

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

Olívia Mendonça-Furtado^{a,*}, Mariana Edaes^a, Rupert Palme^b, Agatha Rodrigues^c, José Siqueira^a, Patrícia Izar^a

^a Institute of Psychology, University of São Paulo, Av. Prof. Mello Moraes, 1721, CEP 05508-030 São Paulo, Brazil

^b Institute of Medical Biochemistry, University of Veterinary Medicine, Veterinärplatz 1, 1210 Vienna, Austria

^c Institute of Mathematics and Statistics, University of São Paulo, Rua do Matão, 1010, CEP 05508-090 São Paulo, Brazil

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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 (FTM¹) and cortisol (FCM²) 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.

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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 (Cowlshaw and Dunbar, 1991; Gogarten and Koenig, 2013). However, in unstable hierarchies males generally engage in agonistic interactions in order to monopolize estrus females (Cowlshaw 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).

* Corresponding author. Tel.: +55 11 3091 0022.

E-mail addresses: olimendonca@gmail.com (O. Mendonça-Furtado), edaes.mariana@gmail.com (M. Edaes), Rupert.Palme@vetmeduni.ac.at (R. Palme), agatha.srodrigues@gmail.com (A. Rodrigues), siqueira@usp.br (J. Siqueira), patrizar@usp.br (P. Izar).

¹ Fecal testosterone metabolites.

² Fecal cortisol metabolites.

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 (FBV³), 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 from 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 intra-group 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.

February and March/2009 and ZA was not found from January to April/2010 and in August/2010), between January 2009 and December 2010. We used the scan sampling method (Altmann, 1974) of 1 min at 5 min intervals, and we also recorded all occurrences of agonistic behaviours (vocalizations, intra-group conflicts; for details on observation conditions, see Izar et al., 2012). Actor and recipient were specified whenever possible. Observations were made by OMF and two field assistants trained by the Ethocebus researchers until inter-observer reliability reached 85% (see Verderane et al., 2013 for details).

Behavioural data were used to calculate: (1) monthly rate of agonism directed towards any group member from each adult male (directed rate); (2) monthly rate of agonism received from any group member by each adult male (received rate). To calculate rates we divided the monthly agonistic events of each subject by the monthly hours the group was observed. Agonistic interactions were used to calculate rank using the Dominance Direct Tree method (Izar et al., 2006; for more details see Section 2.5).

2.4. Faeces collection and analyses

To evaluate the endocrine status of each individual male a non-invasive method was applied (Sheriff et al., 2011). Faeces were collected opportunistically, only when it was possible to identify which individual produced it, depending on the presence and visualization of the subjects. For this reason, hormone data were not collected on a regular basis and a GzLMM⁴ test (for more details see Section 2.6) was used to deal with missing data. Medians were used instead of means because data were not normally distributed.

A total of 287 samples was collected: 84 from CHam1, 86 from CHam2, 52 from CHam3, 34 from ZAam1, 11 from ZAam2, 15 from ZAam3 and 5 from ZAam4 (see Supplementary Tables 1 and 2 for more details). Faeces were placed in eppendorf tubes and stored on ice until the arrival at the camp lab, where they were stored at -20°C .

Faecal metabolites were extracted according to the methanol-based protocol given in Palme et al. (2013). Briefly, a 0.2 g aliquot of each homogenized wet sample was mixture in a multivortex for 30 min with 2 mL of 80% methanol. The suspension was centrifuged at $1950 \times G$ for 10 min. The supernatant was stored at -20°C until assayed. Faecal hormone metabolites were measured in a 50 μL aliquot of the extract (diluted 1:100) with a cortisol and testosterone enzyme immunoassay (EIA). Details of the two EIAs including cross-reactions have been previously described (Palme and Möstl, 1997; Bauer et al., 2008). The cortisol EIA proved suited for monitoring adrenocortical activity in several primate species (Heistermann et al., 2006), and was successfully validated by an ACTH test in this species, too (Mendonça-Furtado, 2012). A lack of a correlation between FCM and FTM following the ACTH test (no increase in FTM) indicated that the testosterone EIA (measuring androgen metabolites with a 17β -hydroxy group) picked up metabolites of testicular origin (Möhle et al., 2002). All intra- and inter-assay coefficients of variation of pool samples were less than 12%. All samples were assayed in duplicate. Concentrations of hormone metabolites are expressed as nanogram per gram of wet faecal matter.

2.5. Dominance trees

To determine the rank of each male within each group, we analyzed dominance relations using the Dominance Direct Tree (DiTree), a method that (1) decides the dominance relationship

between each pair of individuals based on the number of victories in conflicts, and (2) resolves tied relationships applying the transitivity property to the dominance matrix of observed agonistic relations (Izar et al., 2006). For the unstable group, study length was divided into three periods: pre-conflict (January 2009–March 2010), conflict (April–August 2010) and post-conflict (September–December 2010). We conducted one dominance analysis for each period. In the conflict period, behaviours of females (grooming, proceptive behaviour and copulations) were analyzed along with the dominance trees to help solve circular (tied) agonistic relations. For the stable group, we considered the entire study period for one dominance analysis, since there was no rank reversal. For dominance analyses, infants were excluded.

2.6. Statistical analysis

To verify whether aggression rates differed according to hierarchy stability, we performed a GzLMM with monthly rates of agonism (sum of directed and received) as the dependent variable, month as within-subject factor, subject as random factor and group as fixed factor. Because there was a sharp drop on agonistic interactions in the unstable group during the post-conflict period (several months with zero aggression, Fig. 1), jeopardizing the statistical analysis, we excluded the last four months of aggression data of both groups (CH and ZA) to perform the analysis.

Hormone levels data contained outliers. Biologically these outliers stand for a hormone response to an event, and do not represent experimental errors. Therefore we used two kinds of basic statistics: (1) monthly medians were calculated for each subject after outliers were iteratively removed to avoid dragging median levels up; and (2) highest monthly value of each individual (peak values) were calculated keeping the outliers. These were calculated only for months with more than one sample per individual and for both cortisol and testosterone metabolites.

In a first GzLMM analysis, considering male dominance rank order as a fixed factor, we found no ordinal relation between variation of hormone levels and dominance rank. Rather, when there was an effect of rank, significant results pointed either to individual variation among subjects or to an effect of the dominant position versus subordinates. Therefore, we conducted further analyses considering "Status", where subjects were dichotomously classified as dominant (for male ranking 1) or subordinate (for males ranking 2–4).

We did not conduct analyses comparing mating versus non-mating periods because in FBV there is no marked mating period (see Supplementary Tables 1 and 2 for more details). In addition, preliminary analyses showed no influence of presence of proceptive females on hormone levels of males in both groups.

Therefore, we performed a generalized linear mixed model (GzLMM) to test for correlation between median and peak values of testosterone and cortisol metabolites with (1) status (dominant vs. subordinate), (2) hierarchy stability (stable vs. unstable), and (3) the three periods of conflict (only for the unstable group, because preliminary analyses showed hormone levels of males from the stable group did not vary across these periods). In this GzLMM model, fixed factors were status, hierarchy stability and the three periods of conflict, within-subject factor was month, subjects were considered as random factor, and subject hormone levels were the dependent variables. The correlation structure of the random effect was the component of variance. All analyses were performed with IBM SPSS Statistics 20 software.

3. Results

3.1. Aggression rates

Excluding the post-conflict period, hierarchy stability was a predictor of monthly rates of aggression (GzLMM, $F = 4.713$, $p = 0.032$;

⁴ Generalized linear mixed model.

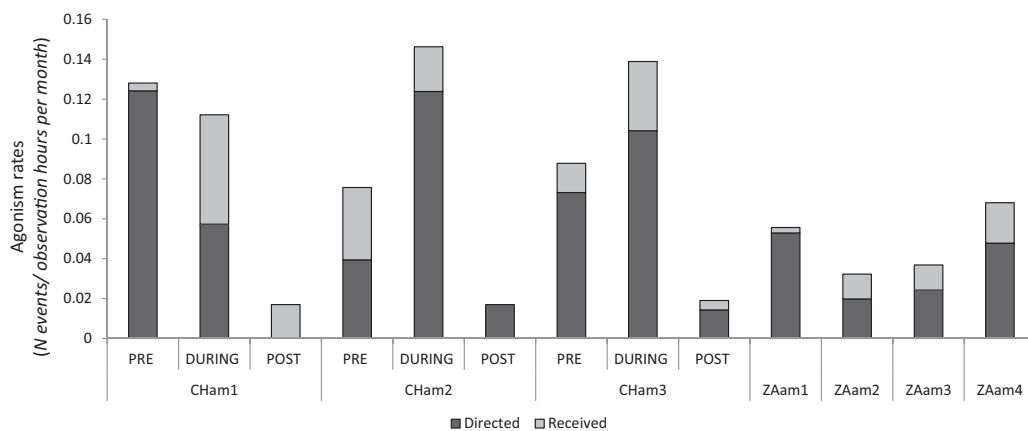


Fig. 1. Aggression rates (directed and received) of adult males (am) from two groups of *S. libidinosus* (CH – unstable hierarchy; ZA – stable hierarchy). Rates were calculated dividing the monthly agonistic events of each subject by the monthly hours the group was observed. For males from CH group, rates were divided into three periods: pre, during and post conflict. CHam1: alpha male on the pre-conflict period; CHam2: alpha male in both during and post conflict periods; CHam3: subordinate male on the three periods. On ZA group, ZAam1 was the dominant and ZAam2, ZAam3 and ZAam4 were subordinates throughout the study.

Fig. 1): rate of aggression was higher in the unstable group (mean = $0.07 \pm \text{CI } 0.014$ events/observation hours) than in the stable group (mean = $0.047 \pm \text{CI } 0.016$ events/observation hours).

3.2. Dominance relations

In the unstable group, during the pre-conflict period, dominance hierarchy was linear and CHam1 was the alpha male (Table 1, see also Supplementary Fig. 1). During the conflict period, agonistic relationships between males were tied, so dominance rank among them could not be determined. DiTrees along with behaviour of females indicated that CHam2 was the dominant male, since he was the individual that received most grooming, proceptive behaviour and was the male that copulated the most. After the conflict period dominance hierarchy became partial (i.e. not all individuals were part of the dominance structure; Izar et al., 2006), frequency of agonistic interactions was much lower than before, and DiTrees indicated that CHam2 consolidated his dominant position until the end of the study period.

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

In the stable group, dominance hierarchy was linear and ZAam1 was the dominant male during the whole study period (Table 1, see also Supplementary Fig. 1).

Table 1

Male hierarchical structure of two groups of *S. libidinosus*: unstable hierarchy CH (pre – pre-conflict period; during – during conflict period; post – post-conflict period) and stable hierarchy ZA. Subjects were identified by group initials (CH and ZA), age (a = adult), gender (m = male), and a subject number. Subject status was determined as dominate (dom) or subordinate (sub), and numbers stand for subordinate position on the hierarchy. CHam3 was not seen during the post conflict period. Although DiTree analysis considered all group members, in order to facilitate visualization, here we show only dominance relationships among adult males.

Subjects	CH		
	Pre	During	Post
CHam1	dom	sub	sub
CHam2	sub2	dom	dom
CHam3	sub1	sub	–
Subjects	ZA		
ZAam1	dom		
ZAam2	sub1		
ZAam3	sub2		
ZAam4	sub1		

3.3. Faecal testosterone metabolites

Hierarchy stability was a predictor of monthly FTM median (GzLMM, $F = 4.100$, $p = 0.047$); males from the unstable hierarchy had higher median FTM levels than males from the stable hierarchy (mean_{unstable} = $216 \pm \text{CI } 87$ ng/g; mean_{stable} = $63 \pm \text{CI } 123$ ng/g). Status was not a predictor of monthly median testosterone (GzLMM, $F = 2.349$, $p = 0.13$), as well as the interaction between status and hierarchy (GzLMM, $F = 1.912$, $p = 0.172$). Although in the unstable hierarchy dominant males clearly had higher FTM levels than subordinates did (mean_{dominant} = $198 \pm \text{CI } 110$ ng/g; mean_{subordinates} = $82 \pm \text{CI } 104$ ng/g; Fig. 2), there was an overlap in the confidence interval of the means of those groups that probably lead to the lack of effect regarding status and FTM monthly medians.

Both hierarchy (GzLMM, $F = 8.833$, $p = 0.004$) and status (GzLMM, $F = 5.658$, $p = 0.02$) were predictors of maximum FTM levels (peaks), and there was an interaction between those variables (GzLMM, $F = 4.080$, $p = 0.048$). In the stable hierarchy FTM peaks were lower than the in the unstable hierarchy, but only in the unstable hierarchy dominant males had higher FTM peaks (mean = $1275 \pm \text{CI } 388$ ng/g) than subordinate males. Furthermore, dominant and subordinate males from the stable hierarchy and subordinates from the unstable one did not differ (mean peaks_{subordinate/unstable} = $303 \pm \text{CI } 332$ ng/g; mean peaks_{dominant/stable} = $171 \pm \text{CI } 510$ ng/g; mean peaks_{subordinate/stable} = $92 \pm \text{CI } 510$ ng/g; Fig. 3).

When analysing the periods that the unstable group went through, the interaction between status and periods was a predictor of the median FTM levels (GzLMM, $F = 3.809$, $p = 0.031$). During the conflict period, the dominant males had higher median FTM levels (mean = $858 \pm \text{CI } 251$ ng/g) than dominant males in the pre- and post-conflict period and subordinate males in all periods. Moreover, dominant males in the pre- and post-period and subordinate males in all periods did not differ in their median FTM levels (mean_{dominant/pre} = $172 \pm \text{CI } 177$ ng/g; mean_{dominant/post} = $49 \pm \text{CI } 280$ ng/g; mean_{subordinate/pre} = $47 \pm \text{CI } 155$ ng/g; mean_{subordinate/during} = $261 \pm \text{CI } 212$ ng/g; mean_{subordinate/post} = $53 \pm \text{CI } 229$ ng/g; Fig. 4).

Still in the unstable group, the interaction between status and periods was not a predictor of FTM peaks (GzLMM, $F = 1.933$, $p = 0.158$). On the other hand status (GzLMM, $F = 9.321$, $p = 0.004$) and periods (GzLMM, $F = 6.965$, $p = 0.003$) were predictors of FTM peaks. Disregarding periods dominant males (mean = $1230 \pm \text{CI } 452$ ng/g) had higher FTM peaks than subordinates (mean = $339 \pm \text{CI } 379$ ng/g). Disregarding status, during the conflicts, males had higher FTM peaks (mean = $1558 \pm \text{CI } 536$ ng/g) than in the

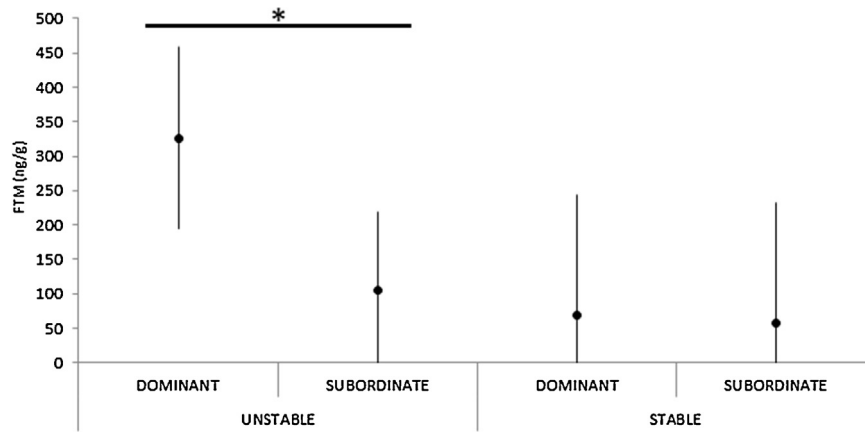


Fig. 2. Means (\pm CI) of monthly median FTM levels of adult males of two groups of *S. libidinosus* (CH – unstable hierarchy; ZA – stable hierarchy), categorized by status. Total samples: $N = 67$ ($N_{\text{unstable/dominants}} = 19$; $N_{\text{unstable/subordinates}} = 26$; $N_{\text{stable/dominant}} = 11$; $N_{\text{stable/subordinates}} = 11$). *Significantly different FTM data ($p < 0.05$).

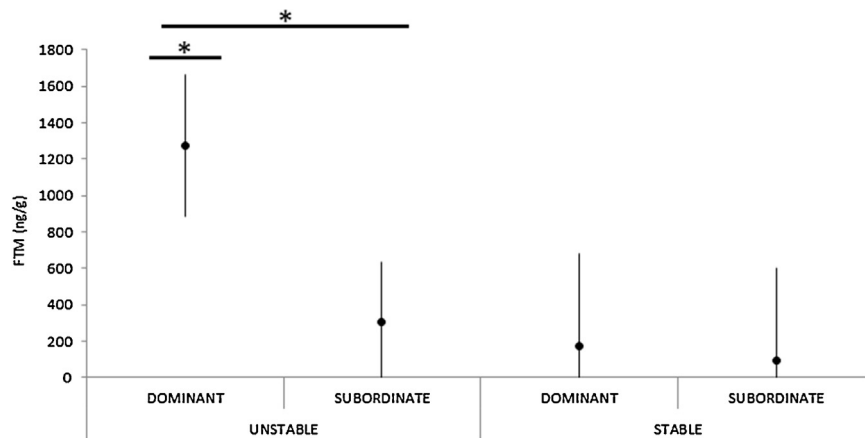


Fig. 3. Mean (mean \pm CI) FTM peak levels of two groups of *S. libidinosus* (CH – unstable hierarchy; ZA – stable hierarchy), categorized by status. Total samples: $N = 67$ ($N_{\text{unstable/dominants}} = 19$; $N_{\text{unstable/subordinates}} = 26$; $N_{\text{stable/dominant}} = 11$; $N_{\text{stable/subordinates}} = 11$). *Significantly different FTM data ($p < 0.05$).

pre- (mean = $663 \pm$ CI 385 ng/g) and the post (mean = $133 \pm$ CI 590 ng/g)-conflict periods (Fig. 5).

3.4. Faecal cortisol metabolites

Status was a predictor of both monthly FCM medians (GzLMM, $F = 9.247$, $p = 0.003$) and maximum (peak) FCM

levels (GzLMM, $F = 18.986$, $p < 0.0001$). Dominant males had higher monthly FCM medians (mean = $6981 \pm$ CI 2168 ng/g) and higher FCM peaks (mean = $16,613 \pm$ CI 4072 ng/g) than subordinates (mean_{FCMmedian} = $2432 \pm$ CI 2058 ng/g; mean_{FCMmaximum} = $4370 \pm$ CI 3866 ng/g; Fig. 6).

Both hierarchy and the interaction between hierarchy and status were neither predictors of the monthly FCM medians

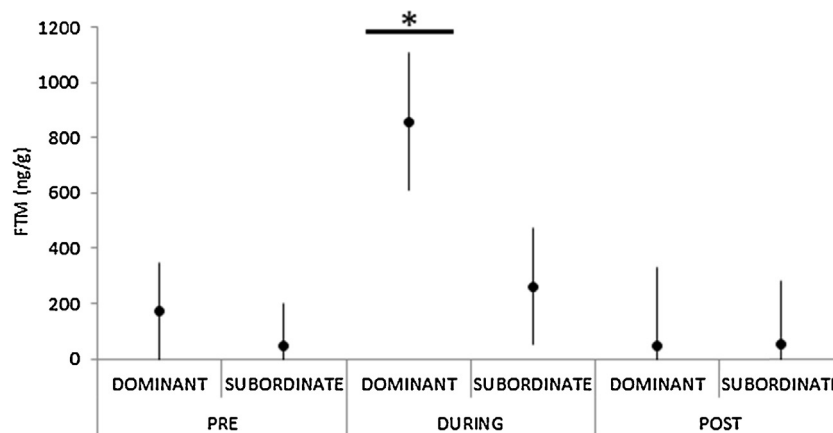


Fig. 4. Means (\pm CI) of monthly median FTM levels of males from the unstable hierarchy group (CH) of *S. libidinosus* in the three periods the group went through: pre, during and post conflict, categorized by status. Total samples: $N = 45$ ($N_{\text{dominants}} = 19$; $N_{\text{subordinates}} = 26$). *Significantly different FTM data ($p < 0.05$).

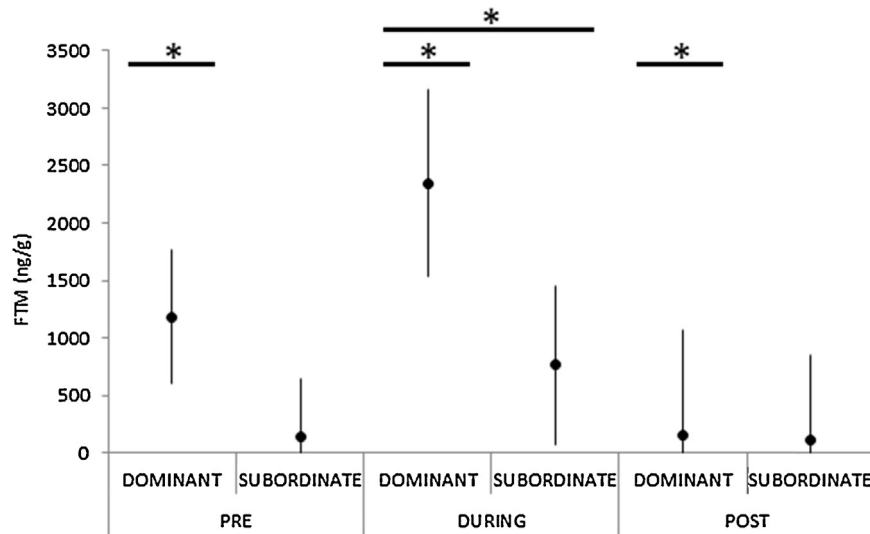


Fig. 5. Mean (mean \pm CI) FTM peak levels of males from the unstable hierarchy group (CH) of *S. libidinosus* in the three periods the group went through: pre, during and post conflict, categorized by status. Total samples: $N = 45$ ($N_{\text{dominants}} = 19$; $N_{\text{subordinates}} = 26$). *Significantly different FTM data ($p < 0.05$).

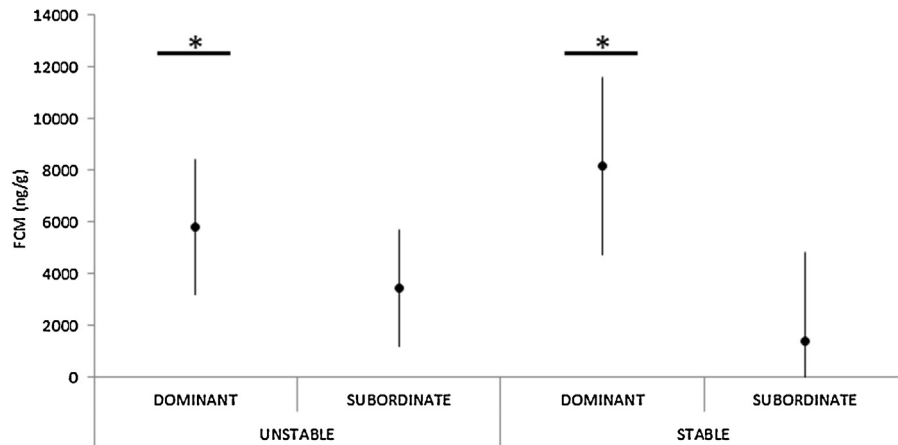


Fig. 6. Means (\pm CI) of monthly median FCM levels of two groups of *S. libidinosus* (CH – unstable hierarchy; ZA – stable hierarchy), categorized by status. Total samples: $N = 67$ ($N_{\text{unstable/dominants}} = 19$; $N_{\text{unstable/subordinates}} = 26$; $N_{\text{stable/dominant}} = 11$; $N_{\text{stable/subordinates}} = 11$). *Significantly different FCM data ($p < 0.05$).

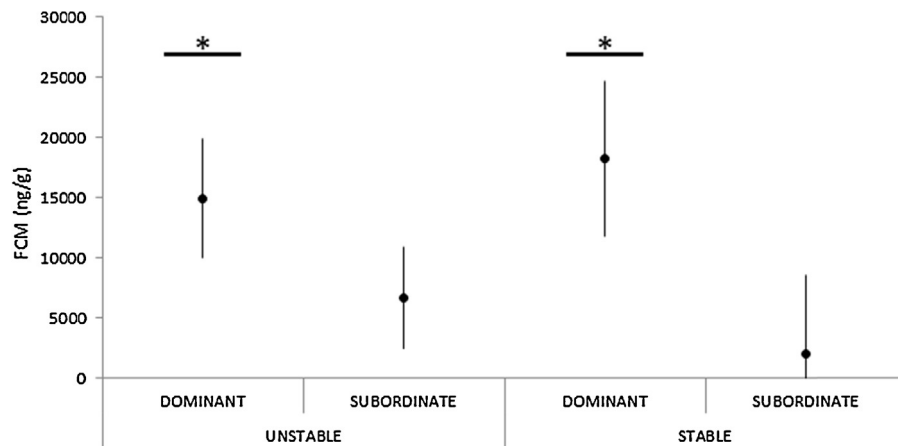


Fig. 7. Mean (mean \pm CI) FCM peak levels of two groups of *S. libidinosus* (CH – unstable hierarchy; ZA – stable hierarchy), categorized by status. Total samples: $N = 67$ ($N_{\text{unstable/dominants}} = 19$; $N_{\text{unstable/subordinates}} = 26$; $N_{\text{stable/dominant}} = 11$; $N_{\text{stable/subordinates}} = 11$). *Significantly different FCM data ($p < 0.05$).

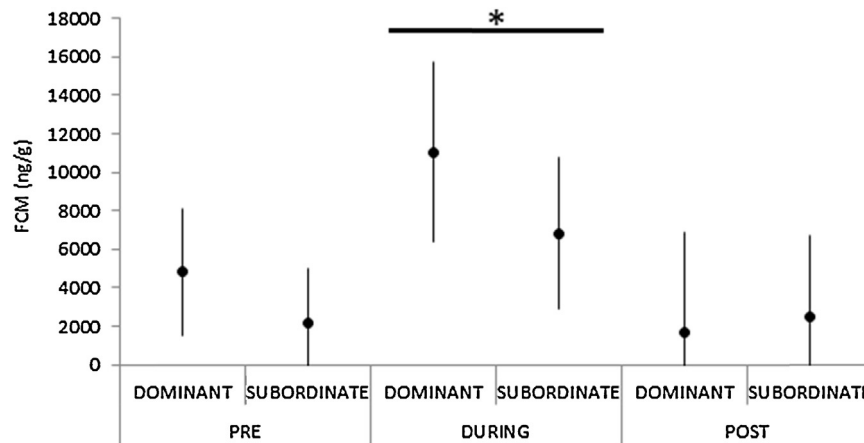


Fig. 8. Means (\pm CI) of monthly median FCM levels of males from the unstable hierarchy group (CH) of *S. libidinosus* in the three periods the group went through: pre, during and post conflict, categorized by status. Total samples: $N=45$ ($N_{\text{dominants}}=19$; $N_{\text{subordinates}}=26$). *Significantly different FCM data ($p < 0.05$).

(hierarchy – GzLMM, $F=0.011$, $p=0.917$; hierarchy \times status – GzLMM, $F=2.181$, $p=0.145$) nor the maximum FCM levels (hierarchy – GzLMM, $F=0.055$, $p=0.815$; hierarchy \times status – GzLMM, $F=1.978$, $p=0.165$; Fig. 7).

Considering only the unstable group, period of conflict was a predictor of median FCM levels (GzLMM, $F=5.798$, $p=0.006$). During the conflict period males had higher median FCM levels (mean = $8917 \pm \text{CI } 3050$ ng/g) than in the pre- (mean = $3475 \pm \text{CI } 2191$ ng/g) and post (mean = $2066 \pm \text{CI } 3363$ ng/g)-conflict periods. Status (GzLMM, $F=1.528$, $p=0.224$) and the interaction between status and period (GzLMM, $F=0.652$, $p=0.526$) were not predictors of median FCM levels. Although in the unstable group dominant males had higher FCM levels than subordinates during the pre-conflict and conflict periods (Fig. 8), there was an overlap in the confidence interval of the means that probably lead to the lack of effect regarding status and FCM across the entire study period.

Still in the unstable group, both status (GzLMM, $F=5.867$, $p=0.02$) and period (GzLMM, $F=6.21$, $p=0.005$) were predictors of maximum FCM levels (peaks). Dominants (mean = $14,526 \pm \text{CI } 4666$ ng/g) had higher FCM peaks than subordinates (mean = $7234 \pm \text{CI } 3911$ ng/g). The interaction between status and period (GzLMM, $F=1.677$, $p=0.2$) was not a predictor of maximum FCM levels. However, during the conflict period

(mean = $18,489 \pm \text{CI } 5526$ ng/g) males had higher FCM peaks when compared to the pre- (mean = $9326 \pm \text{CI } 3970$ ng/g) and post (mean = $4825 \pm \text{CI } 6092$ ng/g)-conflict periods (Fig. 9).

4. Discussion

In this study, we presented a behaviourally and physiologically documented rank reversal in a group of bearded capuchin monkeys. With the help of non-invasive sampling methods (faecal hormone metabolites levels), we analyzed this event in the light of the hypothesized relationship between male dominance status and hierarchy stability, and levels of testosterone and cortisol of males.

The first hypothesis that in a stable hierarchy, with formal dominance relationships, direct competition is resolved without costly overt aggression (Bernstein, 1981) was supported by the results: aggression rates were higher in the unstable hierarchy group than in the stable group. We also observed that the intensity of aggression in the conflict period of the unstable group was much greater than in the other periods, and greater than in the stable group, including not only threats but also fierce physical combats. In fact, as a result of one of the fights between CHam1 and CHam3, CHam1 lost his right foot and CHam3 had a severe cut in his inferior lip.

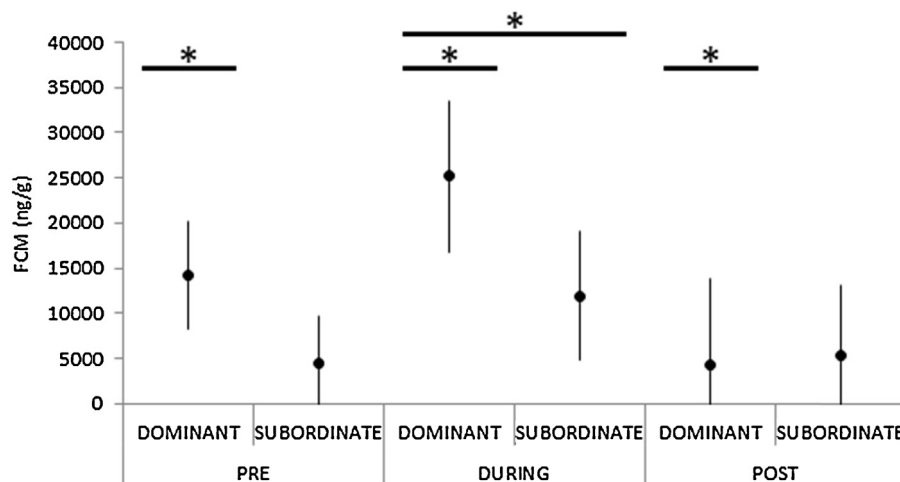


Fig. 9. Mean (mean \pm CI) FCM peak levels of males from the unstable hierarchy group (CH) of *S. libidinosus* in the three periods the group went through: pre, during and post conflict, categorized by status. Total samples: $N=45$ ($N_{\text{dominants}}=19$; $N_{\text{subordinates}}=26$). *Significantly different FCM data ($p < 0.05$).

These observations contrast with the general pattern of low intensity aggression found in captive and wild capuchin monkeys (*Cebus* and *Sapajus*, Fragaszy et al., 2004; Lynch et al., 2002), but is similar to the injuries suffered by a dominant male during a rank reversal in *C. capucinus* (Perry, 1998), what is further evidence that dominance hierarchy lowers the risk of injuries.

The second hypothesis was that hierarchy stability and status would affect testosterone levels of males in *S. libidinosus*. The prediction that males in an unstable hierarchy would have higher FTM than males in a stable hierarchy due to the higher rate of aggressive interactions was confirmed for both median and peak testosterone levels. This result is in accordance with the Challenge Hypothesis that predicts an increase in testosterone levels when males face social instabilities, as well as reproductive challenges (Goymann et al., 2007). Because in tufted capuchin monkeys reproductive success is strongly skewed towards the dominant male due to female choice (Izar et al., 2009, 2012), fights for rank acquisition might be considered ultimately related to competition for reproduction. Our findings for *S. libidinosus* are in accordance with several studies on cercopithecoids (e.g. Teichroeb and Sicotte, 2008) but differ from a previous study with the sister species *S. nigritus*, for which the only correlate of testosterone increase was female proceptive behaviour, but not male–male aggression related to female monopolization (Lynch et al., 2002). We suggest that in capuchin monkeys testosterone levels increase only at times of male–male aggression in the context of rank acquisition (instability in the hierarchy), and not in the context of direct competition for receptive females.

The prediction that status would affect testosterone levels only in the unstable hierarchy was also confirmed. Indeed the dominants from the unstable group had higher peak levels than subordinates, and the dominant male of the stable group had similar values as subordinate males (of both groups). The fact that dominants only had their testosterone levels elevated in the unstable hierarchy might be related to their directed aggressive interactions rate which was higher than those of subordinates (see Fig. 1) (Sapolsky, 1993). For example, in Assamese macaques (*Macaca assamensis*) testosterone levels were associated with higher directed aggression and rank acquisition (Ostner et al., 2011), and in chimpanzees (*Pan troglodytes*), lower testosterone levels were related to strong aggression received (Klinkova et al., 2004). In addition, the results from the post-conflict period (possibly a stable phase for the unstable group) and from the stable hierarchy (ZA) show that when aggression rates are lower, median testosterone is low and similar in both dominant and subordinates.

Results for *S. libidinosus* once again differ from the previous study with *S. nigritus* (Lynch et al., 2002), where dominant and subordinate males had similar testosterone levels. The authors hypothesized that this lack of difference could be due to the short dominant tenure, since a dominance take-over had happened just before the beginning of their study. Our results suggest otherwise that the lack of difference could be a consequence of hierarchy stability and the reported low agonism rates (Lynch et al., 2002) already reached.

Findings for *S. libidinosus* also differ from findings for *C. capucinus*, a closely related capuchin species in which dominant males always have higher testosterone levels than subordinates (Schoof and Jack, 2013; Jack et al., 2014), even when dominance is achieved through a non-aggressive rank reversal (Schoof et al., 2012). We suggest that this difference between species could be related to the short male tenure in *C. capucinus* (Jack and Fedigan, 2004) when compared to *Sapajus* (Izar et al., 2009). Physiologically, *C. capucinus* would respond as if they were permanently in an unstable condition, and therefore dominants would maintain their testosterone levels higher all the time (Schoof and Jack, 2013). More studies are necessary to

address factors related to interspecific differences in capuchin monkeys.

The hypothesis that hierarchy stability and status would affect cortisol levels of males in *S. libidinosus* was partially confirmed. We predicted that: (1) males from the unstable hierarchy would have higher cortisol levels than males from the stable hierarchy; (2) dominant males from the unstable hierarchy would have higher cortisol levels than subordinates from the same hierarchy; and (3) subordinate males from the stable hierarchy would have higher cortisol levels than dominants from the same hierarchy. Results supported only the second prediction. Although in the unstable group there was an increase in cortisol levels of males during the conflict period, there was no difference in cortisol levels of males from stable and unstable hierarchies. Overall results suggest dominants carry a larger allostatic load than subordinates regardless of hierarchy stability. Only during the post-conflict period in the unstable group dominant and subordinate males had similar cortisol levels. This result was probably due to the severe injuries suffered by the two subordinate males (see description in Section 2.2).

Goymann and Wingfield (2004), using data from Lynch et al. (2002) on *S. nigritus* showing no effect of status on male cortisol levels, suggested that in the genus *Sapajus* dominant and subordinate males would not differ in their allostatic load. In contrast to that, our results indicate that alpha males of *S. libidinosus* had higher allostatic load than subordinates. This is consistent with the central role dominant males of *Sapajus* occupy within the group (e.g. group protection against predators [Izar, 2004], elevated vigilance and alert behaviour [Hirsch, 2002], protection of food sources from other groups or species [Janson, 1984; Verderane, 2010], to control of intra-group conflicts [Ferreira et al., 2006]). Higher cortisol levels in dominant than in subordinate males was observed in other primate species such as white-faced capuchins (*C. capucinus*; Schoof et al., 2012), chimpanzees (*P. troglodytes schweinfurthii*; Muller and Wrangham, 2004), cynomolgus monkeys (*Macaca fascicularis*; Czoty et al., 2009), and Verreaux's sifakas (*Propithecus verreauxi*; Fichtel et al., 2007). However other species show an opposite pattern (olive baboons [*Papio anubis*], Sapolsky, 1982; squirrel monkeys [*Saimiri sciureus*], Manogue et al., 1975; talapoin monkey [*Miopithecus talapoin*], Eberhart et al., 1983; mandrill [*Mandrillus sphinx*], Setchell et al., 2010). These diverse findings in many distant clades, with a wide diversity of social features, support the idea that differences in cortisol levels between dominants and subordinates not only vary according to social systems exhibited by each species or population, but depend on the dominant/subordinate allostatic load ratio (Abbott et al., 2003; Goymann and Wingfield, 2004; Gesquiere et al., 2011). In addition, the dominant male allostatic load might vary between populations in relation to ecological features such as distribution of food resources and predation risk. Therefore environmental differences between *S. nigritus* and *S. libidinosus* habitat could account for different results reported here and by Lynch et al. (2002). Finally, because both studies report data from a few dominant males, another possible explanation for the difference in results is the influence of personality modulating physiological profiles of dominant males (Sapolsky, 2011).

Summing up, in the unstable group, all males had an increase in both FCM and FTM levels during the conflict period. The elevation of both hormones at the same time may indicate that in unstable periods, *Sapajus* males are less vulnerable to testosterone suppression by cortisol or may have a higher secretion of the first one (Sapolsky, 2011). This same pattern was observed in the black horned capuchin monkeys (Lynch et al., 2002), as well as in many other species (Sapolsky, 2005) when there is male–male competition during the mating season. Our findings are in accordance with this framework, because the conflict period involved fighting for the dominant position and indirectly for female access.

5. Conclusion

Our results provide support for hypotheses in the literature regarding both testosterone and cortisol levels. The relation between testosterone and aggression predicted by the Challenge Hypothesis (Wingfield et al., 1990) was corroborated by our results. Rank-based predictions on testosterone levels (Sapolsky, 1993) were also confirmed. Our data support the idea that variation in cortisol levels is also closely related to specific features of social structure (Abbott et al., 2003; Goymann and Wingfield, 2004; Sapolsky, 2005) and add that in *Sapajus libidinosus*, the allostatic load of dominants is higher than that of subordinates, even in a stable hierarchy. Finally, this is the first study to compare hormone profiles of two groups of Neotropical primates from the same population varying in hierarchy stability, including a male rank reversal. This is a rare event in the wild, especially in the genus *Sapajus* (Carosi et al., 2005), and the fact that we were able to track the hormone changes during this transition provides breakthrough knowledge to understand how the physiological profile responds to changes in social system.

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