Behavioural Processes 109 (2014) 79–88

Contents lists available at ScienceDirect

Behavioural Processes

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

Does hierarchy stability influence testosterone and cortisol levels of bearded capuchin monkeys (*Sapajus libidinosus*) adult males? A comparison between two wild groups

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ARTICLE INFO

Article history:
Available online 16 September 2014

Keywords:
Aggression
Dominance
Hormones
Challenge hypothesis
Allostatic load

ABSTRACT

Testosterone and cortisol are hormones expected to play a major role in competitive behaviours (i.e. aggression), and are related to rank and hierarchical stability. Through a non-invasive technique, we analyzed faecal testosterone (FTM[1]) and cortisol (FCM[2]) metabolites of dominant and subordinate males from two wild groups of bearded capuchin monkeys. One group had a stable dominance hierarchy while the other had an unstable hierarchy, with a marked conflict period related to a male take-over. In the unstable hierarchy group (1) the dominant male had higher FTM peaks than subordinates, and (2) basal FTM levels were higher than in the stable group. These findings are in accordance with the Challenge Hypothesis and rank-based predictions, and confirm that in *Sapajus libidinosus* hierarchy stability, social status, aggression rates and testosterone are closely related. Dominants of both groups had higher basal and peak FCM levels, suggesting that in *S. libidinosus* the dominant male has a higher allostatic load than subordinates, related to his role in protection against predators, intragroup appeasement, and control of food sources. Finally, we suggest that males of *S. libidinosus* are resistant to testosterone suppression by cortisol, because in the unstable group in spite of an increase in FCM there was also an increase in FTM during the conflict period.

This article is part of a Special Issue entitled: Neotropical Behaviour.

1. Introduction

In social species, group members are subject to constant competition for limiting resources, which led to the evolution of hierarchical social structures in many social taxa, in which competitive relations are formalized in dominance relationships (Chase et al., 2002). Stability of hierarchies can increase or reduce the yielded benefits. In a stable hierarchy there is no reversal in dominance and no change in rank among subjects (Sapolsky, 1993); subjects can predict the outcome of an intra-group interaction and consequently save energy and avoid possible deleterious results (see Clutton-Brock and Huchard, 2013 for a review on social competition). In many primate species access to females occurs via dominance rank, with low levels of overt aggression (Cowlishaw and Dunbar, 1991; Gogarten and Koenig, 2013). However, in unstable hierarchies males generally engage in agonistic interactions in order to monopolize estrus females (Cowlishaw and Dunbar, 1991).

Hierarchy stability and dominance rank are expected to be linked to hormone levels of males (Mehta and Josephs, 2010). Testosterone is related to behaviours such as aggression, mate seeking and guarding, and courtship (Wingfield et al., 1990). According to the Challenge Hypothesis (Wingfield et al., 1990), because testosterone is involved in the aggression necessary to compete for high rank but might reduce health (e.g. Muehlenbein and Watts, 2010), males from stable hierarchies would have lower testosterone levels than males from unstable hierarchies, and testosterone levels would be similar in both dominants and subordinate males. In unstable hierarchies (high aggression rates), higher rank subjects are expected to have higher basal testosterone concentration (Sapolsky, 1993).

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[1] Fecal testosterone metabolites.
[2] Fecal cortisol metabolites.

http://dx.doi.org/10.1016/j.beproc.2014.09.010
0376-6357/

Cortisol is another hormone important in mediating relationships between aggression, social rank, and reproductive function (Muehlenbein and Watts, 2010). Features of social structure such as dominance style, means of maintaining dominance, breeding system, hierarchy stability and availability of coping outlets for subordinates may influence how dominants and subordinates perceive stress (Sapolsky, 2005). Dominants are expected to experience more stress than subordinates in an unstable hierarchy while the opposite is expected in a stable hierarchy (Sapolsky, 2005). However, findings concerning this prediction are divergent, reflecting the wide diversity of primate social systems (Abbott et al., 2003). Goymann and Wingfield (2004) suggested that cortisol levels would depend on the benefits or costs (allostatic load) of being a dominant or a subordinate in a given species, population or sex. If allostatic load is higher in dominants than in subordinates their cortisol levels are expected to be higher and vice versa.

Capuchin monkeys (the two sister genera *Cebus* and *Sapajus*; Lynch-Alfaro et al., 2012a,b), although known for their high diversity in social systems related to ecological variation (Fragaszy et al., 2004; Izar et al., 2012), generally present a clear male dominance hierarchy, and reproductive skew towards the dominant male (Izar et al., 2009). Given these features, this taxon is an interesting model to study the relationship between male hormones, dominance rank, and hierarchy stability. Few studies, however, have addressed this relationship, presenting divergent results (Lynch et al., 2002; Schoof et al., 2012, 2014; Schoof and Jack, 2013). In white-faced capuchins (*Cebus capucinus*), hormone levels differ according to dominance status, so that dominant males present higher cortisol and androgen levels than subordinates (Schoof et al., 2012, 2014; Schoof and Jack, 2013). In black horned capuchin monkeys (*Sapajus nigritus*), Lynch et al. (2002) found no difference between dominants and subordinates in testosterone and cortisol levels.

In the genus *Sapajus*, rank reversals are very rare (Carosi et al., 2005), since male tenure is long and normally ended by death or disappearance (for a review, see Izar et al., 2009). In this study, we took advantage of the observation of a rank reversal in one of the two wild groups of *Sapajus libidinosus* followed on a long term study (e.g. Izar et al., 2012), in Fazenda Boa Vista (FBV[3]), Piauí, Brazil. We analyzed faecal testosterone and cortisol metabolites from all adult males of the two wild groups to test the difference in male hormone levels between a stable and an unstable hierarchy. Social system of *S. libidinosus* follows the general pattern of capuchin monkeys: groups are cohesive during all activities and subordinate individuals are well integrated (albeit may be excluded form favourable food sources); male dominance hierarchy is despotic and the dominant male monopolizes most reproductive activity, due to female choice (Fragaszy et al., 2004; Izar et al., 2012). Male–male relationships between groups are usually aggressive (Verderane, 2010). In FBV, mating might occur throughout the year and most births occur from October to May, with a peak between November and January, the middle of the rainy season (Izar and Fragaszy, unpublished data).

This study aimed at verifying whether hierarchy stability and dominance rank were related to: (1) frequency of agonistic interactions among males; (2) faecal testosterone metabolites levels, and (3) faecal cortisol metabolites levels. According to the Challenge Hypothesis (Wingfield et al., 1990) and rank-based predictions (Sapolsky, 1993), we expected that (1) males would have higher testosterone and cortisol levels in the unstable hierarchy than in the stable one, because agonistic interactions would be more frequent in the unstable group; (2) dominant males would have higher testosterone and cortisol levels than subordinates only in the unstable hierarchy, because dominants would have to aggressively keep their position while in the stable hierarchy aggressive competition would be formalized (Verderane et al., 2013; Fragaszy et al., 2004); and (3) subordinates from the stable hierarchy would have higher cortisol levels than dominants because they are deprived from desirable resources (e.g. food and females; Fragaszy et al., 2004).

2. Methods

2.1. Study site

This study was conducted at FBV, a flat open woodland located in the ecotone between Caatinga and Cerrado in the state of Piauí, northeast Brazil (9°39′ S, 45°25′ W), between January 2009 and December 2010. Vegetation presents areas of shrubs, xerophytic, and palm trees are very abundant in the open woodland (Visalberghi et al., 2007). Rainfall is seasonally distributed, with a clear dry season from May to September and a wet season concentrated from October to April (Verderane et al., 2013). In spite of the marked dry season, food abundance is high throughout the year, and the monkeys' diet consists mainly of fruits and insects. Besides these, the subjects often feed on leaves, flowers and small vertebrates (Spagnoletti et al., 2012; Izar et al., 2012).

2.2. Study groups

The two wild groups (CH and ZA) of bearded tufted capuchin monkeys (*S. libidinosus*) had been studied by the Ethocebus research group since 2006 (Izar et al., 2012) and were therefore habituated to the researchers presence and individually recognized. During this study, CH group size ranged from 17 to 20 individuals: four adult males, five adult females, eight juveniles (two females and six males) and five infants. One of the adult males (CHam0) died due to unknown causes at the beginning of the study and his data were not included here. The other three adult males in this group (CHam1, CHam2, CHam3) participated in an intragroup agonistic conflict, from June to August 2010, that resulted in a takeover of the dominant position. This occurred in the following sequence. Immediately after the death of the former alpha male (CHam0), in October 2008, CHam1 assumed the dominant position until June 2010. In June 2010, he was attacked by CHam3 and during the following months CHam3 and CHam2 engaged in several agonistic conflicts that led CHam2 to assume the dominant position in August 2010. Therefore, CH was considered the unstable hierarchy group. This group was studied for a total of 1331 h and 222 faecal samples from males (see Supplementary Table 1 for more details) were collected and analyzed.

Supplementary Table 1 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.09.010.

Group size of ZA ranged from 15 to 19 individuals: four adult males, four adult females, six juveniles (three females and three males), and six infants. ZAam1 had been the alpha male in this group since its habituation by the Ethocebus research team in 2006 and continued to be so during this study. Two of the other adult males (ZAam2 – immigrated in March 2009 and ZAam3 – immigrated in October 2008) were in the group since the beginning of this study and another (ZAam4) immigrated into the group in July 2010. Therefore, ZA was considered the stable hierarchy group. The group was studied for a total of 732 h and 65 faecal samples from males (see Supplementary Table 2 for more details) were collected and analyzed.

Supplementary Table 2 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.09.010.

2.3. Behavioural data collection and analyses

Data were collected monthly, five consecutive days for each group, whenever we could find the group (CH was not found in

[3] Fazenda Boa Vista.