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Urinary C-peptide levels in male bonobos (*Pan paniscus*) are related to party size and rank but not to mate competition

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ABSTRACT

Within- and between-species variation in male mating strategies has been attributed to a multitude of factors including male competitive ability and the distribution of fertile females across space and time. Differences in energy balance across and within males allow for the identification of some of the trade-offs associated with certain social and mating strategies. Bonobos live in groups with a high degree of fission–fusion dynamics, there is co-dominance between the sexes and a linear dominance hierarchy among males. Males compete over access to females, breeding is aseasonal, and females exhibit sexual swellings over extended time periods. In this study we use urinary C-peptide (UCP) levels in male bonobos (*Pan paniscus*) obtained from 260 urine samples from a wild bonobo community, to quantify male energy balance during mate competition and levels of gregariousness in the species. Although high ranking males are more aggressive, spend more time in proximity to maximally tumescent females, and have higher mating frequencies, we found no indication that mate guarding or mate competition affected male energy balance. Our results showed a positive correlation between monthly mean UCP levels and mean party size. When traveling in large parties, high ranking males had higher UCP levels than those of the low ranking males. These results support the hypothesis that patterns of fission–fusion dynamics in bonobos are either linked to energy availability in the environment or to the energetic costs of foraging. The finding of a rank-bias in UCP levels in larger parties could also reflect an increase in contest competition among males over access to food.

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Introduction

Energetic costs of mate competition

Competition among males over access to fertile females in group-living species often leads to the establishment of dominance hierarchies in the males (Hager and Jones, 2009), with those occupying higher ranks frequently enjoying priority of access to mates (Altmann, 1962). Although there is variation in male mating strategies between species and even within social groups, including coalition formation, queuing and sneaking copulations, a prominent strategy observed in many taxa is mate guarding (insects: Alcock, 1994; reptiles: Ancona et al., 2010; birds: Komdeur, 2001; mammals: Willis and Dill, 2007). Mate guarding, during which dominant males try to maintain sole mating access to fertile females, is one mechanism by which rank differences among males translate into skewed mating among those males. While representing a strategy that increases paternity success, mate guarding has been shown to be a trade-off with elevated metabolic costs due to higher rates of agonistic and sexual activities (Ancona et al., 2010) and due to constrained feeding behavior (Alberts et al., 1996; Komdeur,

2001). Although metabolic costs of mate competition can arise under different mating systems, they seem particularly high among high ranking individuals and in species that mate guard over extended periods as these factors lead to negative energy balances (i.e.: when energy intake is lower than energy expenditure; Lane et al., 2010). The resulting energetic stress may not only result in a substantial decrease in male body mass (Bernstein et al., 1989), but may even lead to a decrease of short-term reproductive success (Lidgard et al., 2005) and to increased male mortality (Hoffman et al., 2008). In some extreme cases (e.g. gray seals: Lidgard et al., 2005; Rhesus macaques: Higham et al., 2011b), termed "endurance rivalry", male mating effort over extended periods is constrained by energy availability. Yet, the metabolic costs of mate guarding and high ranks are not consistent across species. While some studies in primates find that mate guarding and general mating effort are associated with reduced feeding time (Alberts et al., 1996; Georgiev, 2012), weight loss and nutritional stress in high ranking individuals (Bercovitch and Nürnberg, 1996; Higham et al., 2011b; Setchell and Dixson, 2001), others find neither an association with measurements of energy intake and expenditure (Huck et al., 2004; Mass et al., 2009; Weingrill et al., 2003) nor rank related patterns of nutritional stress during mating seasons (Schülke et al., 2014). Variation across studies might be explained by methodological differences (Alberts et al., 1996; Schülke et al., 2014) or by adaptive differences in energy

allocation during mate competition across species (Georgiev, 2012; Girard-Buttoz et al., 2014b; Schülke et al., 2014). Another possibility is that the metabolic costs of mate guarding or high rank can be compensated by a reduction of energetically costly activities in another context such as vertical locomotion (Girard-Buttoz et al., 2014a). Nevertheless, males of species in which the maintenance of high rank depends on physical strength are expected to allocate energy differently than species in which social strategies such as pair-bonding or coalition formation are crucial for reproductive success (Schülke et al., 2014). While most primate studies have focused on metabolic costs in seasonal breeders, little is known about species with aseasonal breeding that might face more persistent costs over extended amounts of time with fewer opportunities for metabolic recovery (Emery Thompson and Georgiev, 2014). This study addresses the question of how male energy balance is affected by long lasting, aseasonal mate competition in bonobos (*Pan paniscus*), a species with fission–fusion dynamics and a lack of male priority of access to food.

Energetic costs of group living

Costs associated with mate competition, and with intragroup competition over food resources, are incurred by males living in groups containing several individuals of both sexes. Since feeding competition is hypothesized to have a stronger effect on female reproductive success, most studies focus on the metabolic costs of female gregariousness (e.g. Ebensperger et al., 2011; Emery Thompson et al., 2012a, 2012b; Pride, 2005; but Isbell and Young, 1993). However, rank related skew in access to food and the consequential costs of increased gregariousness may also lead to rank differences in energy balance among males. This phenomenon might be particularly prominent in species where females are dominant and therefore possess priority of access to food resources. It remains unclear as to whether or not high ranking males would have a more positive energy balance than low ranking males during periods of mate competition in such scenarios.

It has been hypothesized that some group-living species deal with decreases in food availability and increases in competition within groups by temporarily fissioning into smaller parties (Aureli et al., 2008). Consequently, in order to attenuate the effects of reduced food availability in the environment, party sizes are expected to be smaller during times of food scarcity. This function of fission–fusion dynamics has been supported in primates by findings that parties are small when fruit is scarce and large when fruit is more abundant (Anderson et al., 2002; Chapman et al., 1995; Cobden, 2014; but Rimbach et al., 2014; Smith et al., 2008). While a number of other factors have been shown to influence party size including the presence of females that exhibit visual signs of fertility (Anderson et al., 2002; Matsumoto-Oda et al., 1998) and predation pressure (Boesch, 1991), few attempts have been made to quantify the effects of different party sizes on the energy balances of males (Georgiev, 2012). This study explores links between male energy balance and grouping patterns in bonobos.

C-peptide

In wild living populations it is often difficult to quantify rank related metabolic costs or energetic stress. A classic approach to quantifying these costs has been by measuring glucocorticoid levels (e.g. Barrett et al., 2002; Goymann and Wingfield, 2004; Muller, 2004). This method however has the disadvantage that elevated levels can result not only from metabolic stress, but also from social or psychological stress (Abbott et al., 2003; Creel, 2001). For example, in baboons it has been proposed that during times of stable dominance hierarchies, high glucocorticoids in alpha males are primarily caused by energetic stress, whereas high glucocorticoids in low-ranking males are largely caused by social stressors (e.g., high rates of received aggression, a lack of a sense of control, and few coping mechanisms; Gesquiere et al., 2011). While several species seem to share the pattern with baboons, the

generality of this notion is unclear and rank-related glucocorticoid levels are often still hard to interpret. A more specific approach to quantifying metabolic stress is by measuring urinary C-peptide levels (UCP levels; Sherry and Ellison, 2007). C-peptide is cleaved off from proinsulin during the activation of insulin which is produced when glucose levels are elevated in the blood. The C-peptide level of an individual therefore acts as a marker of energy balance, with high C-peptide levels indicative of a more positive energy balance than low levels. Several studies have already demonstrated the use of C-peptide in tracking energy balance in captive and wild living primates (bonobos: Deschner et al., 2008; Georgiev et al., 2011; orangutans: Emery Thompson and Knott, 2008; chimpanzees: Emery Thompson et al., 2009; macaques: Girard-Buttoz et al., 2011; gorilla: Grueter et al., 2014; guereza: Harris et al., 2010).

We measured the UCP levels of wild male bonobos to investigate how mate competition and party size affect the energy balance.

The "Metabolically costly mate guarding" hypothesis

Bonobos live in multi-male, multi-female societies in which males normally remain in their natal community (Kano, 1992; Schubert et al., 2011). Females exhibit visual signs of fertility in the form of extended periods of genital swellings during interbirth intervals (Furuichi and Hashimoto, 2002). As changes of genital swellings do not always correlate with specific reproductive stages (Reichert et al., 2002), detectability of ovulation by males may be constrained, making intense efforts of mate guarding a costly strategy. Nevertheless, there are some indications that mate guarding is a male mating strategy in bonobos: Firstly, high ranking males spend more time in proximity to females with maximally tumescent swellings (Surbeck et al., 2012b). Secondly, staying in close proximity of maximally tumescent females is associated with an increase in male cortisol levels (Surbeck et al., 2012b). These elevated cortisol levels may be indicators of elevated metabolic stress due to mate guarding activity since the feeding time of bonobo males close to maximally tumescent females is also decreased (Surbeck et al., 2012b). While such a decrease in feeding time has been associated with increased vigilance and male aggression in other species (Ancona et al., 2010; Chuang-Dobbs et al., 2001), the latter does not apply to bonobos because the general presence of maximally tumescent females does not increase male aggression (Surbeck et al., 2012a). However, reduced aggression towards fertile females in the form of mate guarding without coercive mating may also result in decreased feeding opportunities (Surbeck and Hohmann, 2013). This "Metabolically costly mate guarding" hypothesis implies that energetically costly mate-guarding is a male mating strategy in bonobos and predicts rank related patterns of UCP levels only in the presence of maximally tumescent females with high ranking males having lower UCP levels.

"Metabolically costly aggression" hypothesis

Energetic costs of aggression have been demonstrated in several vertebrates (Southwick, 1967; Marler and Moore, 1989). In chimpanzees, energetically costly aggressive behavior is essential for the maintenance of high ranks even in the absence of maximally tumescent females (Georgiev, 2012). Aggressive behavior is more likely to explain differences in male energy balances than other energetically costly behaviors such as traveling (Emery Thompson et al., 2009). Results from one bonobo community indicate that high ranking males are also more aggressive than low ranking males and that the presence of maximally tumescent females that are close to conception (potentially fertile females) leads to an overall increase in male aggression (Surbeck et al., 2012a). The "metabolically costly aggression" hypothesis assumes that aggression is always energetically costly and, consequently, predicts that aggression negatively influences the energy balance of males. Therefore, we would expect permanently lower C-peptide levels in

high ranking males. Given that the presence of potentially fertile females is associated with elevated levels of male aggression, a decrease in C-peptide levels in all males is predicted. Furthermore, as aggression frequency increases on mating days (Hohmann and Fruth, 2003), we would also expect copulation rates to correlate with C-peptide levels.

Metabolic costs of grouping hypotheses

The energy balance of males may vary with changes in male gregariousness rather than mate guarding effort and a variety of scenarios concerning male grouping costs are possible.

If larger parties are due to the presence of maximally tumescent females, predation pressure, or proximity to neighboring communities and not to higher food availability, we would expect that males are more likely to experience higher metabolic costs and lower UCP levels when traveling in larger parties because per capita food availability decreases. The same pattern would emerge if overall individual energetic expenditure increases with party size. However, if larger parties are mainly formed during times of high food abundance, we would not expect a decrease in mean UCP with increasing party size because per capita food availability would remain constant. While the relationship between party size and energy balance in males allows for distinguishing some main hypotheses concerning the grouping dynamics of bonobos, data on energy expenditure such as travel distance, general food availability and female energy balance are necessary to explore these factors in more detail.

Male energy balance might also vary according to dominance rank independent of male mating strategies because high ranking males have priority of access to monopolizable food over low ranking males or occupy qualitatively better feeding spots (Kahlenberg, 2006). This would lead to observing rank related differences in UCP levels with higher ranking males having higher UCP levels. Furthermore, in bonobos, the presence of mothers has been shown to influence male mate access (Surbeck et al., 2011) and it is possible that the presence of mothers might also affect a son's access to other resources such as food. For an overview of the hypotheses and predictions see Table 1.

Material and methods

Ethics statement

Permits to conduct research at LuiKotale in Salonga National Park, Democratic Republic of Congo were granted by the Institut Congolais pour la Conservation de la Nature (ICCN) in Kinshasa, Democratic Republic of Congo.

Study site and subjects

Data collection was conducted on the Bompusa bonobo community between December 2007 and July 2009 at the LuiKotale field site in Salonga National Park, Democratic Republic of Congo. During the study period, the community consisted of 33–35 individuals, which included five adult (older than 15 years) and four subadult (older than ten years) males, eleven 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 could be individually identified and were habituated to human presence before the start of the study period. Subadult and adult males were included in this study, because all engaged in competition over access to maximally tumescent females and actively participated in dominance interactions with other males (Surbeck et al., 2011). Phenology data were not available for the study period. Genetic analyses from a previous study revealed that six of the nine males had their mothers in the community (Schubert et al., 2013).

Behavioral observation

Parties including males were followed from the time the 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 and mating behaviors were recorded during party follows and during focal follows (2112 h of party 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 focal's activity (feeding, moving, resting, grooming) was recorded. Focal individuals were randomly chosen from the males traveling in the same party.

Aggressive behaviors included both contact and non-contact aggression with a giver and a receiver. Branch dragging displays were also included because we assume that their metabolic costs are similar to some other types of aggression. In situations when it was difficult to determine whether they were directed at another individual, no receiver of this aggression was scored. Rates of giving and receiving aggression were calculated as hourly rates, daily for each individual. Rates were based on both records from focal follows and party follows, corrected for the time each male was present in the focal party. Submissive behavior included different forms of retreat, such as fleeing and jumping aside.

We assessed dominance relationships among male community members on the basis of dyadic interactions (Vervaecke et al., 2000). Within a

Table 1
Overview of the hypotheses and predictions for bonobo males.

Hypotheses	Predictions
Mate competition	
"Metabolically costly mate guarding" hypothesis	1.1 High ranking males have lower UCP levels than low ranking males, but only in the presence of maximally tumescent females
"Metabolically costly aggression" hypothesis	2.1 High ranking males have always lower UCP levels than low ranking males
	2.2 All males have decreased UCP levels in the presence of a maximally tumescent female close to conception (potentially fertile female)
	2.3 Aggression and copulation rates correlate negatively with UCP levels
Grouping pattern ("Metabolic costs of grouping hypotheses")	
Larger parties form due to maximally tumescent females, predation pressure or proximity to neighboring communities	3.1 All males show a decrease in UCP levels with increasing party size
Larger parties form during times of higher food availability	3.2 No decrease in male UCP levels with increasing party size
Male rank influences access to food within parties	3.3 High ranking males have always higher UCP levels than those of low ranking males
Mother presence influences access to food within parties	3.4 Males with a mother present in the party have higher UCP levels than those of males without mother

dyad, individuals showing submission in response to aggression or to a non-aggressive approach by another individual were classified as subordinate. Multiple aggressive interactions with the same outcome occurring within the same ten minute period were counted as one single event.

We scored genital swellings daily and distinguished between four swelling stages ranging from minimal (stage 1) to maximal (stage 4) and scores were based on firmness of swelling (tumescence) and skin surface structure (Hohmann and Fruth, 2000). Female bonobos can have swelling cycles for several years without giving birth and it is common for multiple female party members to show maximal tumescence at any given time (Kano, 1992). Therefore, maximally tumescent females are likely to vary in their probability to conceive. In order to relate changes in male behavior and physiology to mate competition, we used two different approaches: (1) The presence of maximally tumescent females has previously been shown to influence male stress physiology (Surbeck et al., 2012b). Therefore we compared the morning energy balance of individuals who had spent the previous day with maximally tumescent females to those who had not. (2) We classified the maximally tumescent females for the period six months prior to conception as potentially fertile. We then compared male morning UCP levels after days when none of the females were potentially fertile to situations when at least one female was potentially fertile. This second classification was used because the presence of potentially fertile females has been shown to affect male testosterone physiology and aggressive behaviors (Surbeck et al., 2012a). Furthermore, a special focus on these six-months prior to conception swelling cycles allows for a comparison with results from East African chimpanzees where parous females exhibit only a mean of five swelling cycles before each conception (approximately six months: Muller and Wrangham, 2004a). If the mother of a given male was the only maximally tumescent female in the community, the son was not considered to be in the presence of a maximally tumescent female, because adult and subadult males were never observed competing over mating access to their mothers or copulating with them at LuiKotale.

Urine collection

For UCP measurements we used early morning urine samples collected opportunistically from the nine males during the party follows over the entire study period (N = 251, 18 to 40 samples per individual). Early morning samples were chosen as they likely reflect the energy balance of the previous day (mean collection time ± SD: 7:00 AM ± 1.84 h; Muller and Wrangham, 2004b). The selected samples for hormone measurements were distributed evenly throughout the data collection period and the number of samples per male was comparable (N = 27.9 ± 8.1). For 200 of these samples the behavior of the individual was observed on the previous day (N per individual 22.2 ± 7.4, mean observation time per individual 4.9 h ± 2.5 h) (Table 2).

Whenever possible, we collected samples on the underside of large *Haumania* leaves to prevent sample contamination. 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. Because urine samples contaminated with feces have been shown to produce erroneous results, we did not collect such samples (Higham et al., 2011a). 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 for Evolutionary Anthropology (MPI-EVA) in Leipzig, Germany, where UCP analyses were performed. Permits to export urine samples from the Democratic Republic of Congo (DRC) and import them into Germany were issued by the ICCN and the head veterinarian of DRC in Kinshasa. The permit for importing samples into Germany came from the state ministry for social affairs and consumer protection of Saxonia/Germany.

Sample preparation and C-peptide measurement

Frozen urine samples were thawed at room temperature. After shaking for 10 s (VX-2500 Multi-tube Vortexer) the samples were centrifuged for 10 min at 2.000 g (Multifuge Heraeus). We measured C-peptide levels with C-Pep-EASIA KAP0401, a commercially available solid phase enzyme amplified sensitivity immunoassay kit from DIAsource, designed to measure C-peptide in human serum. 100 μl of pure urine was added in duplicates into the wells and assay instructions followed. Intra- and inter-assay coefficients of variation of low and high value quality controls were 9.4% and 7.4% (N = 5) and 9.1% and 7.9% (N = 9), respectively.

Assay validation for bonobo urine

While C-peptide measurements have previously been validated in bonobos (Deschner et al., 2008), the use of a different assay required the validation of certain assay parameters. Three sets of pooled samples were prepared and serially diluted. Serial dilutions of urine samples gave displacement curves parallel to those obtained with standards from the assay kit. To assess the accuracy of the C-peptide measurement in bonobo urine, recovery experiments were performed with the three pooled samples. Each pool was prepared with urine from five different individuals. For spiking (adding a known amount of the hormone), the five external standards of the assay kit were used. For the two lower standard concentrations (0.21 ng/ml and 0.6 ng/ml) recovery was 89% (N = 3; SD. = 3.1%) and 91% (N = 3; SD. = 2.1%), respectively. The pool samples spiked with higher standard concentrations (1.68 ng/ml, 5.1 ng/ml, and 15.3 ng/ml) resulted in 83% (N = 3; SD. = 2.0%), 71.3% (N = 3, SD. = 3.2%) and 68% (N = 3; SD. = 1.5%) recoveries. While recoveries were lower in the two higher standard concentrations, only seven (2.8%) samples fell in this range. The average C-peptide concentration of the individually measured samples was 1.26 ng/ml with a standard deviation of 1.80 ng/ml.

To adjust for the variation in the volume and concentration of the urine, we measured creatinine (Cr) concentrations in each urine sample (Bahr et al., 2000) and expressed all C-peptide values in nanogram/milligram creatinine. To avoid overestimation of C-peptide concentrations by a correction with very low creatinine values, all urine samples with creatinine levels <0.05 mg/ml were excluded (2.3% of all measured samples). Because studies on chimpanzees produced conflicting results concerning the comparability of hormone concentrations from individuals of different age classes using creatinine concentration correction (Anestis et al., 2009; Emery Thompson et al., 2012a, 2012b), we previously demonstrated that there are no significant differences between the creatinine/specific density ratios of adult and subadult male bonobos (Surbeck et al., 2012a, 2012b). We therefore included both, adults and subadults in our analysis.

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).

Behavioral and social correlates of UCP levels

We used Generalized Linear Mixed Models (GLMMs; Baayen, 2008) with the log transformed UCP levels to examine the independent effects of several predictor variables. In a first set of models we examined the effects of social predictor variables (predictions 1.1, 2.1, 2.2, 3.1, 3.2, 3.3, 3.4 in Table 1), while in a second set of models we tried to examine the effects of three possible behavioral correlates (prediction 2.3 in Table 1).

Models for social predictors of UCP levels

In the first model, we examined the effects of three social predictor variables: the male's dominance rank, presence or absence of maximally tumescent females in the community during the previous day of sample collection and mean party size during the day prior to sample collection. We included these predictors as test variables as well as the two, two-way-interactions between rank and party size and between rank and presence of maximally tumescent females into the model. Male rank was incorporated in two different ways in two separate models. Firstly we included the overall rank of a given male in the male hierarchy and secondly we included the male rank relative to the other males present on the day prior to sample collection to account for fluctuation in rank due to the fission–fusion nature of the bonobo society. Because party size and presence of maximally tumescent females were correlated (either because maximally tumescent females attract more individuals or because these females traveled in larger parties), we also ran two separate models with either party size or presence of maximally tumescent females as a predictor variable, and then compared the AIC indices of the two models (Bumham and Anderson, 2002). To investigate the potential impact of varying numbers of maximally tumescent females observed in the party on male UCP levels, we incorporated this parameter as a predictor variable instead of presence/absence of maximally tumescent females in the first model. In order to investigate the influence of the effect of potentially fertile females, we incorporated them instead of the maximally tumescent females into the first model.

To investigate the possible impact of a mother on a male's energy balance, we incorporated mother presence on the day prior to sample collection as a test variable in all models.

While we assumed that there are periods that are nutritionally richer for the bonobos and that these relate to changes in UCP levels, we are unable at this point to precisely quantify when these periods occurred. As a result, we took a mathematical and a non-mathematical approach to account for the possible effects of such times in the model and compared their outcomes:

1) To control for season, we included a simple sine shaped curve with the maximum at a previously undefined date during the year. This was done by first transforming the days within a given year to a variable ranging from 0 to 2*pi. We then included the sine and cosine of this variable as additional fixed effects into the model (Surbeck et al., 2012b).
2) To allow for asymmetric seasonal fluctuations in UCP levels, not easily captured by using sine and cosine transformations, we built a semi-parametric model (Hastie and Tibshirani, 1986; Wood, 2006). Here, the seasonal term was modeled as a periodic curve over the year but allowed to be quite flexible throughout the year. These models were implemented in the gamm4 package (Wood, 2012).
3) Because we assume that monthly difference in food availability has an influence on feeding time of individuals, we calculated a monthly proportion of scans during which males were feeding on fruits and non-fruits and a monthly proportion of scans during which males were feeding only on fruits (Chaves et al., 2011; Girard-Buttoz et al., 2014a; Masi et al., 2009). These two measurements were incorporated separately as predictor variables instead of the seasonal term.

Because there might be relatively low seasonality in the habitat (although there is a yearly dry season), we incorporated an autocorrelation term, which accounts for temporal patterns in the residuals that are not explained by the annual periodicity of the first two models but vary at an intermediate temporal scale. All three approaches revealed very similar results concerning the social predictor variables (party size, dominance rank and presence of maximally tumescent females, presence of mother), confirming the robustness of the results from the approaches reported herein, we therefore only present the results of the first approach incorporating season as a sine shaped curve. To rule out collinearity between other factors such as party size and presence of maximally tumescent females, we determined Variance Inflation Factors (VIF, Field, 2005) for a standard linear model excluding the random effects which revealed VIF of 1.2 for the presence of maximally tumescent females, 1.0 for overall rank, 1.0 for mother presence and 1.2 for party size.

Model for behavioral correlates of UCP levels

In this model, we tried to examine the effects of three possible behavioral correlates of energy expenditure, aggression given, aggression received and copulation rate on changes in UCP levels. All behavioral variables were incorporated as predictor variables in a way that allowed us to distinguish within- versus between-subject effects; i.e., to distinguish whether daily aggression rates influenced a given individual's daily UCP levels or whether differences between individuals in average rates of aggression can explain their differences in UCP levels (van de Pol and Wright, 2009). In this model we also included season as the simple sine shaped curve with the maximum at a previously undefined date during the year.

We included an autocorrelation term as control variable in all the models, as well as 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 biased effect size estimates and P-values (Forstmeier and Schielzeth, 2011). In order to achieve reliable P-values for the individual effects, we dropped one test variable at a time and compared the reduced and the full model using a likelihood ratio test (Barr et al., 2013). We explicitly decided against using a stepwise approach, because of the many shortcomings of this procedure (Mundry and Nunn, 2009; Whittingham et al., 2006).

Results

UCP levels of male bonobos

The medians of individual UCP levels ranged from 0.98–2.80 ng/mg Cr (overall range of UCP levels is from 0.18 to 57.65 ng/mg Cr). Although we only used early morning samples, we additionally included collection time into our analysis. The time of sample collection was not significant (daytime: GLMM estimate $\pm$ SE $= 0.128 \pm 0.06$, P $= 0.11$). Furthermore, UCP levels did not exhibit significant seasonal variation (season as the simple sine shaped curve with the maximum at a previously undefined date: GLMM model comparison with and without seasonal term using a chi-square test: Chisq $= 2.70$, Df $= 2$, P $= 0.26$; season as a periodic term over the year but flexible throughout the year: GLMM, Df $= 0.95$, F $= 3.2$, P $= 0.08$; season as a monthly variation in percentage time spent feeding or spent feeding on fruits GLMM estimates $\pm$ SE, time spent feeding: 0.01 ± 0.07, P $= 0.92$, time spent feeding fruits: 0.07 ± 0.07, P $= 0.32$). Mothers' presence on the previous day did not influence male UCP levels (mother presence: GLMM estimate $\pm$ SE $= -0.09 \pm 0.21$, P $= 0.64$).

Table 2
Overview of the sample size for each individual.

Male ID	Dominance rank (note that 9 refers to the highest ranking individual and 1 to the lowest ranking one)	Number of measured urine samples (days with maximally tumescent females/days without maximally tumescent females)
Ca	9	15/13
Ti	8	8/16
Ja	7	16/15
Da	6	14/11
Be	5	15/17
Ap	4	8/5
Pn	3	9/6
Em	2	10/8
Mx	1	10/4

UCP levels and the presence of maximally tumescent females

During 58% of the observation days, at least one maximally tumescent female was present, and about half of the urine samples were from days when maximally tumescent females were present on the previous day (N = 120). The monthly proportion of days during which maximally tumescent females were present did not correlate with monthly mean UCP levels (Spearman rank correlation: $r_s = -0.36$, N = 18, P = 0.13). Neither the presence nor the number of maximally tumescent females on the previous day had an influence on UCP levels when controlling for the mean party size on the previous day (presence of maximally tumescent female: GLMM estimates ± SE, 0.10 ± 0.15, P = 0.48; number of maximally tumescent females: GLMM estimates ± SE, 0.03 ± 0.05, P = 0.67). Furthermore, there was also no effect of the presence of potentially fertile females on male UCP levels (presence of potentially fertile females: GLMM estimates ± SE, −0.05 ± 0.17, P = 0.73).

UCP levels, party sizes and male ranks

Mean monthly party size correlated positively with the monthly medians of UCP levels (Spearman rank correlation: $r_s = 0.68$, N = 18, P = 0.003, Fig. 1). Male UCP levels were higher during months with larger party sizes. A more detailed analysis, combining individual UCP levels with a focal's party size on the previous day of sample collection and male overall rank, revealed that changes in party sizes affect males of different dominance ranks differently. High ranking individuals show a significantly stronger increase in UCP levels as party size increases than that of lower ranking individuals (two-way interaction between individual party size and overall male dominance rank, estimate ± SE = 0.12 ± 0.06, P = 0.03, Table 3, Fig. 2). Subsequently, the difference in UCP levels in small parties between high and low ranking individuals was considerably smaller than those in large parties where high ranking individuals had much higher UCP levels than low ranking individuals. If we incorporate a male's relative rank on the previous day of sample collection instead of his overall rank, we find a very similar result (two-way interaction between individual party size and relative male dominance rank, estimate ± SE = 0.31 ± 0.16, P = 0.05).

Table 3

Overview of the results from the general linear mixed models (GLMMs) examining the effects of socio-ecological variables on UCP levels in male bonobos. For definition of terms, see the Materials and methods section.

	Estimate	SD	P-value
Intercept	0.60	0.20	
Season[a]			0.76
Presence of maximally tumescent female in the party of the previous day	0.10	0.15	0.48
Overall male dominance rank	0.13	0.09	
Presence of mother of the previous day	−0.05	0.19	0.79
Mean party size of focal of the previous day	0.13	0.07	
Autocorrelation	−0.05	0.06	0.40
Overall male dominance rank: Mean party size of focal of the previous day[b]	0.12	0.06	0.03

[a] The P-value of the comparison between the models with and without season is shown (Chisq = 18.61, Df = 7).
[b] Indicates the significant two-way interaction between relative male rank of the previous day and individual party size on UCP levels. This shows that the influence of party size differs depending on male dominance rank and vice versa.

Party sizes and the presence of maximally tumescent females on UCP levels

The daily party sizes correlated significantly with the number of maximally tumescent females present on a given day (Spearman rank correlation: $r_s = 0.20$, N = 8, P < 0.001). To test which of the two predictors, presence of maximally tumescent females or party size, was more closely related to the observed UCP levels we built two models by removing each predictor from the main model and compared the results: While the significant effect of party size and male rank remained after removing the presence of maximally tumescent females completely from the main model (two-way interaction between individual party size and relative male dominance rank, estimate ± SE = 0.30 ± 0.16, P = 0.02), the interaction between the presence of maximally tumescent females and male rank did not become significant after removing party size completely from the main model (two-way interaction between individual party size and relative male dominance rank, estimate ± SE = −0.17 ± 0.36, P = 0.98) nor did the presence of maximally tumescent female (presence of maximally tumescent female: estimate ± SE = 0.26 ± 0.14, P = 0.052). Furthermore, a model without party size revealed a significantly higher AIC than a model without the presence of maximally tumescent females (AIC model: maximally tumescent females 504.2 vs. party size 497.9). Therefore, differences in UCP levels are more strongly related to changes in party sizes than to the presence of maximally tumescent females.
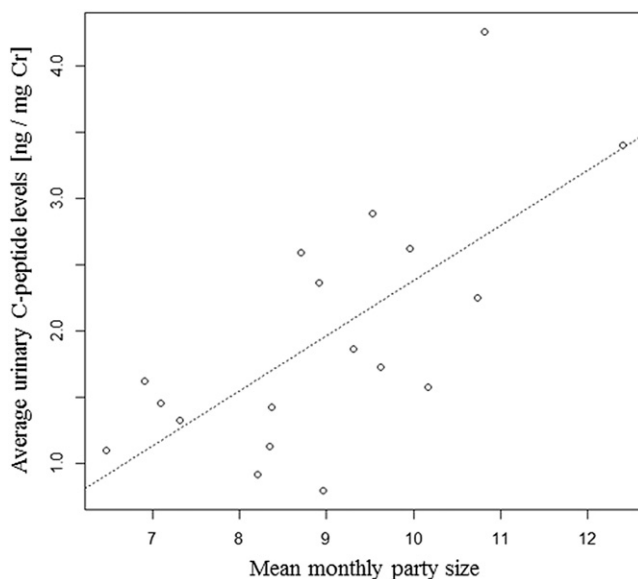

Fig. 1. Monthly mean party sizes correlate positively with monthly medians of UCP levels of male bonobos (Spearman rank correlation: $r_s = 0.68$, N = 18, P = 0.003).
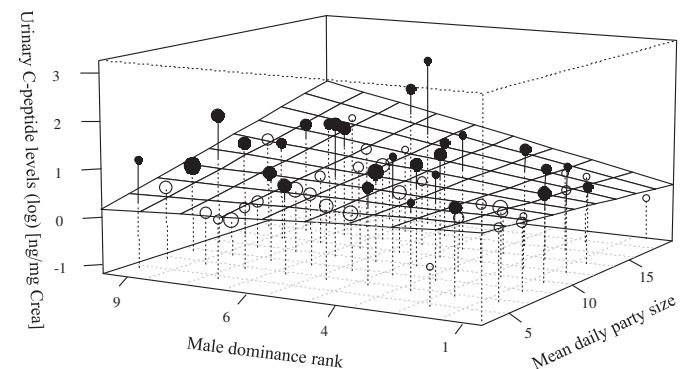

Fig. 2. Morning UCP levels of male bonobos in relation to overall male rank and mean individual party size on the day prior to sample collection (two-way interaction between individual party size and relative male dominance rank, GLMM: estimate ± SE = 0.12 ± 0.06, P = 0.03; note that rank 9 refers to the highest ranking individual and 1 to the lowest ranking individual).

Behavioral correlates of UCP levels in males

A model incorporating rates of aggression given and received, as well as the copulation rate of the previous day of urine collection did not explain the observed UCP levels better than the Null model including only random effects (full model and the null model comparison: Chisq = 12.75, Df = 8, P = 0.12). Consequently, we were prevented from drawing the final conclusions about the behavioral correlates of UCP levels in male bonobos, but it is likely that none of the predictors had a very strong influence on UCP levels as this would have improved the full model.

Discussion

Measuring UCP levels in male bonobos, a species with linear male dominance hierarchies, we found no indication that mate competition negatively affects the energy balance of males. The positive correlation between mean monthly UCP levels and mean party size indicates a link between energy balance and fission–fusion dynamics in male bonobos, that is, males exhibit increased gregariousness when they can afford to do so. Comparing mean daily party sizes with UCP levels early next morning shows that high ranking males have a more positive energy balance when traveling in larger parties, while the energy balance of low ranking individuals is not affected by party size. These UCP pattern would not be expected if party size is mainly determined by social factors. If party size was based on the presence of maximally tumescent females and not on resource abundance, individuals would likely experience higher metabolic costs in larger parties.

Role of energetically costly behavior in bonobo mate competition

Variation across species in male energy balance can indicate differences in adaptive behaviors during mate competition (Schülke et al., 2014). In eastern chimpanzees, the presence of a maximally tumescent parous female leads to a decrease in the UCP levels of all males, independent of their mate guarding activity (Georgiev, 2012). This has been attributed to similar metabolic costs of increased aggression and longer travel distances in larger parties during mate competition (Georgiev, 2012; Georgiev et al., 2014). However, because of the metabolic cost of rank maintenance, high ranking chimpanzee males exhibit lower UCP levels than low ranking ones only in the absence of maximally tumescent females (Emery Thompson et al., 2009; Georgiev, 2012).

In this study on male bonobos we find that neither the presence of maximally tumescent females nor the presence of potentially fertile females influenced UCP levels. Furthermore, since high ranking males spend more time in the proximity of maximally tumescent females but do not exhibit lower C-peptide levels than those of the low ranking males, there is no indication that energetic costs of mate guarding affect male energy balance. While we found that the presence of maximally tumescent females is related to party size, the observed pattern of increased UCP levels in high ranking males in larger parties likewise contradicts the predictions of the "energetically costly mate guarding" hypothesis and the "metabolically costly aggression" hypotheses. If mate guarding or aggression would be energetically costly, we would expect aggression and copulation frequency to influence UCP levels. Because these parameters do not explain the variation in UCP levels, energetically costly mate guarding or other energetically costly behaviors do not seem prominent during mate competition in bonobos. In the case temporal changes of genital swellings do not always reflect changes in fecundity such as time of ovulation (Reichert et al., 2002), males may refrain from energetically costly forms of mate competition and adopt alternative strategies of mate guarding and mate competition.

A previous study in bonobos conducted during the same time period found increased cortisol levels in high ranking males in the presence of maximally tumescent females (Surbeck et al., 2012b). This pattern had been linked to the duration that individuals spent in the proximity of maximally tumescent females. Using only behavioral correlates of male bonobos during this time, we were not able to distinguish between two possible causes of elevated cortisol levels: psychological stress due to the unpredictability of the social environment or physiological stress due to reduced feeding. Combining the previous results with the results of this study that the presence of maximally tumescent females does not affect male UCP levels and that high ranking male bonobos have a better energy balance in larger parties (which often include maximally tumescent females) strongly suggests that metabolic stress in proximity to maximally tumescent females is unlikely to have caused the cortisol patterns. Therefore, the high cortisol levels are likely linked to psychological stress in males of high dominance ranks. This is in contrast to results from studies in baboons, chimpanzees and macaques which relate stress in high dominance ranks mainly to metabolic costs and in subordinates to psychological factors (Barrett et al., 2002; Gesquiere et al., 2011; Muller, 2004; but Girard-Buttoz et al., 2014b). A possible explanation for this species-specific trait is the high dominance rank of female bonobos, which renders social interactions less predictable even for high ranking males in dense social environments such as the proximity to maximally tumescent females (Abbott et al., 2003; Crockford et al., 2008).

While previous studies in bonobos indicate a strong role of mothers as coalition partners during mate competition (Furuichi, 1997; Surbeck et al., 2011) which might apply to other contexts such as access to food resources, we found no indication in UCP levels that maternal support would affect the energy balance of their sons (no influence of mother presence on UCP levels). Therefore, male bonobos neither seem to compensate for the lack of their mother as coalition partners through investment in energetically costly behavior during competition, nor does mother presence lead to an increase in energy balance in sons.

Metabolic costs of gregariousness

Party sizes in fission–fusion species have been shown to vary according to a variety of factors (e.g. limited roost (Kerth, 2008), foraging and mating strategies (Connor et al., 2000), resource competition and defense (Holekamp et al., 1997; Wittemyer et al., 2005)). In chimpanzees one of the factors influencing party size is food availability (Anderson et al., 2002; Mitani et al., 2002). Because chimpanzee males have priority of access to food resources over females and high ranking males occupy better feeding spots than low ranking males (Kahlenberg, 2006), one would expect party size to correlate positively with male energy balance and high ranking males to have higher UCP levels than those of the low ranking males. However, due to the metabolic costs of increased aggression in larger parties, the opposite pattern with high ranking males having lower UCP levels and a general decrease in UCP levels in larger parties has been found (Georgiev, 2012). These findings strongly contrast with our results as male bonobos do not necessarily have priority of access to food over females and where males exhibit increased gregariousness when they can afford to do so. Since we find that aggression frequencies do not explain the variation in UCP levels, it seems that bonobo males, opposite to chimpanzees, do not face metabolic costs of aggression arising from gregariousness.

Due to the positive relationship between party size and UCP levels, our results indicate that grouping patterns in bonobos are linked to changes in food availability or related changes in energy expenditure such as travel costs, extractive feeding, or digestive efficiency. During times of high food availability females are more likely to exhibit sexual swellings which may contribute to the observed increases in party sizes (Anderson et al., 2006; Emery Thompson and Wrangham, 2008). However, if party sizes would be exclusively driven by the presence/absence of maximally tumescent females, we would not expect UCP levels to increase when males travel in larger parties. Likewise, if predation pressure were a main driver of grouping patterns in

bonobos, we would not expect an increase in UCP levels with larger parties. These conclusions based on physiological levels are in line with earlier notions that in bonobos variation in party size is less linked to changes in swelling sizes of the females (Furuichi, 1987; Furuichi and Hashimoto, 2002; Hohmann and Fruth, 2002), while chimpanzee parties including maximally tumescent females tend to be larger regardless of fruit availability (Hashimoto et al., 2001; Nishida, 1979).

The rank related skew in UCP levels in large parties might be caused by age-differences in insulin metabolism, as adult males are generally higher in dominance ranks than sub-adult males (Muller et al., 1996). However, in humans overall insulin production does not increase with age and insulin-reactivity even decreases (Gumbiner et al., 1989). Furthermore, the results of our GLMM incorporating relative male rank and controlling for individual identity, indicate that changes in the relative dominance rank of a given individual were associated with changes in UCP levels. Taken together, it seems unlikely that the observed differences in UCP-levels are linked to age. It could also be argued that a greater difference in UCP levels between high and low ranking males based on relative rank reflects the fact that these relative ranks are more accurately coded in large parties. However, the fact that we found the same results using overall ranks allows us to exclude a potential methodological shortcoming.

The alternative hypotheses would be that high ranking males have better access to food resources than low ranking males in larger parties and that low ranking individuals have a higher energy expenditure in larger parties. The first scenario would be in line with observations in spider monkeys, that traveling in smaller parties reduces not only scramble but also contest competition among community members (Asensio et al., 2008). It is unlikely that high-ranking males actually increase their energy balances in large parties, and it may rather be that large parties coincide with energy surplus and that high-ranking males maintain high energy balance despite traveling in large parties. Overall, further studies including the energy balance of female group members will give more insights into the costs and benefits of gregariousness of different individuals.

Conclusion

Measures of UCP show that rank related differences in behavior during mate competition in male bonobos do not affect the energy balance. This suggests that mate guarding and other forms of mate competition by male bonobos are energetically neutral which might be linked to the low predictability of ovulation in females, which renders costly forms of mate competition ineffective and promotes alternative strategies which are independent of physical strength. When traveling in large parties high ranking males showed an increase in UCP suggesting that dominance status provides benefits in energy gain or reduced costs of energy expenditure.

Acknowledgments

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