) is anxiety-inducing (Di Sorrentino et al., 2012).

Foraging rates were not correlated with spatial position in this study. However, this research was limited to a two month period when food distribution was likely to be consistent. Longer-term studies might reveal different patterns of spatial competition, stress and anxiety with differing amounts and qualities of food resources. Food availability has been seen to play a key role in foraging competition with impacts on the distribution of individuals within a group (Gil-Burmann et al., 1998; Di Bitetti and Janson, 2001; Stahl and Kaumanns, 2003; Quinn et al., 2012). Competition for food and dietary stress can influence fGC levels in wild primates (Foerster et al., 2012; Dunn et al., 2013). A longer study may be able to identify whether social and dietary stressors related to food competition may be an important correlate for higher stress levels in central positions.

This study has several limitations, particularly, the sample size. There were only eight study subjects, with the troop size being around half the average for olive baboons (Napier and Napier, 1985). A larger sample size and the utilisation of tools such as social network analysis may yield stronger evidence of the effect of spatial position on the well-being of animals in relation to stress and anxiety.

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