Social correlates of variation in urinary cortisol in wild male bonobos (*Pan paniscus*)

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ABSTRACT

Cortisol excretion in males of group living species is often associated with social rank and competition for oestrous females. Rank-related patterns of cortisol levels can be used to study mechanisms of rank mainte-nance and costs associated with mate competition. Bonobos (*Pan paniscus*) are interesting because males form a linear dominance hierarchy but are not dominant over females and therefore aggressive male–male competition over access to females alone is not considered to be a successful reproductive strategy. In this study on social correlates of urinary cortisol in wild male bonobos, we investigated the relationship between cortisol levels and several aspects of mate competition, including male rank, aggression rates, and association time with oestrous females. We found that cortisol levels correlated positively with dominance rank when oestrous females were present, but not when they were absent. This result is consistent with the idea that ag-gressive behaviour plays a minor role in maintenance of high rank. While aggression received from males and females explained within-individual variation in cortisol levels, it was the time spent in association with oestrous females that best explained between-individual variation in male cortisol levels. The observed increase in male cortisol may be associated with spatial proximity to oestrous females and could result from anticipated aggres-sion from other group members, reduced feeding time in the males, or a combination of both.

Introduction

In males of group living species, competition for mates often leads to the establishment of dominance hierarchies in which individuals differ in their access to females as well as in other parameters such as exposure to stress. Cortisol is one hormone that fluctuates in re-sponse to stress and is easily detectable in non-invasively collected samples such as urine and faeces. Therefore, measurements of cortisol levels have become a well-established method for quantifying stress-responses in captive and wild animals. During the stress-response, animals respond by mobilising energy from storage sites, enhancing cardiovascular tone, and suppressing costly anabolism (McEwen and Wingfield, 2003; Wingfield and Sapolsky, 2003). While tempo-rary elevations in cortisol levels are adaptive, chronic increases may cause diseases and reproductive failure (Sapolsky, 2002) and thus have detrimental fitness consequences. Stress and related changes in cortisol levels can be caused by both environmental and social fac-tors (Wingfield and Sapolsky, 2003). Measurements of cortisol levels have been used to detect stressful events that affect groups or populations, including changes in temperature and food abundance (Sapolsky, 1986; Weingrill et al., 2004), as well as social parameters that affect single individuals, such as the costs related to the acquisi-tion and maintenance of rank (Goymann and Wingfield, 2004).

Rank-related variation in stress response

Rank-related patterns of cortisol excretion vary within and be-tween species. The physiological costs associated with different dom-inance ranks are related to the way in which dominance is achieved and maintained (Goymann and Wingfield, 2004). High rank is associ-ated with high cortisol levels when dominance rank is achieved and maintained through aggressive behaviour. In contrast, high rank is as-sociated with low cortisol levels when dominance status is formalised and not a matter of dispute. Low rank is associated with high cortisol levels when individuals are exposed to aggression and when coping mechanisms such as social support from other group members is lac-king. In contrast, low rank is associated with low cortisol levels when individuals have social support or are subject to only moderate ag-gression (Abbott et al., 2003; Goymann and Wingfield, 2004). Al-though several species do not exhibit rank-related differences in cortisol values (e.g. Goymann et al., 2003; Lynch et al., 2002; Ostner et al., 2008b), such variations are consistently seen in other species. The *costs of dominance paradigm* refers to species in which high rank is associated with high levels of aggression to maintain rank and subordinates have developed strategies to reduce their high cor-tisol levels. As a result, high-ranking males in such species have higher cortisol levels than subordinates (e.g. social carnivores: Creel, 2005; hyraxes: Koren et al., 2008; bison: Mooring et al., 2006).

The *subordinate stress paradigm* (Abbott et al., 2003) refers to spe-cies in which high-ranking individuals randomly exhibit aggressive behaviours towards subordinates, which have not developed coping

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mechanisms and therefore have elevated cortisol levels. While consistent between-species differences in stress reactivity may exist, dominance relations reflect dynamic processes and during times of rank instability, the rank-related skew in cortisol levels may disappear or shift to the reverse pattern (Bergman et al., 2005; Sapolsky, 1993; Setchell et al., 2010). Gesquiere et al. (2011) found an inverse relationship among male rank and cortisol levels in baboons, regardless of hierarchy stability. However, they also found that the alpha male deviated from this pattern in that he tended to have very high cortisol levels at all times.

Variation in male cortisol levels in the context of mate competition

In addition to rank-related patterns, male cortisol levels have been found to respond in a predictable way in the context of mate competition (Mooring et al., 2006; Ostner et al., 2008a; Sands and Creel, 2004; van der Meij et al., 2010). Changes in cortisol levels have been explained by the increased energetic demands that are associated with aggressive mate competition, the reduction in food intake due to mate guarding activities, and the psychological stress associated with changes in received and anticipated aggression. Reproductive strategies may vary with rank and mate competition may therefore result in rank-related variation in cortisol levels (Anestis, 2010). In sifakas (*Propithecus verreauxi*), dominant males have a higher elevation in cortisol levels during mate competition than subordinates and this bias is thought to reflect rank-related differences in mate guarding effort (Fichtel et al., 2007). In mandrills (*Mandrillus sphinx*), only high-ranking males engage in potentially socially and energetically costly mate guarding behaviours (Setchell et al., 2005) that are associated with increased aggression, loss of body mass, and elevated cortisol levels (Setchell and Dixson, 2001; Setchell et al., 2010). Reduced foraging activity during mate guarding is also observed in male baboons (Alberts et al., 1996) and corresponds with a temporary increase in cortisol levels (Bergman et al., 2005).

Although the induced stress response in the context of mate competition seems to be a logical consequence of temporary changes in energy allocation, reports from other species indicate that rank-related differences in mate guarding effort may not affect male cortisol levels (e.g. tufted capuchins: Lynch et al., 2002).

In conclusion, while the costs related to group living, rank acquisition, and mate guarding are usually unbalanced and may vary in predictable ways, it is obvious that there is no simple relationship between dominance rank and cortisol levels across and within taxa.

Male cortisol levels in relation to social systems in the genus Pan

The two species belonging to the genus *Pan*, *Pan paniscus* (bonobos) and *Pan troglodytes* (chimpanzees), offer an interesting model to study the relationship between mechanisms of rank acquisition, strategies of mate competition, and changes in male cortisol levels. These species share similar traits related to social organisation, including living in multi-male–multi-female groups, fission–fusion grouping patterns, and linear male dominance hierarchies (Stumpf, 2007). However, the two species differ in other traits, including inter-sexual dominance relations, rank acquisition, and the relationship between dominance rank and aggression.

In chimpanzees, males are dominant over females and individual or coalitionary male aggression plays a crucial role in rank acquisition and maintenance (Nishida, 1983). Cortisol levels follow patterns predicted by the costs of dominance paradigm. Rank-related variation in aggression and associated metabolic costs are thought to drive the cortisol response, and high-ranking males have consistently higher cortisol levels than subordinates (Muller, 2004).

In contrast, male bonobos are not consistently dominant over females (Kano, 1992). High-ranking males are more aggressive than low-ranking males, but compared to chimpanzees, physical aggression appears to be less intense (Wrangham and Peterson, 1996). Rank acquisition and maintenance may depend on social parameters such as maternal support and amicable relationships with unrelated females (Furuichi, 1997). Unlike chimpanzees, male bonobos may receive agonistic support from their mothers, and perhaps from unrelated females, but not from other males (Furuichi and Ihobe, 1994; Surbeck et al., 2011). When social support is based on kinship, such as the availability of a mother, it is not contestable and males may have strong partnerships independent of their actual position in the male dominance hierarchy. Under such circumstances, the physiological costs of group living are likely to be similar for males of different social rank, and one would predict that neither the costs of dominance paradigm nor the subordinate stress paradigm explains cortisol levels in bonobos. If the availability of social support decreases overall cortisol levels, we would predict that males with their mothers present in the community may have lower mean cortisol values than males without maternal kin.

In both species of the genus *Pan*, male dominance rank translates into mating success with oestrous females (Boesch et al., 2006; Muller and Mitani, 2005; Surbeck et al., 2011; Takahata et al., 1996). In chimpanzees, access to oestrous females depends on male aggression (Muller and Wrangham, 2004a), and in the context of mate competition, male aggression and testosterone and cortisol levels increase independently of male rank (Muller, 2002; Muller and Wrangham, 2004a). Male bonobos show a similar behavioural response in the presence of oestrous females close to conception (potentially fertile females), but not when these females are unlikely to ovulate (Surbeck et al., 2012). The differential response of male bonobos to oestrous females depending on their potential fertility may be due to the fact that females can exhibit non-conceptive swelling cycles for several years as well as during pregnancy and lactation (Furuichi and Hashimoto, 2002). Studies on captive bonobos have shown that anticipation of competition over food leads to an increase in cortisol (Hohmann et al., 2009; Wobber et al., 2010), and it is therefore reasonable to assume that cortisol levels should also increase when males compete for access to females.

In this study, we combined measurements of urinary cortisol levels with information on variables related to mate guarding and mating success such as spatial association with oestrous females as well as aggression given and received from both males and females. Specifically, we asked the following questions: (1) Are urinary cortisol levels in male bonobos correlated with dominance rank? (2) Do cortisol levels change in the presence of oestrous females, and if so, are these changes related to male rank? (3) Which correlates of mate competition in bonobos are associated with changes in cortisol?

Material and methods

Study site and subjects

Field work was conducted between May and August 2007 and December 2007 and July 2009 at the LuiKotale field site in Salonga National Park, Democratic Republic of Congo (Hohmann and Fruth, 2003b). Members of the Bompusa bonobo community were habituated to human presence from the start of the study period. During the data collection period, the community consisted of 33–35 individuals, which included five adult and four subadult males, 11 parous females, and up to five nulliparous immigrant females. Age estimates were based on physical features such as body size, dentition, and (in females) genital swellings (Furuichi et al., 1998). All community members were identified at the start of the project reported here. Although the exact ages of the males included in this study are unknown, we are confident in our assessment that all of the subadult males were at least 10 years of age, as all of these individuals were present in the community when habituation began in 2002 (see Table 1 for more information on age). Some males disappeared after this study period ended, which prevented

Table 1

Overview of data collection and cortisol levels of the individual male bonobos of the Bompusa community. Rank 1 is assigned to the top ranking individual (CA). Individual codes are written in upper case for adult males and in lower case for sub-adult males. Males with a mother in the community are marked with an asterisk (*) after their individual code. Age classification is based on estimates (see Materials and methods for more details).

Individual	Age class [years]	Rank	Observation hours (absence/presence of oestrous females)	Proximity scans (absence/presence of oestrous females)	Number of urine samples (absence/presence of oestrous females)	Average cortisol levels ± SD [ng/mg creatinine] (absence/presence of oestrous females)	Max/min cortisol levels [ng/mg creatinine]
CA*	26–35	1	466/668	337/508	20/53	64.6 ± 52.5/95.7 ± 60.1	308.95/8.2
TI*	26–35	2	434/600	314/413	19/33	40.8 ± 28.4/69.2 ± 33.8	173.79/11.5
JA	16–25	3	431/541	351/386	27/44	65.96 ± 46.50/82.16 ± 53.15	238.60/10.9
DA	>35	4	446/524	331/368	23/43	41.67 ± 20.16/56.94 ± 42.92	181.0/17.1
BE*	16–25	5	536/640	404/478	28/40	49.50 ± 36.52/54.64 ± 29.17	182.2/9.8
ap*	10–15	6	342/473	245/299	16/26	40.29 ± 26.35/47.45 ± 27.79	119.8/8.2
pn*	10–15	7	256/413	152/186	11/20	52.27 ± 33.46/68.11 ± 40.21	139.0/11.0
em*	10–15	8	323/462	200/263	20/34	57.70 ± 35.75/47.26 ± 30.30	131.4/4.5
mx	10–15	9	279/353	183/195	18/27	94.64 ± 62.60/53.06 ± 29.46	280.8/13.9

us from more precisely adjusting the age classifications. All nine males were included in this study because all engaged in competition over access to oestrous females and actively participated in dominance interactions with other males (Surbeck et al., 2011). An earlier study of the same bonobo community included the four subadult males as the youngest age category of mature males based on their sexual and social maturity (Surbeck et al., 2012). Genetic analyses conducted for another project revealed that six out of the nine males had their mothers in the group (Schubert unpublished data; see also Surbeck et al., 2011).

Behavioural observation

Parties containing males were followed from the time subjects left the nest in the morning until the time they constructed night nests in the evening. Party composition was recorded every full hour (N = 2112 scores of party composition). All instances of aggressive interactions, mating behaviours, and grooming events were recorded during party follows and during focal follows (2112 h of group follows and 470 h of focal follows) (Altmann, 1974). Focal follows lasted for 10 min and were separated for each individual by at least 1 h. At the start and end of each focal follow, the identities of individuals in proximity (within 5 m) to the focal male and the focal's activity (feeding, moving, resting, and grooming) were recorded. Focal individuals were randomly chosen from the males travelling in the same party.

Aggression refers to directed agonistic behaviours, including both contact and non-contact aggression. Branch dragging displays were not included as it was often difficult to determine whether they were directed at another individual. *Rates of giving and receiving aggression* were calculated daily for each individual. They were converted into hourly rates and were based on both records from focal follows and ad libitum observations, corrected for the time each male was present in the focal party. *Submission* refers to different forms of retreat, such as fleeing and jumping aside.

Dominance interactions

We assessed dominance relationships among male community members on the basis of dyadic interactions (Vervaecke et al., 2000). Individuals showing submission in response to aggression or to a non-aggressive approach by another individual were classified as inferior. Multiple unidirectional dominance interactions occurring within the same 10 minute period were counted as one single event.

Oestrous cycle and fertility

In species in which females exhibit genital swellings, the term "oestrous" refers to the period when *female genital swellings* are maximally tumescent (Dixson 1998). We scored genital swellings daily and distinguished between four swelling stages ranging from minimal (stage 1) to maximal (stage 4). Scores were based on firmness

of swelling (tumescence) and skin surface structure (Hohmann and Fruth, 2000). Female bonobos can exhibit non-conceptive oestrous cycles for several years and it is common for multiple female party members to show signs of oestrus at any given time (Kano, 1992). But these oestrous females are likely to vary in their probability to conceive. In order to relate changes in male behaviour and physiology to the time when females were getting closer to conception, we used 3 different approaches: (1) We compared male cortisol levels on days when oestrous females were present versus absent in the community. (2) We calculated for each day when oestrous females were present the number of months until conception of the oestrous female closest to conception, and related this variable to male cortisol levels. The conception date was estimated by subtracting from known birthdates 230 days, which is the mean gestation length in captive bonobos (Drews et al., 2010). (3) We classified oestrous females as *potentially fertile females* during the six months prior to conception and compared male cortisol levels on days when none of the oestrous females were potentially fertile with situations when at least one female was potentially fertile. This classification was done in order to compare our findings with previous data from mate competition in bonobos (Surbeck et al., 2012) and chimpanzees. Previous reports from East African chimpanzees show that parous females exhibit a mean of five swelling cycles per conception (approximately 6 months; Muller and Wrangham, 2004a).

If the mother of a given male was the only oestrous female in the community, the son was not considered to be in the presence of an oestrous female.

Urine collection

Fresh urine samples (N = 1200) were collected opportunistically from the nine males during the party follows over the entire study period. Whenever possible, we collected samples in the underside of large leaves to prevent sample contamination. This technique was tested in another study and found to produce results that were consistent with samples that had been collected directly from the urine stream (Marshall and Hohmann, 2005). If there was no leaf available, we pipetted urine from ground vegetation. To avoid cross-contamination, we only collected urine samples from vegetation if the collection area was not already contaminated by urine from another individual. Urine that had been contaminated with faeces was not collected. Within 12 h of collection, urine samples were transferred into liquid nitrogen. Urine samples were shipped frozen in liquid nitrogen to the Max Planck Institute in Leipzig, Germany, where hormone analyses were performed. Permits to export urine samples from DRC and import them into Germany were issued by the Congolese Wildlife Authority and the head veterinarian of DRC in Kinshasa. The permit for importing samples into Germany came from the head veterinarian of Saxonia/Germany.

Hormone measurements

We followed the methods described by Hauser et al. (2008a) to extract cortisol from urine samples. We used 100 μl urine for extraction and added 50 μl internal standard mixture containing prednisolone (100 pg/μl), a cortisol analogue, to later estimate extraction efficiency. We hydrolysed steroid glucuronides using β-glucuronidase from *Escherichia coli* (activity: 200 U/40 μl), and conducted a separate solvolysis to cleave off the steroid sulphates with ethyl acetate/sulphuric acid in order to avoid enzymatic conversion of androgens as described for β-glucuronidase/sulphates of *Helix pomatia* juice (Hauser et al., 2008b; Massé et al., 1989; Messeri et al., 1984; Venturelli et al., 1995).

Urinary cortisol levels were measured using liquid chromatography–tandem mass spectrometry following the protocol described in Hauser et al. (2008a). We ensured quality control of cortisol concentration measurements by adding control samples with standardised cortisol concentration to the test samples. Measurements of a batch were accepted if control sample measurements deviated less than 15% from the actual cortisol concentration. Samples that lost more than 50% of the internal standard were re-measured. The cortisol concentrations were corrected for differences in extraction efficiency, estimated by the loss of prednisolone from the internal standard. If extraction efficiency was lower than 50%, we re-extracted cortisol from the remaining urine sample. If extraction efficiency was again lower than 50%, which was the case for 3% of the samples, we used the mean value of both measurements as they never deviated from each other by more than 30%. We measured creatinine (Cr) in each sample to correct for water content in the urine (Erb et al., 1970). All hormone levels are given in ng/mg Cr and we excluded urine samples with a creatinine value lower than 0.02 mg creatinine/ml from our analysis.

Subadult males may have lower muscle mass than adult males, which would result in lower creatinine values in urine. A correction of urinary water content to calculate cortisol levels by creatinine could therefore lead to "falsely" high cortisol levels in these males. To test for differences in creatinine production between males, we selected five urine samples from each of the nine males, for a total of 45 urine samples, and tested whether the creatinine/specific density ratio differed between adult and subadult males (this ratio is the equivalent of testing for differences in creatinine levels in samples with equal levels of specific density; Anestis et al., 2009). There was no difference in creatinine/specific density ratio in adult compared to adolescent males (Mann–Whitney *U* test, $U = 5$, $p = 0.2857$, $N = 9$; See Appendix A). Accordingly, it was assumed that individual differences in cortisol levels were unlikely to have been caused by age specific differences in creatinine values.

Data analysis

Dominance rank

We determined male rank by carrying out hierarchical rank order analysis with MatMan (version MfW 1.1; earlier version described in de Vries et al., 1993) and found a highly linear dominance hierarchy among the males (Surbeck et al., 2011). During a four-month study period, the dominance relationship between two males without mothers was subject to multiple reversals before stabilising in the original rank order. This period of social instability was included as a control variable in the analysis of correlates of cortisol (see below).

Behavioural and social correlates of cortisol levels

We used Generalized Linear Mixed Models (GLMMs; Baayen, 2008) to examine the independent effects of several predictor variables on the cortisol levels of given urine samples. In the first model, we examined the effects of five predictor variables: the male's dominance rank, presence or absence of the male's mother in the community, presence or absence of oestrous females in the community during the day of sample collection, aggression rate given by the male, and aggression rate received by the male. Aggression rate given and received were incorporated as predictor variables in a way that allowed us to distinguish within- versus between-subject effects, or, in other words, to distinguish whether these daily aggression rates influenced a given individual's daily cortisol levels or whether differences between individuals in average rates of aggression can explain their differences in cortisol levels (see Appendix A; van de Pol and Wright, 2009). Because rank and individual means of aggression rates given were strongly correlated, we ran a second model with individual means of aggression rates given instead of rank as a predictor variable, and then compared the AIC indices of the two models (Bumham and Anderson, 2002). Because of the time lag between a social interaction and the corresponding change in urinary cortisol, we expected the effects of social interactions on urinary cortisol levels to become stronger over the course of the day. To control for this, we included in both models a two-way interaction of time of urine collection and the value of aggression given and aggression received, residualised against the respective individuals' mean (Bahr et al., 2000; van de Pol and Wright, 2009). To investigate the potential impact of varying numbers of oestrous females present in the community on male cortisol levels, we incorporated this parameter as a predictor variable instead of presence/absence of oestrous females in the first model and ran it only for the samples collected when at least one oestrous female was present.

To analyse whether variation in fecundity among oestrous females influenced male cortisol levels, we (1) conducted an analysis on only those samples taken when an oestrous female was present and included months to conception of the oestrous female closest to conception as a predictor variable in the model with the same variables as the first model; and (2) exchanged the absence/presence of oestrous females in the community of the first model with a categorical predictor with 3 states (i) no oestrous female present, (ii) oestrous female present but no potentially fertile female present, and (iii) potentially fertile female present.

In order to determine whether the rank effects were only the result of the different age classes having different cortisol reactivities, we performed two additional analyses: (1) we exchanged the test variable of rank in the first model with age class (1–4, treated as a quantitative predictor, see Table 1) and compared the resulting AIC values of the two models to see which one better explained the variation in cortisol levels; and (2) to analyse whether the rank-effect remained within each age class, we split the data set by age class (subadult and adult) and ran a simplified model where we included only male rank, the presence of oestrous females, and their two-way-interaction as predictor variables.

As control variables, in all models we included (a) period of rank instability, (b) seasonal effects (see Appendix A), and (c) an autocorrelation term (see Appendix A). While we are certain that there are periods that are nutritionally better for the bonobos than others, at this point we are unable to precisely quantify when these periods occurred. As a result, we have taken a statistical approach to account for the possible effects of such times and incorporated seasonal effects and an autocorrelation term. Furthermore, in all models we have included day and male identity as random effects.

We based our inference on full models (and present their results) in order to avoid false positives as well as biassed effect size estimates and p-values (Forstmeier and Schielzeth, 2011). We explicitly decided against using a stepwise approach because of the many shortcomings of this procedure (Mundry and Nunn, 2009; Whittingham et al., 2006). For more details about the GLMM, see Appendix A.

Results

Male cortisol

Overall, a total of 502 urine samples were analysed (31 to 73 samples per individual). Mean individual cortisol levels ranged between

44 and 87 ng/mg creatinine (range of SD: 27–60 ng/mg creatinine). Maximum values of cortisol levels for the nine males ranged from 120 to 309 ng/mg creatinine (Table 1). Cortisol levels showed a diurnal variation with higher levels early in the morning (daytime: GLMM estimate $\pm$ SE $= -0.30 \pm 0.03$, given a mean daily aggression rate received, p<0.001). Having a mother in the community did not result in lower cortisol levels (mother absent/present: GLMM estimate $\pm$ SE $= -0.04 \pm 0.09$, p $= 0.98$).

Male rank and the presence of oestrous females

In 58% of the observation days, there was at least one oestrous female in the community. Rank was not correlated with cortisol levels in samples collected on days without oestrous females present in the community (Fig. 1; GLMM with oestrous females absent: estimate $\pm$ SE $= -0.04 \pm 0.08$, p $= 0.58$). However, the presence of oestrous females had a significant effect on rank-related patterns of cortisol levels (GLMM, two-way interaction between presence of oestrous females and male rank, estimate $\pm$ SE $= 0.16 \pm 0.05$, p $= 0.004$, Table 2). In the presence of oestrous females, high-ranking males had a larger increase in cortisol than low-ranking males (in fact, the two lowest ranking males exhibited decreases in their cortisol levels), resulting in a significant positive correlation between male rank and cortisol levels in the presence of oestrous females, with dominant individuals having higher cortisol levels than subordinates (Fig. 1; GLMM with oestrous females present: estimate $\pm$ SE $= 0.17 \pm .05$, p $= 0.048$).

Neither the number of oestrous females present in the community, nor the length of time until the oestrous female closest to conception conceived had a significant influence on a male's cortisol levels (number of oestrous females present: GLMM with oestrous females present: estimate $\pm$ SE $= -0.01 \pm 0.05$, p $= 0.56$; number of months until the oestrous female closest to conception conceived: GLMM with oestrous females present: estimate $\pm$ SE $= 0.02 \pm 0.04$, p $= 0.50$). We found
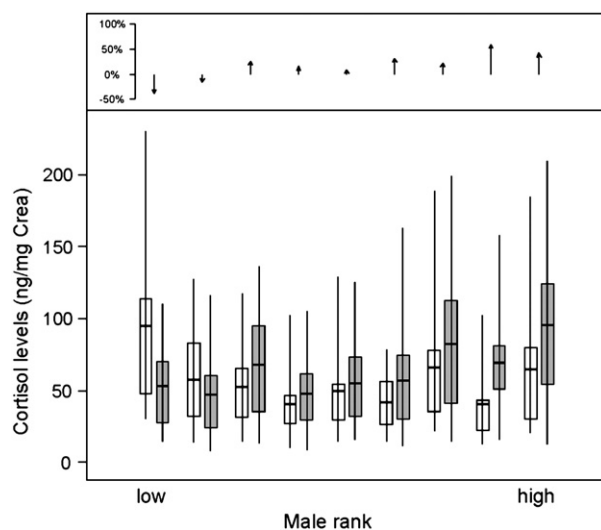

Fig. 1. Lower part: Urinary cortisol levels of bonobo males in relation to rank and absence (white bars) and presence (grey bars) of oestrous females. Horizontal lines indicate means, boxes indicate 50% quartiles, and vertical lines indicate 2.5% and 97.5% quartiles. There was no significant interaction between rank and cortisol levels in the absence of oestrous females (GLMM, estimate $= -0.04 \pm 0.08$, p $= 0.58$), but a significant interaction between rank and cortisol levels was detected in the presence of oestrous females (GLMM, estimate $= 0.17 \pm 0.05$, p $= 0.048 \pm 0.08$).Upper part: arrows indicate the relative cortisol increase in the presence of oestrous females in relation to cortisol values in the absence of oestrous females ([mean cortisol-value present $-$ mean cortisol-value absent]/mean absent). The rise in cortisol becomes significantly larger with increasing dominance rank. Note that presented values in the lower part of the figure are calculated from the raw data, but the test statistics stem from a GLMM: two-way interaction between rank and presence of potentially fertile females in the GLMM: p<0.001.

Table 2

Overview of the results from the GLMM examining the effects of components of mate competition on urinary cortisol in male bonobos. For definition of terms, see Materials and methods.

	Estimate	SE	p-value
Intercept	3.92	0.09	
Test variables:			
Presence of oestrous female: male rank[a]	0.16	0.05	0.004
Presence of oestrous females	0.08	0.06	
Male rank	< −0.01	0.07	
Residual aggression received from females:	0.07	0.03	0.005
Time of sample collection[b]			
Residual aggression received from females	0.05	0.03	
Time of sample collection	−0.30	0.03	
Residual aggression received from males:	0.06	0.03	0.045
Time of sample collection[b]			
Residual aggression received from males	0.01	0.03	
Residual aggression rate given[c]	−0.01	0.03	0.626
Individual mean of being aggressed by females	<0.01	0.05	0.960
Individual mean of being aggressed by males	0.03	0.06	0.829
Mother's presence in the community	−0.04	0.09	0.987
Control variables:			
Rank instability	0.005	0.11	0.890
Season of the year[d]			<0.001
Autocorrelation term	0.07	0.03	0.001

[a] Indicates the significant two-way interaction between male rank and oestrous female presence on urinary cortisol levels. This shows that the influence of rank differs depending on the presence of oestrous females and vice versa.

[b] Indicates the significant two-way interaction between residual aggression received (within individual centred daily aggression rate received, which stands for the deviation of a given day's aggression received from the mean aggression received by an individual over all days) and time of urine collection: This shows that the influence of the daily behaviour frequency on cortisol levels was stronger later in the day.

[c] Refers to the within-individual centred daily aggression rate given, which stands for the deviation of a given day's aggression given from the mean aggression given by an individual over all days.

[d] The p-value of the comparison between the model with and without season is shown (Chi^2 = 21.20, df = 2).

corresponding results when replacing the month to conception of oestrous female closest to conception with a categorical variable for the presence or absence of a potentially fertile female: There were no significant differences in the rank-dependence of male cortisol levels in the presence of oestrous females whether a potentially fertile female was present or not (two-way interaction between presence of potentially fertile females/presence of oestrous females far from conception and male rank, estimate $\pm$ SE $= -0.09 \pm 0.07$, p $= 0.35$)

Male age and the presence of oestrous females

The model that included the four age classes (see Table 1) instead of male rank revealed substantially larger AIC values, indicating that rank explained the variation in cortisol better than age classes (AIC of model including rank: 886.7; AIC of model including age classes: 894.3, evidence ratio based on Akaike weights $= 42.3$). Analysing subadult and adult males separately showed that the basic overall patterns of rank influencing cortisol patterns in the absence/presence of oestrous females also remained within the age classes such that (1) the cortisol response of subadult males to the presence/absence of oestrous females was rank-dependent (GLMM in subadult males, two-way interaction between presence of oestrous females and male rank, estimate $\pm$ SE $= 0.26 \pm 0.09$, p $= 0.0052$); and (2) while the rank of adult males correlated positively with cortisol levels when oestrous females were present but not when they were absent (GLMM on adult males with oestrous females present, estimate $\pm$ SE $= 0.15 \pm 0.04$, p $= 0.049$: GLMM on adult males with oestrous females absent, estimate $\pm$ SE $= 0.03 \pm 0.05$, p $= 0.66$), the two-way interaction between rank and oestrous female presence did not

reach significance (estimate $\pm$ SE $= 0.06 \pm 0.06$, p $= 0.19$). For more details, see Appendix A.

Aggression and cortisol

Rates of aggression given during the day of sample collection were not associated with an individual male's cortisol levels (GLMM, estimate $= -0.01$, p $= 0.63$, Table 2). However, both daily rates of aggression received from males and from females had a significant influence on individual cortisol levels and this effect appeared to depend on the time of day when samples were collected, as samples collected later in the day reflect the behaviour better than samples collected earlier in the day (aggression received from males dependent on collection time: GLMM estimate $= 0.06$, p $= 0.044$; aggression received from females dependent on collection time: GLMM, estimate $= 0.07$, p $= 0.005$, Table 2). Specifically, male cortisol levels decreased less on days when the individual received more aggression from males or females. Mean rates of aggression given correlated with male rank (Surbeck et al., 2012). However, the explanatory power of aggression given appeared to be moderate because a model incorporating it instead of male rank had higher AIC values, which indicates slightly lower explanatory power (AIC from model incorporating rank $= 886.5$, AIC from model incorporating mean aggression given $= 889.2$; evidence ratio based on Akaike weights $= 6.3$). In addition, mean rates of aggression received from males or females did not relate to the observed variation in cortisol levels *between* individuals (mean aggression received from males: GLMM, estimate $\pm$ SE $= 0.03 \pm 0.06$, p $= 0.83$; mean aggression received from females: GLMM, estimate $\pm$ SE $= 0.001 \pm 0.05$, p $= 0.96$, Table 2).

Proximity to oestrous females and its correlates

Independent of the presence or absence of oestrous females, male rank correlated strongly with how often males were in proximity to unrelated females (Spearman rank correlation: $r_s = 0.85$, N $= 9$, p < 0.01). Specifically, male rank correlated positively with how often a male was close to oestrous females (Spearman rank correlation: $r_s = 0.78$, N $= 9$, p $= 0.017$, Fig. 2). In addition, when the focal male was in proximity to an oestrous female, the number of total males and females that were in proximity was larger than in scans with no oestrous female in proximity (number of males in proximity: exact Wilcoxon test, $T^+ = 45$, N $= 9$ males, p < 0.01; additional females in proximity: exact Wilcoxon test, $T^+ = 45$, N $= 9$ males, p $= 0.019$). Incorporating the frequency of being close to oestrous females in parties containing oestrous females as a predictor variable instead of male rank into the GLMM for cortisol levels revealed substantially lower AIC values compared to the model incorporating
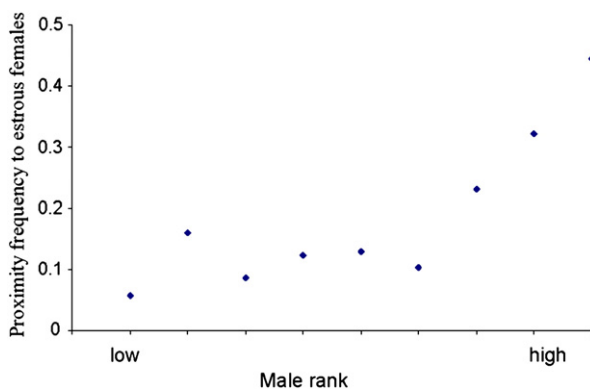

Fig. 2. Variation in the frequency of being in proximity to oestrous females in relation to male rank. Proximity frequency was calculated by dividing the number of scans with at least one oestrous female in proximity by the total number of scans in parties containing at least one oestrous female.

male rank (AIC for GLMM with male rank: 886.51, AIC for GLMM with male proximity to oestrous females: 880.63; evidence ratio based on Akaike weights $= 18.9$), indicating a better fit of the former model to the measured cortisol levels.

Looking at the frequency of aggression during focal follows, we found that males tended to receive more aggression when they were in proximity to an oestrous female compared to times when they were not (exact Wilcoxon test, $T^+ = 38$, N $= 9$ males, p $= 0.074$). However, males were not more aggressive when in proximity to oestrous females (exact Wilcoxon test, $T^+ = 25$, N $= 9$ males, p $= 0.82$).

Using scans of focal males activities, we found that males in proximity to oestrous females fed significantly less often compared to times when these males were not in proximity to oestrous females (exact Wilcoxon test, $T^+ = 43$, N $= 9$ males, p $= 0.01$).

Discussion

In this study on correlates of urinary cortisol in wild male bonobos, we found that cortisol levels were independent of male rank at times when oestrous females were absent. This result is in agreement with previous assumptions concerning the minor role of aggression in the context of rank maintenance (Furuichi, 1997). When oestrous females were present, changes in cortisol levels correlated positively with rank, and high-ranking, older males, which were found to be more aggressive and to copulate more frequently with oestrous females (Surbeck et al., 2012), had higher cortisol levels than low-ranking, younger males.

While changes in the frequency of aggressive behaviour appeared unlikely to account for the observed changes in cortisol, proximity to oestrous females turned out to be associated with high levels of cortisol and explained the observed cortisol better than male rank.

Relationship between dominance rank and cortisol levels

Two comparative studies, one in mammals and birds and one in primates, explained variation in rank-related cortisol patterns between species as a result of the costs of acquiring and maintaining high ranks as well as the frequency and intensity of aggression that subordinates are exposed to (Abbott et al., 2003; Goymann and Wingfield, 2004).

The absence of a link between rank and cortisol levels at times when no oestrous females were present, a situation that makes up about 40% of the observation time, is in line with the notion that rank maintenance in male bonobos is not based on constant aggression (Furuichi, 1997). It highlights an important difference between the two sister species of *Pan*; unlike bonobos, high-ranking male chimpanzees exhibit elevated cortisol levels independent of the presence of oestrous females (Muller and Wrangham, 2004b). The relationship between cortisol and rank in male chimpanzees has been related to the energetic costs of aggressive behaviour in the context of maintaining high rank in the unpredictable social environment of a fission–fusion society (Muller and Wrangham, 2004b). Bonobos also engage in a fission–fusion grouping pattern, and the findings of our study indicate that high-ranking male bonobos experience fewer challenges from subordinates and male coalitions than high-ranking chimpanzees do.

Rank-related cortisol patterns in males are known to vary in many contexts, including mate competition (Fichtel et al., 2007; Ostner et al., 2008a; Sapolsky, 1982; Setchell et al., 2010). Although high-ranking bonobo males copulate more often with oestrous females than do low-ranking males, there is no indication that the presence of such females per se leads to an increase in aggression (Takahata et al., 1996; Surbeck et al., 2012). However, when potentially fertile females are present, male aggression does increase (Surbeck et al. in press) and it seems reasonable to assume that under such conditions,

cortisol levels may also increase. The data presented above show that rank effects on cortisol levels emerged in the presence of oestrous females that were still far from conception and did not change when these females approached conception. Therefore, unlike in species in which mate competition is associated with both increased aggression and elevated levels of cortisol, male bonobos show increasing levels of cortisol in the absence of an increase in male aggression. From this, we infer that the presence of oestrous females may lead to non-aggressive forms of male competition for access to mates that are independent of the likelihood that these oestrous females conceive. A more detailed assessment of the impact of physiological and behavioural cues from females related to the reproductive cycle on male cortisol levels would require corresponding data from females but this was beyond the scope of the current study.

In humans, the presence of social partners may attenuate acute stress levels (De Vries et al., 2003), and, therefore, the presence of close kin may also affect stress levels in nonhuman primates. Contrary to this prediction, our results do not indicate that the presence of mothers lowered the cortisol levels of their sons. To investigate the influence of interactions with different social partners, one would need to consider direct acts of social support (e.g. alliance formation or consolation), which require a refined protocol with individual focal follows and urine sampling over the course of the entire day.

At this stage, we cannot exclude the possibility that differences in age had an influence on cortisol reactivity in males. This is relevant as our age estimates and male rank largely correlate. However, the finding that a model incorporating age classes instead of rank had lower explanatory power suggests that rank explains cortisol levels better than estimated age in this study. Furthermore, rank effects depending on the presence of oestrous females remained even when subadult and adult males were analysed separately. Finally, given that we did not find significant differences between adult and subadult males in terms of creatinine/specific gravity ratio, we feel confident that differences in physiology and behaviour such as muscle mass, bladder size, or water intake were not responsible for the observed cortisol patterns. While the observed differences in behaviour and physiology require a more complex approach, the lack of precise information on age prevents a more detailed analysis and further studies are needed to address the question of how cortisol reactivity in bonobos changes with age and other developmental parameters.

Correlates of competition for oestrous females

Elevated cortisol levels are sometimes associated with investments in relationships with females and the costs of mate guarding (Bergman et al., 2005; Fichtel et al., 2007; Lynch et al., 2002). In howler monkeys, maintaining close spatial association and affiliative relationships with females during and outside of the mating season can result in permanently elevated cortisol levels in dominant males (Van Belle et al., 2009).

Bonobo females are known to control access to preferred food (Fruth and Hohmann, 2002), to actively exclude males from accessing contestable resources (Parish, 1996), and to intervene in male mate competition (Hohmann and Fruth, 2003a; Surbeck et al., 2011). Under such circumstances, the quality of inter-sexual social relationships can be very important for a male's reproductive success. While there is no evidence for consortships or sexual coercion in bonobos (Paoli, 2009; Takahata et al., 1999), close long-term associations between unrelated females and males do exist and may even enhance male mating success (Furuichi, 1997; Hohmann and Fruth, 2003a). The finding that proximity to oestrous females explained the observed between-individual differences in cortisol levels better than dominance rank did indicates that these male–female associations are likely related to the cortisol response in male bonobos. Maintaining long-term relationships with oestrous females, even

when those females are not close to conception, may represent a non-aggressive but challenging form of mate competition (Furuichi, 1997; Hohmann and Fruth, 2003a). But how could these associations with oestrous females lead to elevated cortisol levels?

In addition to mate guarding, male cortisol levels also increase in response to actual or anticipated aggression (Abbott et al., 2003; Ostner et al., 2008a). In line with these studies, we found that the decline in cortisol over the day was reduced on days when rates of aggression from females and/or males were high. Furthermore, proximity to oestrous females enhanced the likelihood of males becoming targets of aggression.

While our data collection protocol was not designed to link specific behavioural events to acute changes in cortisol levels, in our analysis we considered the overall temporal relationship between relevant behavioural interactions and time of urine sample collection, assuming that the influence of stress-related social interactions was stronger later in the day (Bahr et al., 2000).

An interesting question is whether the male cortisol response differs according to the sex of the aggressor. The alpha male was never attacked by other males during this study. Therefore, we can rule out the possibility that being the victim of male aggression while in close proximity to oestrous females drives his high cortisol levels. For males other than the alpha, we cannot exclude the possibility that received or anticipated aggression by males in proximity to oestrous females drove the rank-related cortisol response.

Previous reports suggest that female aggression against males may have fatal consequences for the victim (Hohmann and Fruth, 2003a). Rates of female aggression against males tend to be low and prevent more systematic analyses of their effect on intersexual relationships. In our study, we noted that three out of the four highest cortisol levels detected in the samples from the highest ranking male were collected after he had been attacked by females in the context of mate competition. While these observations do not allow us to make any firm conclusions, they can be used to generate hypotheses that can be tested in future studies. One such hypothesis is that aggression from females may have a stronger effect on male cortisol levels than aggression from other males. Another is that close proximity to oestrous females may expose dominant males to an increased risk of aggression from females more often than lower ranking males, which could explain elevated cortisol levels even in the alpha male.

The results of this study indicate that, when in proximity to oestrous females, males spent less time feeding. This may reflect efforts to monitor the activity of the oestrous females or that of other male and/or female party members. Reduced food intake can strongly affect cortisol levels, and the frequent proximity between certain males and oestrous females may have contributed to the observed increase in these male's cortisol levels. However, shortened feeding time may be compensated with high rates of food intake, selectivity for high-quality food, or changes in digestive efficiency. More detailed studies are required to explore individual costs of male–female associations and related constraints in terms of energy acquisition, nutrition, and metabolism.

Overall, our results suggest that being in proximity to and investing in relationships with oestrous females exposes males to the risk of potential aggression from other group members and is likely to reduce feeding opportunities. Compared to the maximum cortisol values, as shown in Table 1, the increased cortisol levels in the high-ranking males that were induced by the presence of an oestrous female appear moderate. However, considering that oestrous females were present for about 60% of the time, it is premature to exclude the possibility that long-term exposure to elevated cortisol levels has a fitness effect. Since high rank enhances mating success, it is reasonable to infer that the cost of elevated cortisol in higher ranking males is offset by the potential reproductive benefits they derive from these long term close associations with oestrous females.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yhbeh.2012.04.013.

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