



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

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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

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