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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.

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

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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