Animal Behaviour 87 (2014) 195–202

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Rank effects on social stress in lactating chimpanzees

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ARTICLE INFO

Article history:
Received 27 May 2013
Initial acceptance 3 July 2013
Final acceptance 10 October 2013
Available online 6 December 2013
MS. number: A13-00450R2

Keywords:
chimpanzee
Gombe National Park
lactation
Pan troglodytes schweinfurthii
rank status
stress

Given the deleterious consequences associated with chronic stress, individual differences in stress susceptibility can have important fitness implications. These differences may be explained in part by dominance status because high rank is typically associated with decreased aggression and improved nutrition. Here, we examined the relationship between dominance and social stress in lactating chimpanzees, *Pan troglodytes schweinfurthii*, at Gombe National Park, Tanzania. We did so by pairing daily demographic and behavioural data with faecal glucocorticoid metabolite (FGM) concentrations collected over 37 months. While there was no main effect of rank, interesting differences emerged by adult subgroup size and adult sex ratio (males/females). We found that differences in FGM concentrations between high- and low-ranking females were most pronounced as adult subgroup size and sex ratio increased. Low-ranking females had higher FGM concentrations in larger subgroups and in subgroups biased towards adult males; we observed no comparable change in FGM concentrations amongst high-ranking females. Because low-ranking females were the recipient of significantly more male aggression relative to females of high rank, these patterns may be driven by psychosocial stress in low-ranking females. There was no significant change in diet quality across subgroup sizes; this finding suggests that nutritional stressors were not driving differences in female FGM concentrations. Being susceptible to social stress has important fitness implications as it may constrain low-ranking females from 'choosing' optimal subgroups to take advantage of food resources and/or for the socialization of their offspring.

Although an animal's physiological stress response can be adaptive because it mobilizes energy reserves to cope with immediate demands, chronic exposure to elevated stress hormones can have deleterious consequences, including immunosuppression, muscle wasting and reduced reproduction (reviewed in Sapolsky, 2002). Identifying factors promoting individual differences in susceptibility to stress can thus have important implications for understanding the proximate causes underlying variation in health, survivorship and reproductive success.

Numerous studies have demonstrated that rates of aggressive interactions and diet quality are correlated with glucocorticoid concentrations in wild animals (reviewed in Creel, Dantzer, Goymann, & Rubenstein, 2013). Because high rank typically confers reduced rates of received aggression and priority of access to food (reviewed in Clutton-Brock, 1988; Ellis, 1995; Sapolsky, 2001), early studies of rank and physiological stress responses were based on the hypothesis that low rank is stressful. However, subsequent research, particularly on males, has demonstrated a more equivocal relationship. Although some species show a negative correlation between rank and glucocorticoid concentrations (e.g. Faulkes & Abbott, 1997), others are characterized by a positive correlation (e.g. Carlson et al., 2004; Cavigelli, Dubovick, Levash, Jolly, & Pitts, 2003; Creel & Sands, 2003; Holekamp & Smale, 1998). Primary factors contributing to this variability across species in the relationship between rank and glucocorticoid concentrations include the stability of the social hierarchy and the manner in which high rank is attained and maintained (reviewed in: Creel et al., 2013; Sapolsky, 2005).

Fission–fusion systems provide a unique opportunity to investigate rank effects on stress physiology. In fission–fusion societies, fluidity in subgroup size is a strategy by which individuals respond to immediate constraints and opportunities. The general consensus is that time spent alone or in small subgroups minimizes intragroup competition for food when foraging resources are scarce (e.g.

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0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.10.031

reviewed in Aureli et al., 2008). Although subordinates can thus reduce the likelihood of aggression by avoiding dominants, they may, as a result, be relegated to lower-quality food patches, miss opportunities for cooperative infant care, or be more vulnerable to predation (Krause & Ruxton, 2002; Murray, Eberly, & Pusey, 2006; Murray, Mane, & Pusey, 2007). Analysing individual behaviours and stressors in the context of fission–fusion dynamics can thus reveal the strategies used by animals to balance their social and ecological environments.

Chimpanzees, *Pan troglodytes*, live in multimale, multifemale communities characterized by fission–fusion social organization in which subgroup composition within a permanent community changes frequently over time (Goodall, 1986; Nishida, 1968). Subgroup size is positively correlated with food supply (Goodall, 1986; Isabirye-Basuta, 1988; Mitani, Watts, & Lwanga, 2002; White & Wrangham, 1988; Wrangham, 1977), which suggests that taking advantage of temporally abundant food resources can impose costs associated with maintaining close proximity to others (i.e. nutritional benefits may be offset by aggression and anxiety). Theory predicts that these costs may be particularly pronounced among low-ranking individuals (reviewed in Creel et al., 2013). However, whether individuals of varying rank within a community differentially respond to the costs and benefits of grouping is poorly established.

In this study, we examined the relationship between rank and social stress in lactating East African chimpanzees, *Pan troglodytes schweinfurthii*. Dominance hierarchies in female chimpanzees are stable over time, and high rank status confers fitness benefits, including improved infant survival, faster-maturing daughters and shorter interbirth intervals (Pusey, Williams, & Goodall, 1997). These benefits are thought to be the result of differential access to food resources because a female in better condition can invest more energy in reproduction and offspring care (Emery Thompson & Wrangham, 2008; Pusey et al., 1997).

We focus our analyses on lactating females primarily because lactation is the most energetically demanding reproductive phase (Clutton-Brock, Albon, & Guinness, 1989; Gittleman & Thompson, 1988; Hanwell & Peaker, 1977) and is a critical component of female reproductive success (e.g. Lee, 1996; chimpanzees: Emery Thompson, 2013; Emery Thompson, Muller, & Wrangham, 2012). Furthermore, by focusing exclusively on lactation, we minimized complications of stress associated with sexual coercion (Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007) and avoided known variation in cortisol concentrations across reproductive states in chimpanzees (Emery Thompson, Muller, Kahlenberg, & Wrangham, 2010).

Despite the importance of off-setting the costs of offspring care (Dufour & Sauther, 2002; Gittleman & Thompson, 1988; Pond, 1977), lactating females may be constrained from capitalizing on food resources if doing so is costly in terms of increased aggression received from conspecifics. In chimpanzees, mothers with dependent offspring are typically less gregarious, particularly with males (Otali & Gilchrist, 2006), than other female chimpanzees (Goodall, 1986; Murray, Lonsdorf, Eberly, & Pusey, 2009; Wrangham & Smuts, 1980). This may be due to the vulnerability of young to aggressive attacks ('infant safety hypothesis': Otali & Gilchrist, 2006) and/or the costs of travelling with an infant: travel distance and subgroup size are positively correlated, and mothers with dependent offspring may not be able to keep pace with larger subgroups (Wrangham, 2000). In either case, evidence suggests that lactating mothers face unique social and ecological trade-offs relative to other females, yet little is known about how female rank status influences this trade-off.

Our study addresses two main objectives. First, we examined social stress in lactating chimpanzees by determining the effects of rank, adult subgroup size and adult subgroup sex ratio on faecal glucocorticoid metabolite (FGM) concentrations. Given the documented fitness benefits of rank in female chimpanzees, we predicted that low-ranking females would be more susceptible to social stress than high-ranking females. Second, we analysed how two possible sources of stress in lactating chimpanzees vary with rank and subgroup size: rates of received aggression and diet quality. Chimpanzees are ripe fruit specialists (Goodall, 1986), and the percentage of fruit in the diet indicates quality such that diets higher in fruit are considered better quality relative to diets lower in fruit (e.g. Chapman, Wrangham, & Chapman, 1995; Emery Thompson & Wrangham, 2008). We predicted that high-ranking females would have lower rates of received aggression and higher diet quality relative to low-ranking females, and that these differences would be most pronounced in larger subgroups, which typically form in response to fruit availability but foster greater opportunities for conflict (i.e. more potential aggressors). These two variables (rate of received aggression and diet quality) provide insight into the costs and benefits of grouping, and whether socioecological trade-offs are experienced equitably by individuals of varying rank.

METHODS

Tanzanian field assistants and M. Heintz collected demographic and behavioural data on chimpanzees at Gombe National Park, Tanzania, as a part of a long-term research project. Faecal samples were collected and processed as part of a broader study addressing the effects maternal stress on offspring health and development. Each observation day, researchers followed one lactating female and collected data on (1) subgroup composition every 5–15 min and (2) the female's activity every 1 min (using instantaneous scan samples: Altmann, 1974). Observation began when a female descended from her sleeping nest or was first located, and continued (at maximum) until the female ascended into a sleeping site in the evening. Mean $\pm$ SE duration of observation days included in analyses was 8.6 $\pm$ 0.25 h, and mean duration between consecutive observation days was 75 $\pm$ 10.3 days.

Aggression received by the female was recorded ad libitum on observation days. For a 37-month period (1 January 2009–31 July 2012), researchers followed the mother again the next day to collect faecal samples for hormone quantification (see below). Because circulating glucocorticoid metabolites manifest in faeces after 12–24 h in chimpanzees (Murray, Heintz, Lonsdorf, Parr, & Santymire, 2013), this 2-day pairing of observational data with physiological samples allowed us to link FGM levels to demographic and behavioural data with finer temporal resolution than in previous studies.

We categorized females as lactating from the birth of an infant until the earliest of the following: infant's death, the conception of the female's next infant, or the infant's fourth birthday (infant chimpanzees are typically not fully weaned until 4–5 years: Clark, 1977; Pusey, 1983; van de Rijt-Plooij & Plooij, 1987). Long-term behavioural observations of immigrant females indicate that females are well integrated into their new community after they have given birth; spatial site fidelity and permanent residence occur after a female gives birth (Williams, Pusey, Carlis, Farm, & Goodall, 2002). Because all females included in this study were either natal to the study community (64.3%; $N = 9$), or they conceived after immigration (35.7%, $N = 5$), immigration status was not a variable tested in our analyses.

Female Rank Status

We categorized females as either 'high-ranking' or 'low-ranking' based upon their position in the female dominance hierarchy. The