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Original Article

The "tolerant chimpanzee"—towards the costs and benefits of sociality in female bonobos

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Humans share an extraordinary degree of sociality with other primates, calling for comparative work into the evolutionary drivers of the variation in social engagement observed between species. Of particular interest is the contrast between the chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*), the latter exhibiting increased female gregariousness, more tolerant relationships, and elaborate behavioral adaptations for conflict resolution. Here, we test predictions from 3 socioecological hypotheses regarding the evolution of these traits using data on wild bonobos at LuiKotale, Democratic Republic of Congo. Focusing on the behavior of co-feeding females and controlling for variation in characteristics of the feeding patch, food intake rate moderately increased while feeding effort decreased with female dominance rank, indicating that females engaged in competitive exclusion from high-quality food resources. However, these rank effects did not translate into variation in energy balance, as measured from urinary C-peptide levels. Instead, energy balance varied independent of female rank with the proportion of fruit in the diet. Together with the observation that females join forces in conflicts with males, our results support the hypothesis that predicts that females trade off feeding opportunities for safety against male aggression. The key to a full understanding of variation in social structure may be an integrated view of cooperation and competition over access to the key resources food and mates, both within and between the sexes.

Key words: **C-peptide, energy balance, feeding competition, *Pan paniscus*, social foraging.**

INTRODUCTION

Complex sociality is a hallmark feature of the human condition with evolutionary roots in our primate heritage (Brown et al. 2011; Freeberg et al. 2012; Bergman and Beehner 2015). Our closest living relatives, bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) diverged approximately 1.5–2.6 million years ago, long after the *Homo-Pan* split occurred 7–13 million years ago (Langergraber et al. 2012; de Manuel et al. 2016). Nevertheless, the two *Pan* species differ in several important aspects of their sociality. Understanding the drivers of these differences and the factors underlying bonobo sociality may inform us about the evolutionary pressures leading to characteristic traits of human sociality.

Bonobos and chimpanzees live in relatively large multi-male, multi-female groups (Miller et al. 2014; Surbeck et al. 2017) with male philopatry and female dispersal (Morin et al. 1994; Gerloff et al. 1999; Eriksson et al. 2006), and a high degree of fission–fusion dynamics (Sugiyama 1968; Kuroda 1979; Aureli et al. 2008). Despite the considerable diversity among chimpanzee subspecies (Boesch et al. 2002; Boesch 2009; Gruber and Clay 2016), differences between bonobos and chimpanzees remain salient. Compared with chimpanzees, bonobo females are more gregarious (Hohmann et al. 1999; Hohmann and Fruth 2002), more central in the social network (Wrangham 1986; Furuichi 1989; White 1989; Tokuyama and Furuichi 2017), and travel in mixed sex subgroups more often (Wrangham 1986; White 1988; Furuichi 1989). In stark contrast to chimpanzees, female bonobos are codominant with males (Furuichi 1997; Surbeck and Hohmann 2013) and evolved elaborate sociosexual behaviors that mitigate conflicts and facilitate gregariousness

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and coalition formation (Kano 1980; Hohmann and Fruth 2000; Clay and de Waal 2014), which may explain why levels of overt aggression between females are low (Furuichi 1997; Surbeck and Hohmann 2013). In contrast to chimpanzees, agonistic coalitions among bonobos are more prevalent among females than males (Stevens et al. 2006; Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016).

Increased gregariousness and cooperativeness may result from higher social tolerance in bonobo compared to chimpanzee females. However, feeding experiments comparing captive groups of bonobos and chimpanzees have produced inconclusive results concerning tolerance towards conspecifics, partly because they concern both male and female behavior. Parish (1994) and Hare et al. (2007) both found bonobos to be more tolerant than chimpanzees during co-feeding experiments, whereas Cronin et al. (2015) found that bonobos exhibit less social tolerance than chimpanzees. In a food transfer-situation, bonobos were found to share less and unidirectionally whereas chimpanzees tended to share more actively and reciprocally (Jaeggi et al. 2010). Hare and Kwetuenda (2010) found that bonobos actively provided unrelated individuals with access to food, but Bullinger et al. (2013) were not able to replicate these results.

Rooted in theory of optimal foraging in patchy environments (Charnov 1976) and socioecological models (Jarman 1974), three feeding ecology hypotheses have been put forward to explain patterns of agonistic behavior in bonobos that all emphasize female competition (Stockley and Bro-Jørgenson 2011). These hypotheses borrow from ecological theory (Bradbury and Vehrencamp 1976) in predicting that characteristics of limiting food resources determine how animals compete for access to these resources, both within and between groups, and propose that the competitive regime shapes the rules of social engagement (Wrangham 1980; van Schaik 1989; Isbell 1991). If food resources occur in patches small enough to be economically monopolized against group mates and qualitatively worth defending, within-group contest competition over access to these resources ensues promoting competitive exclusion if alternative patches close by provide lower nutritional yield. Experimentally clumped resources cause increased direct competition in mammals (Monaghan and Metcalf 1985) birds (Sol et al. 1998), fish (Ward et al. 2006), and invertebrates (Cameron et al. 2007) and the resulting competitive exclusion selects for the evolution of despotism (Milinski and Parker 1991), steep linear dominance hierarchies, and coalition formation (Sterck et al. 1997). If patches are too large, of low quality, or too small to be defended economically, within-group scramble competition will prevail like in social spiders fed very small or very large prey (Sharpe and Avilés 2016), promoting an adjustment of group size or feeding party size to patch size without affecting agonistic behavior (Wrangham 1980; van Schaik 1989; Isbell 1991; Koenig 2002).

The first hypothesis, hereafter referred to as Resource Abundance hypothesis, was developed specifically to explain differences between chimpanzees and bonobos and has evolved over time, resulting in a number of verbal models supplementing and expanding the original idea as proposed by Badrian and Badrian (1984). The untested premise of this hypothesis is that bonobo food patches are too large and too narrowly spread to cause diminishing returns for the consumer over realistic residence times (Charnov 1976; Chapman 1988). Different versions of the Resource Abundance hypothesis highlight the size of fruit bearing trees or the widely available, terrestrial herbaceous vegetation (THV) occurring in large, undefensible patches both of which are thought to prevent contest competition, diminish within-group scramble competition, and reduce the costs of grouping among female bonobos (Badrian and Badrian 1984; Wrangham 1986; White and Wrangham 1988). The THV sub-hypothesis suggests that contest competition effects, possibly occurring during exploitation of smaller fruit patches, can be compensated by subordinates feeding more on overabundant THV. Indeed, bonobos regularly consume THV at all major study sites (Kuroda 1979; Kano 1983; Badrian and Malenky 1984), but data concerning differences in THV consumption between bonobos and chimpanzees are inconclusive (Wrangham 1986; Malenky and Stiles 1991; Malenky and Wrangham 1994; Malenky et al. 1994) and rank effects on THV feeding have not been assessed yet. The fruit patch size sub-hypothesis invokes the size of fruit patches to be larger in bonobo habitat than chimpanzee habitat (Badrian and Badrian 1984; White and Wrangham 1988). The validity of the fruit patch size hypothesis is debated (e.g. Chapman et al. 1994; Furuichi et al. 2015) but it is implicitly used as a reference for species differences in female–female social relationships in *Pan* (Russon and Begun 2004; Heilbronner et al. 2008; Hare and Yamamoto 2017) and crucial elements regarding bonobo feeding behavior remain untested. From the Resource Abundance hypothesis, we predict that contest competition over highly prized defendable fruit patches prevails only when patches are small whereas in large patches, contest competition is moderate or absent (White and Wrangham 1988). Apart from behavioral measures (e.g. food intake, searching time) the patch-related difference in competition can be assessed as a dominance effect on energy intake (Table 1). However, if small patch size constrains food intake, the fission–fusion system allows subordinate females to compensate for reduced intake in small patches by feeding more often or for longer time away from high-ranking females (either in nearby fruit trees or on THV) resulting in dominance rank not being related to energy balance. Accordingly, we do not expect to find dominance rank effects on food intake, feeding efficiency or energy balance, but on time spent feeding on THV and on how often a female is missing from the main party.

The other two hypotheses aim at the proximate level of competition and explain patterns of conflict and association in bonobos

Table 1

The 3 hypotheses for the evolution of bonobo social structure with predictions

	Resource abundance	Cooperative defense	Priority of access
Female coalitions target	—	Males	Females
Food patch depletion*	No	Yes	Yes
Food intake in patch	Not related to rank	Increases with rank	Strongly increases with rank
Movements in patch	Not related to rank	Decreases with rank	Strongly decreases with rank
Energy balance (uCP)	Not related to rank	Increases with rank	Strongly increases with rank

*intake rates decrease with increasing patch residence time coupled either with unchanged or increasing movements within the patch/foraging effort from resource characteristics and the way the animals compete over food but do not explain why these differ between the *Pan* species. While the Resource Abundance hypothesis does not specify what females can gain from grouping, the Cooperative Defense hypothesis makes a clear prediction about the trade-offs deriving from female bonding (Parish 1996). It assumes that bonobos face strong within-group contest competition for food and that females benefit from forming coalitions with other females to defend access to food resources against males. As this implies that males are dominant over females in dyadic conflicts, the additional proposed advantage for coalition formation among females is the suppression of conditioning sexual aggression (Parish 1996). The hypothesis rests on observations of captive females of both *Pan* species provided with a defensible food source in which female bonobos monopolized access to the food patch, exhibited high rates of co-feeding, and had a higher feeding success than the male, whereas the male had a similar feeding success as females in the chimpanzee group (Parish 1994). Although these data provide convincing evidence concerning the benefits derived from female bonding, the causes for species-differences in female bonding remain ambiguous. One possible explanation is that the driving force for female bonding in bonobos is that social bonds prevent male harassment and coercion in bonobos but not in chimpanzees (Wrangham 1993). Captive female bonobos tolerate subordinate ones during co-feeding (Vervaecke et al. 2000), and intersexual dominance relations may change with partner availability (Vervaecke et al. 1999). The Cooperative Defense hypothesis predicts that contest competition over access to limited food yields dominance rank effects on energy balance, but that the effect is weak, because females exhibit tolerance towards other females in exchange for their cooperation against males. Coalitions should mainly be formed by females and should mainly target males. This is in line with data showing that it is primarily the rate of socio-sexual behavior between female bonobos that increases at times when the potential for contest competition is high (Hohmann and Fruth 2000; Hohmann et al. 2009).

The Priority of Access hypothesis derives from the common cercopithecine pattern of females forming coalitions against other females to exclude them from food resources (Wrangham 1980; Strier 1994; Cords 2012). The hypothesis assumes strong within-group contest competition for limiting food resources and female competition to be primarily intrasexual. By forming close affiliative and supportive relationships, female alliances are thought to gain an advantage against other individuals and alliances, yielding increased net energy intake to its members. Given that most females disperse from their natal group, kin support will not generate linear hierarchies to begin with. Instead, hierarchies will be stratified, with females engaging in conflict only with females from other strata but not from their own (such as the bonobo hierarchy constructed with the ADAGIO method following Douglas et al. 2017). Like the Cooperative Defense hypothesis, the Priority of Access hypothesis predicts that bonobos face strong contest competition over access to food. In contrast to the other hypotheses, the Priority of Access hypothesis predicts conflicts over food to occur equally often between females and between the sexes, females to form coalitions mainly against other females, and strong rank effects on food intake and feeding effort. Furthermore, the resulting energy balances would be expected to vary according to rank strata, instead of diminished variation resulting from general tolerance among females.

Here, we test the competing predictions (Table 1) of the three hypotheses laid out above with data on polyadic conflicts, feeding behavior in fruit patches and THV, as well as information on individual energy balance in female bonobos in their natural habitat at LuiKotale, Democratic Republic of Congo. We use the recently refined focal tree method (Vogel and Janson 2011), which combines information on the size and quality of individual food patches with data on feeding and agonistic behavior of all co-feeding consumers. We first test whether feeding in fruit patches is associated with diminishing returns resulting from patch depletion by regressing intake rate and feeding effort over residence time. Then we relate food intake rates and feeding effort within patches to female dominance rank as a function of patch size and number of competitors. These data offer a window into food patch characteristics that are relevant to the consumer, a perspective that has been applied to other primates (Snaith and Chapman 2005; Heesen et al. 2014) but was previously not applied to bonobos. As indicators of conflict avoidance and compensation for reduced food intake, we relate female dominance rank to average party size and to the time spent in THV patches, respectively. Finally, we assess the energetic consequences of direct and indirect forms of feeding competition with data on variation in urinary C-peptide (uCP) levels within and among individuals. The C-peptide of insulin, as shed in urine, has been established as a noninvasive biomarker for energy balance (Deschner et al. 2008; Girard-Buttoz et al. 2011) and energetic status (Sherry and Ellison 2007; Emery Thompson and Knott 2008), including in wild bonobos (Georgiev et al. 2011; Surbeck et al. 2015).

METHODS

Ethics statement

All methods applied were strictly noninvasive and noncontact. The Institut Congolaise pour la Conservation de la Nature (ICCN) granted the permission to conduct research at LuiKotale, Salonga National Park, Democratic Republic of Congo (0683/ICCN/DG/ADG/014/KV/2012). Permits for exporting the samples from the Democratic Republic of Congo were issued by the ICCN (0521/ICCN/DG/CWB/05/01/2014), whereas the permits for importing the samples to Germany were issued by the state ministry for social affairs and consumer protection of Saxony/Germany.

Study site and study subjects

Data were collected at the LuiKotale field site near Salonga National Park, Democratic Republic of Congo, from August 2012 to April 2013 and November 2013 to August 2014. A description of the field site can be found in Hohmann and Fruth (2003). During this period, the fully habituated Bompusa West community consisted of five adult and two subadult males along with 16 adult females and three subadult females. Of the adult females, 13 were parous, of which two gave birth during the study period, and the remaining three were nulliparous. Our subjects were 14 adult females resident in the community at the onset of the study.

Behavioral observations

We followed bonobos during half day shifts (N = 223 days, 577 h focal animal sampling), either from the morning nest site until noon or from noon until the evening nest site. Due to the fission-fusion dynamics of the species, most follows were at the party level. We define a party as a subgroup of the community that may vary in size and composition of individuals over time. All data were collected by 2 observers working as a team using notebooks and a voice-recorder, with pre-assigned methods of data collection and consistent roles throughout the field season. For baseline data, each half hour interval, one observer recorded the party composition, as well as the activity, location (ground or tree), and any food items being consumed by each individual in sight ($N = 3644$ scans). All occurrences of agonistic behavior in the party were recorded, including the context as well as the identities and roles of opponents (Altmann 1974). Both observers carried Garmin GPS devices (GPSMAP® 62 and GPSMAP® 60CSx) for recording bonobo ranging data and marking the food patches visited during shifts.

Food patch characteristics. We collected data on bonobo feeding behavior with a modified version of the focal tree method (Vogel 2005; Vogel and Janson 2007; Vogel and Janson 2011). We included all arboreal and terrestrial feeding patches as focal trees (Chapman 1988), in order to account for instances such as a terrestrial patch where food had fallen on an area roughly equal to the tree crown above. In a few cases, we also included adjoining tree crowns of the same species as a single focal tree, when we clearly observed that the bonobos fed and moved easily among 2 closely connected crowns. Each focal tree was tagged physically using clearly visible plastic flagging tape with a hand-written unique identifier code (focal tree identity) to facilitate reliable recording of potential re-visits. We estimated focal tree size based on the diameter at breast height (DBH) for single trees in centimeters (Chapman et al. 1992), the DBH (cm) of the "mother" tree from which the food had fallen, or the sum of DBHs for adjoining tree crowns. The latter practice may have over-estimated the size of multi-stem crowns but was used for 5% of focal trees only. We visually estimated focal tree food crop size on a 5-point logarithmic scale (1 = 1–9 items, 2 = 10–99, 3 = 100–999, 4 = 1000–9999, and 5 = 10 000–99 999; Janson and Chapman 1999). Focal tree observations began when the first bonobo entered the feeding patch and ended when the last individual departed the patch. One observer recorded the identities and times of entries and exits for each individual of the feeding group, which were then used in defining the "feeding bout duration" and "feeding party size" of each focal tree observation. When there was a clear pause in feeding such that most bonobos started resting or grooming, the time between the pause and resumption of feeding was subtracted from the total feeding bout duration. Bonobo food plants were identified with the help of local field assistants and by using reference herbaria at camp. We visited remaining unidentified focal trees at the end of the field season with a local botany expert in order to identify the remaining plant species.

Food intake. The second observer recorded feeding behaviors during five-minute focal protocols, rotating among all focal females feeding in the patch. Feeding was defined as ingesting, chewing, swallowing, and short handling/processing times (10 s), as well as short pauses (10 s) and short movements between consecutive food items. Intake rates were calculated as the number of food items (e.g. fruits, seeds) ingested per unit of time of uninterrupted feeding behavior. For dry seeds, such as those of *Scorodophloeus zenkeri*, we counted the number of seed pods processed per unit time. In the case of leaves and flowers, we recorded the number of handfuls ingested.

Movement. To quantify feeding costs, movement in the focal tree that briefly interrupted feeding activity was recorded as a dichotomous variable (moved vs. did not) for every one-minute interval of focal animal observation in a focal tree protocol.

Rank. A novel graph based method, ADAGIO, was developed recently by Douglas et al. (2017) to construct a dominance hierarchy among female bonobos. We used an ADAGIO chart based on the overt and subtle agonistic interaction data from our observation period to rank the 14 study females into eight rank categories. The rank categories were based on an ADAGIO top–down approach such that the highest rank $r = 1$ was assigned to the females at the root nodes of the graph and the direct child-nodes of these females were assigned rank $r + 1$ etc. This method is particularly well suited to female bonobo dominance relationships, as it allows a quantification of nonlinear as well as linear dominance hierarchies.

Urine collection

Urine samples were collected from all focal individuals throughout the study period opportunistically for C-peptide measurement, with a focus on obtaining the first morning urine voids, as these samples better represent nocturnal fasting (Sherry and Ellison 2007). We used the underside of large *Marantaceae* leaves to capture urine samples ($N = 230$) or pipetted them from foliage on the ground ($N = 8$). Urine sample collection was conditional on the absence of urine from other individuals to avoid cross contamination, and on the sample not coming into contact with feces (Higham et al. 2011). All samples were frozen in liquid nitrogen on the day of collection and shipped to the laboratory on dry ice, where they were stored in −20 °C until analysis.

Hormone analyses for energy balance

We assayed $N = 238$ urine samples with matching behavioral data from the previous day for C-peptide levels at the Endocrinology laboratory of the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. Thawed urine samples were shaken for 10 s (VX-2500 Multi Tube Vortexer) and then centrifuged for ten minutes at 2000 g (Heraeus Multifuge). We then used solid phase Enzyme Amplified Sensitivity Immunoassay kits (C-PEP-EASIA KAP0401) commercially distributed by DIAsource. The immunoassay was designed to measure C-peptide levels in human serum, and has been validated for bonobo urine (Surbeck et al. 2015). Intra-assay coefficients of variation (CV) based on the mean CVs of 4 replicates were 3.89% for low- and 3.75% for high-value quality controls. Inter-assay CVs were 2.66% for low- and 8.85% for high-value quality controls ($N = 15$ plates). To adjust for the variation in the volume and concentration of the urine, we corrected the C-peptide levels by Creatinine (Crea) levels in each sample (Bahr et al. 2000) and reported all hormone measurements as ng C-peptide/mg Crea. Samples with Crea values lower than 0.05 mg Crea/ml were omitted from further analyses ($N = 2$ samples, 0.84% of all assayed samples). In addition, $N = 1$ (0.42%) sample was excluded because it failed to yield detectable C-peptide levels.

In humans, plasma insulin levels increase dramatically from middle and late pregnancy (Spellacy and Goetz 1963; Spellacy et al. 1965) due to the necessity of diverting maternal glucose towards optimal fetal growth. Seven of the resident females gave birth during our field sampling seasons. Because elevated insulin levels do not reflect energy balance, we excluded 17 urine samples from pregnant females from our analyses. To do so, we assessed pregnancy retrospectively from observed birth events. Reproductive status of 10 of the 14 females was also monitored with pregnancy tests strips (hCG strip Artron Bioresearch Inc.) and with urinary steroid hormone analyses for another project (Douglas et al. 2016) rendering the likelihood of undetected pregnancy to be very low.

The final sample size was $N = 218$ with 15.6 ± 6.8 SD samples per female (range = 5–28).

To test whether the C-peptide assay detected known patterns of C-peptide level variation, we first compared mean uCP values during the last pregnancy trimester with mean values when not pregnant for seven females with a Wilcoxon matched pairs test and found late pregnancy values to be significantly higher ($T^+ = 28$, $N = 7$, $P = 0.016$; Figure 1a) which was expected from the human literature (Spellacy and Goetz 1963). Secondly, to assess whether our assay was sensitive enough to pick up day-to-day variation in feeding behavior, we compared two clearly distinct dietary regimes; days when females consumed mainly *Dialium* spp. and days when they were feeding mainly on the dry seeds of *Caesalpinioideae* trees such as *Scorodophloeus zenkeri*. *Dialium* fruits offer easily accessible pulp, are small fruits that require minimal handling time and are easy to harvest because they are clustered in tree crowns. Moreover, they contain a relatively high amount of sugar compared to the average sugar content of other fruits consumed by bonobos (Beaune et al. 2013a). *Caesalpinioideae* seeds are often encased in comparably hard seed pods requiring longer handling times, and are difficult to harvest because they occur widely dispersed over the tree crown and should therefore have a much smaller effect towards a positive energy balance than *Dialium*. We found that average individual uCP morning values following days when the bonobos fed mainly on *Dialium* fruits were significantly higher than morning values following days when dry seed consumption was the main diet (Wilcoxon matched pairs test $T^+ = 35$, $N = 8$, $P = 0.016$; Fig. 1b), in line with similar results from another bonobo community in Kokolopori (Georgiev et al. 2011).

Statistical analyses

We tested our predictions (Table 1) concerning the competitive regime of female bonobos with two Generalized Linear Mixed Models (GLMM; Baayen 2008) based on the behavioral data from females during focal tree observations. We then constructed a linear mixed model (LMM; Baayen 2008) to test for a potential energetic signature of competition among the females through our physiological measure, urinary C-peptide.

Food intake model. In our first model, we evaluated whether social factors and food patch characteristics have an effect on female feeding gain. As an index of food intake, we used individual intake rate (bites or items/min) measured during the focal tree protocols as our *response variable*. We had initially built this model as an LMM with a Gaussian error structure, in which the response variable was set as the deviation of individual intake rate/min from the average intake rate for each food species, but this Gaussian model did not meet its assumptions about residuals, as the model residuals against fitted values were structured along diagonal lines. We then used a GLMM with a Poisson error structure with the counts of individual intakes as the response such that each minute of intake within the feeding focal protocols per female represented a single data point. We excluded incomplete intake rate minutes, unless they were preceded and followed by a minute of continuous intake. We included dominance ranks as standardized ranks per observation ranging from zero (lowest stratum) to one (highest stratum), converted from the eight rank strata derived from the ADAGIO plot and the number of individuals in the patch as our *test predictors of social effects*. Because the pattern of dominance among females tends to be nonlinear and nulliparous, young females are typically lower ranking than older females, we included rank as a squared term to account for a potential nonlinear effect of rank on food intake resulting from only the lowest-ranking females having decreased food intake compared to mid- and high-ranking females. The number of adult and subadult individuals in the patch was determined from the continuous records of focal tree entries and exits to obtain a point score for each intake minute. After inspecting the distribution of the number of individuals, we log-transformed it to reduce the skew in its distribution.

Our *test predictors accounting for food patch characteristics* included the log-transformed size of the focal tree as DBH (cm) and the food crop size score. To test for the effect of food patch depletion, we included the proportion of time into the feeding bout as an additional predictor along with its squared term in case of a nonlinear effect. The nonlinear effect could be expected based on the empirical observations that cumulative food intake follows a negative exponential curve due to satiation (McCleery 1977). We calculated

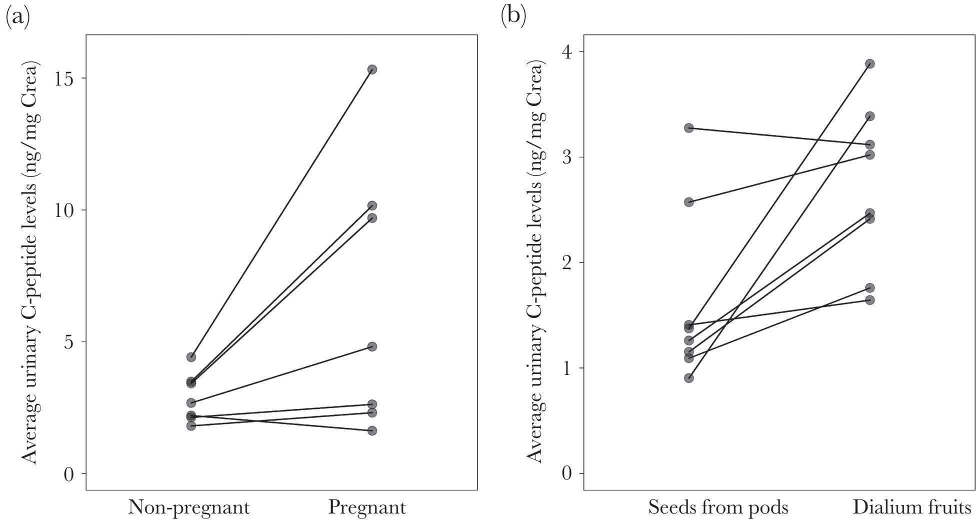

Figure 1
Average urinary C-peptide levels (ng/mg Creatinine) (a) in nonpregnant ($N = 7$ females) and pregnant bonobo females ($N = 7$ females) and (b) during periods of *Dialium* fruit consumption and seeds of dry pods (*Monopetalanthus*, *Hymenostegia*, *Scorodophleus*) consumption ($N = 8$ females).

the temporal variable by taking the difference between the time the focal tree bout ended and the time when the intake rate was recorded and expressed it as the proportion of time into the feeding bout. We standardized the predictor to range from 0 (time when the intake was recorded) to 1 (time when the focal tree bout ended). Due to our interest in the mode of feeding competition among female bonobos, we wanted to test whether dominance rank, our main test predictor, would have a different effect on intake rate depending on patch size, varying level of crowding or food availability. Thus, we added the following three interaction terms in to our model of food intake: 1) rank squared (and rank) with the number of individuals in the patch, 2) rank squared (and rank) with DBH, and 3) rank squared (and rank) with food crop size score. Time elapsed since midnight and its square were added as *control predictors* because time of day has been shown to have an influence on primate feeding behavior (Carlson et al. 2013). Feeding bout identity (date combined with a running number for *n*th focal tree of the shift), focal tree identity, focal tree species and bonobo identity were added as *random effects*.

Movement model. Our second model examined the influence of the same social factors and food patch characteristics on female feeding costs. As an index of feeding cost, we tested the movement of females within focal tree food patches as a *response variable* in a GLMM with a binomial error structure. Each data point was one of either binary outcome "yes" or "no", corresponding to whether an individual female moved during a 1-min feeding focal recorded during the focal tree observations. We included the same *test predictors* as in the intake model, with the 2 following differences: 1) we did not include a quadratic dominance rank term as we did not expect a nonlinear effect of rank on movement, and 2) we included the group patch occupancy time as minutes until end of feeding bout, instead of using the proportion in to bout. Our interaction terms and *random effects* were the same as in the food intake model.

Energy balance model. As a final test to evaluate the mode of feeding competition among female bonobos, we used an LMM with a Gaussian error structure with the log-transformed urinary C-peptide levels, a proxy of energy balance, as the *response variable*. In line with our two models of behavior, we included dominance rank as our *main test predictor*. As an *additional social test predictor*, we used mean party size from the day preceding urine sample collection. Mean party sizes were calculated from the half-hourly party scan data, with the condition that the female (sampled the following morning for urinary C-peptide level) was observed in over 60 % of scans, as party size and composition can fluctuate throughout the day due to the fission-fusion dynamics of bonobo communities. We included the proportion of party scans the party spent feeding and the number of focal tree food patches visited per hour by the party as *test predictors* accounting for energy intake of the previous day. To calculate the proportion of feeding scans, we divided the number of half-hour party scans where most individuals of the party were observed feeding by the total number of scans recorded during the respective shift. The number of patches visited per hour variable was log-transformed due to its skewed distribution.

Because terrestrial herbaceous vegetation availability has been proposed to relax feeding competition among female bonobos (Wrangham 1986), we included the proportion of party scans the party spent feeding on terrestrial herbaceous vegetation during the prior day as an additional *test predictor*. We calculated the proportion from the half-hour party scans by dividing the number of scans where most individuals of the party were observed feeding on terrestrial herbaceous vegetation by the total number of scans recorded during the respective shift, and square-root transformed the variable to make the its distribution more symmetrical.

To examine potential effects of energy expenditure on urinary C-peptide levels, we included distance travelled by the party in meters per hour of observation as a *test predictor*. Calculation of this parameter was based on the GPS track log of the day prior to urine sample collection; each track was first cleaned to avoid artificial increases in track length due to GPS points recorded while the party was stationary in a feeding patch. The cleaned track distance was then divided by the total duration of track recording to obtain the mean speed.

While the bonobo habitat exhibits some degree of seasonality in terms of predictable dry seasons (Beaune et al. 2013b) and there may be periods that are nutritionally better in terms of food availability, we were not able to test for effects of seasonality based on phenology data. We therefore followed Emery Thompson et al. (2014) and modeled as a *test predictor* the variation in food abundance as the proportion of fleshy fruit in the feeding time budget measured with 30-min group scans.

Recent work on bonobos at LuiKotale by Surbeck et al. (2015) showed that urinary C-peptide levels in male bonobos varied with dominance rank depending on the party size of the previous day, with higher-ranking males showing greater increases in urinary C-peptide levels with increasing party size. We therefore included a 2-way interaction term between rank and party size to account for the possibility that female dominance rank affects energy balance differently depending on the size of the party. We tested for 2 additional 2-way interactions; one between dominance rank and duration of feeding and another between dominance rank and number of patches visited.

As uCP levels have been shown to be lower during the first 6 months of lactation in wild chimpanzees, (Emery Thompson et al. 2012) we included a dichotomous variable "lactating" vs. "non-lactating" (N = 28, 12.9 %) into our model as a *control predictor*. Bonobo identity and date were included as random effects to account for uneven sampling and repeated measures of individual females.

Model implementation. All of our mixed models were implemented in R (version 3.3.1.; R Core Team 2016) with the package "lme4" (Bates et al. 2015) for model fitting. As a preparatory step prior to fitting the models, we normalized our numeric and ordinal input variables by z-transforming them to a mean of zero and standard deviation of one. This facilitates the interpretability of the resulting parameter estimates and squared terms (Schielzeth 2010). In addition, we included random slopes for every model between all those pairs of random and fixed effects, where one fixed effect varied within one level of a random factor in order to keep the Type I error rate at the nominal rate of 5% (Schielzeth and Forstmeier 2009; Barr et al. 2013). For example, the same female fed in trees with different DBH's, so a random slope was modeled for the random effect of bonobo ID and the fixed effect of DBH. The same female had always only one rank, so the random slope was not included for bonobo ID and rank.

We obtained Variance Inflation Factors (VIFs; Field 2005) determined for standard linear models (excluding the random effects, interactions, and squared terms) with the package "car" (Fox and Weisberg 2011) in order to rule out potential collinearity issues among the predictor variables. We did not find any issues with collinearity among our predictors (maximum VIF = 1.77). For the energy balance model with Gaussian error structure, we made a visual assessment of a quantile–quantile plot and the distribution of residuals plotted against fitted values to verify the assumptions of normally distributed and homoscedastic residuals, and did not detect any deviations from these assumptions. We checked model stabilities by omitting each level of random effects one at a time and comparing the derived model estimates with those of the full model estimates. The comparison of estimated coefficients did not reveal any influential cases. We checked that the food intake model with Poisson error structure complied with the model assumption of absence of overdispersion (Cameron and Trivedi 1990) and did not detect any issues with overdispersion ($\chi^2 = 2392.91$, $P = 1$, dispersion parameter = 0.528).

As an initial test of significance (Forstmeier and Schielzeth 2011), we compared each of our full models against its respective null model (excluding test predictors but including random effects and respective random slopes) with a likelihood ratio test using the anova function with the test argument set to "Chisq." Our threshold for statistical significance was set to $P = 0.05$. On the condition that the full model was significant against the null model, we proceeded to test for the significance of each variable one at a time (Barr et al. 2013) using the drop1 function in R. We tested the significance of interaction terms first, removing all nonsignificant interactions and only then testing the lower order variables that had been involved in the interactions. Our samples sizes were $N = 4550$ for the food intake model, $N = 4500$ for the movement model, and $N = 218$ for the energy balance model. Details concerning the number of levels per random effect for each model can be found in Table 2.

RESULTS

During the study period, females showed joint aggression against a common target 17 times (i.e. they formed a coalition sensu de Waal and Harcourt 1992) and a female supported another female in a conflict twice. The target in these conflicts was a male in 17 cases and a female in 2. Considering only those conflicts that could be clearly assigned to a feeding context, 10 female–female coalitions were observed and 9 targeted an adult male. Thus, females were more likely to work against males than against females in polyadic conflicts with low probabilities that these outcomes were the result of a random process (Binomial test for all conflicts $N = 19$,

Table 2
Summary of models tested

Model (type/error structure)	Data point	Units	Sample size	Test predictors	Control predictors	Random effects (number of levels)
Food intake (GLMM/ Poisson)	Focal min	Bites/handfuls/items	4550	Interaction: Rank^2 * # individuals in patch (*log*) Interaction: Rank^2 * Patch size in DBH Interaction: Rank^2 * Food crop size score (*log*) Rank Rank^2 # individuals in patch (*log*) Patch size in DBH Food crop size score (*log*) Proportion time into bout Proportion time into bout^2	Time of day Time of day^2	Bonobo ID (14 levels) Focal tree ID (328 levels) Bout ID (404 levels) Food sp. (18 levels)
Movement (GLMM/ Binomial)	Focal min	Move (y/n)	4500	Interaction: Rank * # individuals in patch (*log*) Interaction: Rank * Patch size in DBH Interaction: Rank * Food crop size score (*log*) Rank # individuals in patch (*log*) Patch size in DBH Food crop size score (*log*) Time until end of bout	Time of day Time of day^2	Bonobo ID (14 levels) Focal tree ID (328 levels) Bout ID (404 levels) Food sp. (18 levels)
Energy balance (LMM/ Gaussian)	uCP (log)	ng/mg Crea	218	Interaction: Rank * Mean party size of previous day Interaction: Rank * # of food patches per hour (*log*) Interaction: Rank * Proportion of feeding scans Rank Mean party size of previous day # food patches per hour (*log*) Proportion of feeding scans Meters travelled per hour Proportion of THV scans (*sq.rt*) Monthly average proportion of fruit scans	Lactation (y/n) Behavior shift (am/pm)	Bonobo ID (14 levels) Date (115 levels)

$P = 0.0007$, and for conflicts in feeding context $P = 0.014$). All 14 females engaged in joint aggression against male targets in a total of 17 different dyads. Comparing raw counts from all occurrences data matched per female, in dyadic conflicts in a feeding context females did not aggress males more often than females (median and interquartile range for male targets = 6 (3–10), for female targets = 4 (2–11), Wilcoxon matched pairs test $N = 14$, $T = 43$, $P = 0.86$). This pattern remained stable after exclusion of the three lowest ranking females that exhibited low or no aggression to other females in dyadic feeding conflicts ($T = 26$, $P = 0.88$).

During the 2 field seasons we sampled a total of 683 focal patches, consisting of the following food types: fruits, leaves, flowers, pith, tree bark and animal matter. Most food items were fruits (611 patches; 45 taxa), including dry fruit pods (64 patches; 6 taxa) of the family *Fabaceae*, from which bonobos extracted seeds only (except for *Scorodophloeus zenkeri*). Bonobos consumed leaves (53 patches; 9 taxa), with some of the taxa appearing also in other food types, for instance, the leaves and fruit of *Dialium* spp. were consumed, and the leaves, flowers (6 patches) and dry fruit pods of *Scorodophloeus zenkeri* were consumed. The remaining focal patch observations involved the consumption of animal matter (8 patches; 4 taxa), tree bark (1 patch; 1 taxon) and waterlily (4 patches; 1 taxon).

Table 3

Food intake rate increases with increasing dominance rank and increasing food crop

	Descr. Stats. mean (range)	Estimate ± SE	z	P
Intercept		1.575 ± 0.209	7.546	[a]
# individuals in patch	5 (1–17)	−0.014 ± 0.012	−1.210	0.235
Patch size as DBH (cm)	62 (4–350)	−0.013 ± 0.025	−0.496	0.632
Food crop size score	**3.6 (2–5)**	**0.068 ± 0.030**	**2.245**	**0.046**
Rank		**0.034 ± 0.011**	**3.202**	**0.023**
Proportion into bout	0.4 (0–1)	−0.071 ± 0.008	−8.559	[a]
Proportion into bout^2		**0.028 ± 0.010**	**2.716**	**0.010**

The proportion of time remaining until the end of a feeding bout has a non-linear relationship with individual food intake rate. Results are an overview of a GLMM ($N = 4550$ focal minutes; mean minutes per female ± SD = 325.0 ± 217.7, range = 89.0–935.0), with the significant effects displayed in bold. The full model was highly significant as compared to the null model (likelihood ratio test $\chi^2 = 43.26$, df = 13, $P < 0.001$). All interaction terms were non-significant and we therefore removed them from the model. [a]Significance test not indicated because of not having a meaningful interpretation.

Bonobos consumed *Dialium* in 16 % (110 observations of 683) of focal trees, relatively consistently throughout both field seasons. The second most frequently used focal tree species was *Polyalthia suavolensis* (12 %, 80 observations), which was consumed almost exclusively during a 2-month period (Nov-Dec) of the first field season, whereas during the second field season it was recorded only on a few days in November. Only 8% of focal tree observations concerned leaf consumption (53 observations), and 9% were on seed feeding in *Caesalpinioideae* trees (64 observations).

In order to investigate the effects of social factors and food patch characteristics on the food intake rates of female bonobos, we analyzed 404 feeding bouts that took place in 328 focal trees from 13 ripe fruit taxa, 3 dry fruit pod taxa, 3 leaf taxa, and 1 flower taxon. We did not include food items such as duiker meat (*Philantomba monticola*), jungle sop (*Anonidium mannii*), or African breadfruit (*Treculia africana*) due to the difficulty to obtain intake rates from a number of different females.

Our full model for the food intake was significant as compared to the null model (likelihood ratio test: $\chi^2 = 43.26$, df = 13, $P < 0.001$, Table 3). We found that the proportion of time until the end of a feeding bout had a significant, nonlinear effect on intake rate (Table 3). Intake rates declined steeply from the beginning of a bout towards the middle and continued to decline on a shallower curve towards the termination of a bout (Figure 2b). Together with the observation that the probability of moving in food patches increased as the minutes until the end of the bout decreased (Table 4, Figure 3b; see the movement model below), these results suggest that the bonobos depleted their food patches.

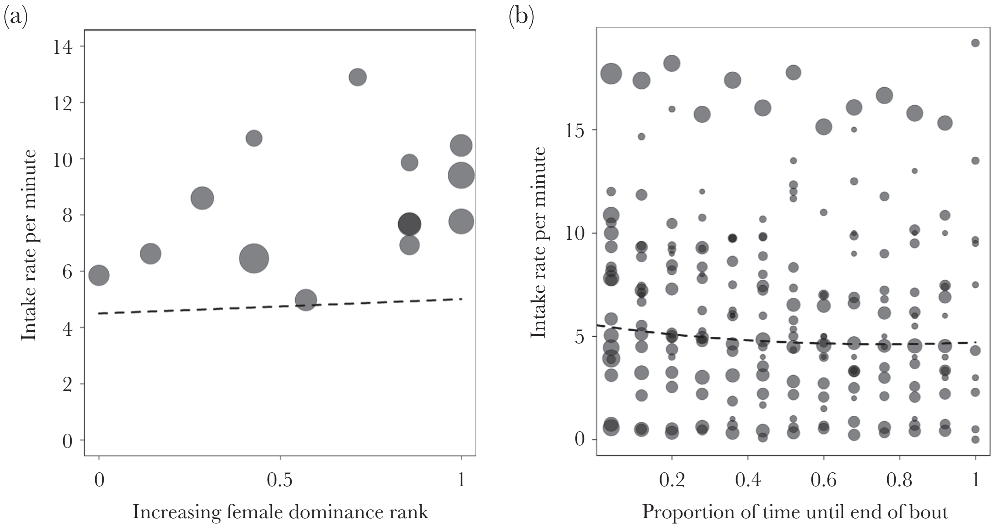

Figure 2

Food intake rate in focal trees in relation to (a) female dominance rank (GLMM: estimate ± SE = 0.034 ± 0.011, $\chi^2 = 5.21$, df = 1, $P = 0.023$), and (b) the proportion of time until end of bout with 1 on the x-axis indicating the termination of bout (GLMM: estimate ± SE = 0.028 ± 0.010, $\chi^2 = 6.73$, df = 1, $P = 0.010$). The area of each circle in a) is in proportion to the number of data points per female. The area of each circle in (b) is in proportion to the number of data points per food type. The dashed line in both (a) and (b) depicts the fitted model.

The food intake model also revealed a significant positive effect of female dominance rank on intake rates (Table 3), lending support to the Cooperative Defense and the Priority of Access hypotheses but running against the Resource Abundance hypothesis (Table 1). Across all food patches, the higher ranking a female was, the more food she ingested per unit time spent in the patch, though the effect was modest (Figure 2a). The interaction between rank (including rank squared) and the number of individuals in a patch was nonsignificant, suggesting that the effect of rank on intake rate was similar across feeding group sizes, in support of the Cooperative Defense hypothesis. In addition, we found that the amount of food crop had a significant effect on intake rates (Table 3) such that animals feeding in focal patches with a larger crop size enjoyed higher intake rates. The observed rank effects on intake rates were not affected negatively by food crop size, as evidenced by the nonsignificance of the interaction between rank (including rank squared) and crop size, indicating that contest competition was not generally increased in patches containing less food.

Using the same subset of N = 404 feeding bouts as the intake model and the same ecological and social predictors, we modeled the probability that a female moved during a minute of feeding in a focal tree which occurred in 18% of cases. Overall, our full model for movement was significant as compared to the null model (Table 4). We found a significant relationship between female dominance rank and movement, with lower ranking females being more likely to move in food patches than higher-ranking females (Figure 3a). None of the interaction terms between dominance rank and factors promoting contest competition (patch size, crop size, and feeding party size) reached significance. Thus, patches did not differ much in the strength of contest competition caused. Therefore, the nonsignificant interaction terms were excluded from the movement model. Interestingly, we observed a statistical trend for the interaction of dominance rank and the number of co-feeding individuals to have an effect on movement probability, indicative of interference between individuals.

Our behavioral models suggest that increasing dominance rank is associated with increasing food intake rate and reduced feeding effort when co-feeding. Next, we investigated whether these effects translated in to variation in energy balance by modelling uCP levels as a function of social and ecological factors. For the N = 218 urine samples included in the analyses, the median uCP level per individual (N = 14) ranged from 1.49 to 3.30 ng/mg Crea with an overall range of values from 0.39 to 11.12 ng/mg Crea.

The full energy balance model was significantly different from the null model (χ^2 = 20.029, df = 10, P = 0.029, Table 5). None of the interaction terms of dominance rank with a possible predictor of contest competition intensity was a significant predictor of urinary C-peptide, and neither was dominance rank as a main effect in the reduced model (Table 5). The sole significant predictor of uCP levels was the monthly proportion of fruit in the diet as a measure of the seasonal abundance of these high-quality resources (Figure 4).

Female dominance rank and the average party size she travelled in were not correlated (Pearson's r = 0.12, N = 8, P = 0.78; Figure 5a); maximum (25) and minimum party size (1 to 3) were

Table 4

The probability of movement in food patches decreases with dominance rank

	Descr. Stats. mean (range)	Estimate ± SE	z	P
Intercept		−1.349 ± 0.194	−6.948	[a]
# individuals in patch	5 (1–17)	−0.102 ± 0.104	−0.977	0.383
Patch size as DBH (cm)	62 (4–350)	0.088 ± 0.133	0.666	0.522
Food crop size score	3.6 (2–5)	0.047 ± 0.128	0.366	0.729
Rank		**−0.150 ± 0.069**	**−2.192**	**0.049**
Minutes until end of bout	**46 (0–249)**	**−0.261 ± 0.088**	**−2.976**	**0.010**

The probability of movement has a negative, linear relationship with time remaining until the end of a focal tree bout, indicating that movement in focal trees increases towards the end of a feeding bout. Results are an overview of a GLMM (N = 4500 focal minutes), with the significant effects displayed in bold. The full model was highly significant as compared to the null model (likelihood ratio test χ^2 = 21.43, df = 5, P < 0.001). All interaction terms were nonsignificant and we therefore removed them from the model. [a]Significance test not indicated because of not having a meaningful interpretation.

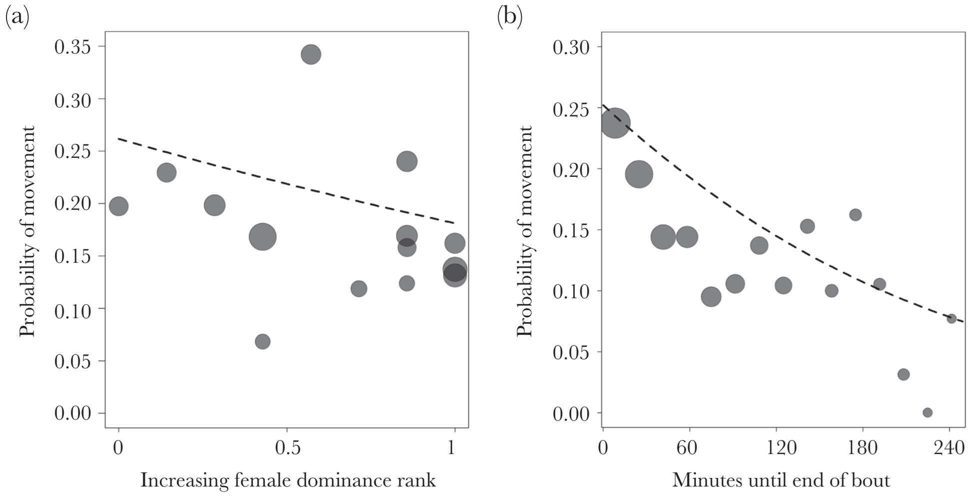

Figure 3

Probability of movement in focal patches as a measure of feeding effort in relation to (a) female dominance rank (GLMM: estimate ± SE = -0.150 ± 0.069, χ^2 = 3.89, df = 1, P = 0.049), (b) how many minutes remain until the end of the focal patch feeding bout (GLMM: estimate ± SE = -0.261 ± 0.008, χ^2 = 6.65, df = 1, P = 0.010). The area of each circle in (a) is in proportion to the number of data points per female. The area of each circle in (b) is in proportion to the number of data points across food type. The dashed line in both (a) and (b) depicts the fitted model.

Table 5

Urinary c-peptide level increases as the monthly average proportion of fleshy fruits in the diet increases

	Descr. Stats. mean (range)	Estimate ± SE	*t*	*P*
Intercept		0.561 ± 0.186	3.012	[a]
Mean party size	9.0 (3.0–20.7)	0.063 ± 0.061	1.022	0.311
# food patches per hour	0.70 (0.16–2.89)	−0.061 ± 0.042	−1.457	0.150
Proportion feeding scans	0.39 (0–0.88)	−0.022 ± 0.049	−0.448	0.674
Rank		−0.052 ± 0.065	−0.792	0.431
Meters travelled per hour	281.9 (5.1–1083.8)	0.049 ± 0.050	0.978	0.346
Proportion of THV scans	0.13 (0–0.43)	0.059 ± 0.051	1.145	0.266
Monthly average proportion of fruit scans	**0.68 (0.38–0.88)**	**0.174 ± 0.043**	**4.075**	**<0.001**

Results are an overview of a LMM (N = 218 urine samples), with the significant effect displayed in bold. The full model was highly significant as compared to the null model (likelihood ratio test χ^2 = 20.029, df = 10, P < 0.029). All interaction terms were nonsignificant and we therefore removed them from the model.
[a] Significance test not indicated because of not having a meaningful interpretation.

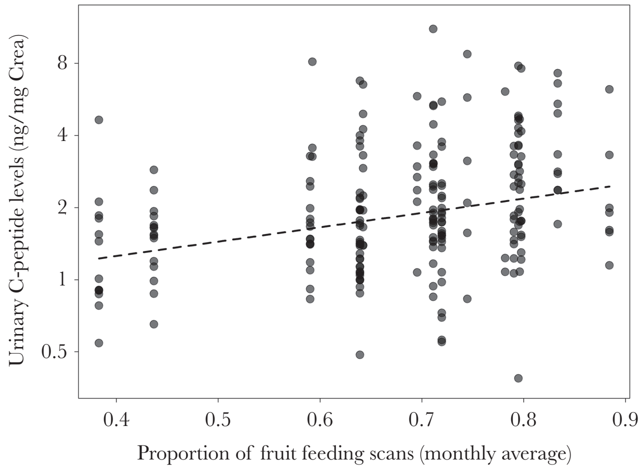

Figure 4

The effect of monthly average proportion of fleshy fruit on urinary C-peptide levels (LMM: estimate ± SE = 0.174 ± 0.043, χ^2 = 11.29, df = 1, P < 0.001). Urinary C-peptide levels are log-transformed. The dashed line depicts the fitted model.

nearly identical for all females. There was also no rank effect on how often females were missing from group scan observations (Pearson's correlation between number of scan observations and female dominance rank r = 0.19, N = 14, P = 0.52). At least one individual visited a THV patch in 7.2 % of all group scans. Dominance rank did not have an effect on the time a female spent feeding on THV while travelling (Pearson's correlation between proportion of scans with THV feeding and female dominance rank r = 0.16, N = 14, P = 0.59; Figure 5b).

DISCUSSION

Our study revealed that females cooperated against male targets in agonistic coalitions, increasing female dominance rank was associated with decreasing feeding effort but moderate increases in food intake rates across a range of different food items and tree species, and that these rank effects did not translate into rank effects on female energy balance. Instead, variation of energy balance reflected the proportion of fruit in the diet with changes in uCP being independent of rank. In the following, we discuss these results in light of the 3 socioecological hypotheses for the evolution of bonobo female sociality and agonistic behavior.

The key prediction of the THV sub-hypothesis is that consumption of terrestrial herbs (THV) compensates for differences in food intake in fruit trees and that differences in access to such herbs are causally linked to the species-differences in female sociality (Wrangham 1986). However, in our study the use of THV was neither associated with dominance rank nor did dominance rank predict how often females were missing from the main party (our proxy to signal that subordinates would have opted to feed alone more often). A lack of rank effect on party size could be explained by rank assortative association in 2 or more parties of rather homogenous ranks. As strong evidence against such assortativeness, we have shown elsewhere that neither the social nor the rank relationship between females predicted their post fission association (Moscovice et al. 2017).

It has been suggested that rather than feeding on THV when others consume fruit, it could be that low-ranking females compensate for the lower energy gain from fruit trees by feeding on THV when parties travel between fruit trees (Wrangham et al. 1996). The premise of this feed-as-you-go hypothesis is that either THV is uniformly distributed or that that patches are large enough to accommodate large parties, two conditions that are not always met (Malenky et al. 1994). The model also suggests that unlike chimpanzees, bonobos slow down travel velocity when moving between fruiting trees (Wrangham 2000) which implies that most party members consume THV. However, in this case, it is reasonable to infer that the energetic gain from THV would be similar across

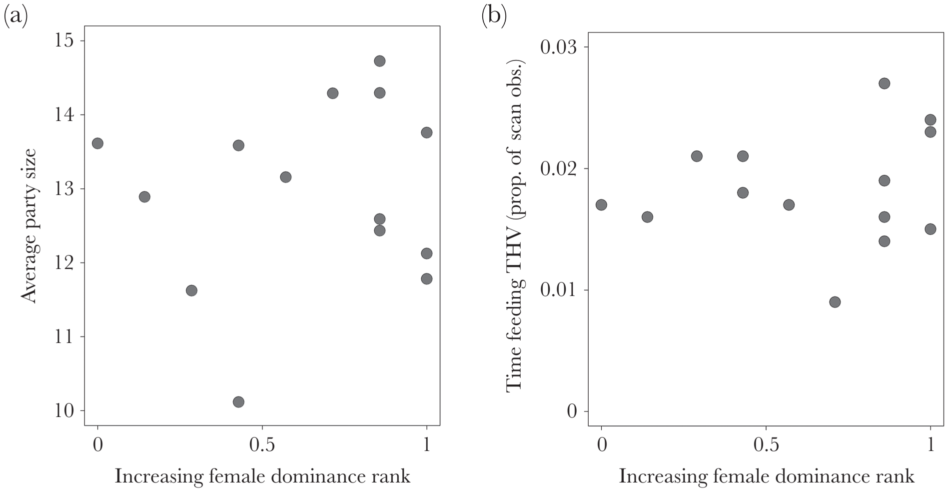

Figure 5

Relation between female dominance rank and (a) average party size the female was seen in (Pearson's r = 0.12, N = 8, P = 0.78), and (b) time spent feeding terrestrial herbaceous vegetation (THV), as the proportion of THV feeding scans over all scan observations including each female (r = 0.16, N = 14, P = 0.60).

individuals and that low ranking females would gain extra energetic benefits only if they had higher food intake or profit from enhanced fiber digestibility. Individual focal follows of females, including combined data on THV intake rates and food patch residence times, could yield a more rigorous test for potential rank effects on THV feeding. To specifically target potential compensation processes, comparative data are needed from females temporally leaving the party and those maintaining close proximity to others.

The key premise of the fruit patch size sub-hypothesis is that bonobos feed in fruit trees large enough to avoid direct and indirect feeding competition (Badrian and Badrian 1984; White 1986, as cited in White and Wragham 1988, as cited in White and Wragham 1988). Support for this is restricted to one data set (White and Wrangham 1988), with subsequent studies finding that both *Pan* species use fruit tree patches of comparable sizes (e.g. Chapman et al. 1994; Furuichi et al. 2015). Our data also speak against the fruit patch size hypothesis because we found diminishing returns coupled with increasing effort suggesting that bonobos depleted fruit patches independent of their size, which evidently caused competition. Our behavioral data clearly show rank effects on female food intake and feeding effort, suggesting that females engage in contest competition over food. These rank effects should not prevail under the Resource Abundance hypothesis if competitive exclusion had no benefit (energy balance not affected by dominance rank) but carried any costs for the dominants over evolutionary time. If our assumption about contest effects fading over evolutionary time is wrong, then the Resource Abundance hypothesis would predict that subordinates would compensate for ingestion deficits in fruit patches by THV consumption, which was not the case either.

In support of the Cooperative Defense hypothesis and in agreement with earlier studies (Parish 1996; Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016), female agonistic collaboration targeted mainly males and this was not a byproduct of females being generally more aggressive towards males than females, because females targeted males and females equally often in dyadic conflicts. Further support for the Cooperative Defense hypothesis came from the observation that food patches were depleted by feeding parties, and that dominance rank effects on food intake and feeding effort in fruit patches were moderate. The one prediction not supported by our data is that energy balance should vary with dominance rank. This could indicate either that high-ranking female bonobos do not profit through contest competition in terms of energy balance, or that effects exist but are too small to be detected by the analysis. Yet, we were able to detect individual changes in uCP between gestation and other reproductive phases. We also detected a nutritional signal with significantly higher uCP levels on days when bonobos mainly fed on abundant, easy to harvest, high sugar fruits versus days when feeding mainly on difficult to harvest starch rich fruits. Accordingly, the only significant predictor of uCP levels in our energy balance model was the proportion of fleshy fruit in the monthly diet. As a further point supporting the sufficient sensitivity of our energy balance measure, we have previously shown for the males of the same bonobo group that dominance rank effects on uCP can be picked up, but depend on the size of the party a male was travelling in, which can be interpreted as a proxy for food abundance (Surbeck et al. 2015). Another possibility is that high-ranking females indeed had energetic advantages from contest competition, but immediately transferred these gains to their offspring. If dominant females provided more or richer milk, differences would not be expected in female energy balance but rather in inter-birth interval or offspring survival. Our combined findings bear resemblance to the pattern observed in female mountain gorillas; despite clear behavioral indications of feeding competition (Wright et al. 2014; Wright et al. 2015; Grueter et al. 2016), uCP did not vary with dominance rank (Grueter et al. 2014). Future studies should try to link behavioral and energetic indicators of feeding competition more directly to assess whether uCP variation is more pronounced on days with more pronounced behavioral variation in terms of feeding times, ingestion rates, and food quality.

The Priority of Access hypothesis predicts that female–female coalitions and female agonistic support in the feeding context should target other females, that dominance rank has strong effects on food intake and feeding efficiency in fruit patches, and on overall energy balance. Rank effects on food intake and feeding effort were significant across a wide range of different food items from many different species with largely varying resource characteristics, but these effects were generally weak. This interpretation is supported by visual inspection of the data for specific, frequently consumed food items, none of which showed pronounced rank effects. If females associated with one another to exclude other females from food resources, as predicted by the Priority of Access hypothesis, large differences in food intake rates between such alliances should ensue. Consequently, subordinates should be excluded from food patches and parties, yielding highly differentiated association patterns. However, subordinates were not missing from parties more often than dominants and lower ranking individuals did not avoid travelling in larger parties. Socioecological theory would also predict females to form strong affiliative relationships with their cooperation partners (Sterck et al. 1997; Ostner and Schülke 2014). Agonistic support, however, is not correlated with the strength of dyadic affiliative relationships in female bonobos at LuiKotale (Moscovice et al. 2017). This is partially supported by findings from bonobos at Wamba, where female coalition formation is facilitated by being associated in the same party yet coalitions did not correlate with proximity or grooming (Tokuyama and Furuichi 2016). Hence, female bonobos seem to choose partners for cooperation and affiliation (Hohmann et al. 1999) rather opportunistically.

Our predictions derived from the Cooperative Defense and the Priority of Access hypotheses do overlap to some extent. Both hypotheses received some support from the result that 1) food resources were depleted by the bonobos, a prerequisite for feeding competition to occur (Snaith and Chapman 2005; Heesen et al. 2014) and that 2) dominance rank was a positive predictor of food intake and a negative predictor of feeding effort in food patches albeit we predicted strong effect from the Priority of Access Hypothesis and observed weak effects. Our findings are not so different from what has been described for female chimpanzees in terms of rank-effects on feeding efficiency (reviewed in Pusey and Schroepfer-Walker 2013). Lower-ranking females of the Gombe community spent significantly more time foraging, and consumed a lower quality diet compared to high-ranking females (Greengrass 2005; Murray et al. 2006). Female chimpanzees at Gombe tend to concentrate their use of the community range by establishing overlapping core areas, with high-ranking females occupying smaller, higher quality core areas than low-ranking females (Murray et al. 2007). Differentiated use of the community range occurs also at Kanyawara where high-ranking chimpanzee females are significantly more likely to occupy core areas containing high-quality forage, and tend to exhibit shorter inter-birth intervals and higher levels of ovarian hormones (Emery Thompson et al. 2007; Kahlenberg et al. 2008a). At Taï National Park, where female chimpanzees tend to be more sociable than is typically reported for chimpanzees, and where they use the entire territory, often in mixed parties, contest competition was found to increase with increasing number of competitors, or when food was monopolizable. In the latter case, high-ranking females possessed food significantly more frequently following a conflict than low-ranking females (Wittig and Boesch 2003).

Dominance rank effects on feeding behavior are highly variable within and between primate species independent of their broadly categorized diet. Among frugivores female olive baboons (*Papio cynocephalus anubis*) exhibit strong rank effects on supplant rates, food intake rates and energy intake (Barton 1993; Barton and Whiten 1993), whereas Assamese macaques (*Macaca assamensis*) exhibit none of these effects (Heesen et al. 2013). Dominance rank predicts energy intake in folivorous Hanuman langurs (*Semnopithecus entellus*, Koenig 2000) and rank effects are variable within folivorous Mountain gorillas (*Gorilla beringei beringei*). Dominance rank affects THV feeding site residence times in one population (Grueter et al. 2016) and fruit feeding time in another (Wright et al. 2014), which translates into rank effects on energy intake/balance in one case but not the other. Together these results suggest that the drivers and consequences of feeding competition can only be understood with an integrated view combining detailed knowledge about food resource characteristics, differential feeding behavior within food patches, inter-individual variation occurring between patches, and a full picture of the energetic consequences of differential resource use and how it is traded-off against other benefits.

The prediction most clearly differentiating between the two hypotheses is that under the Priority of Access hypothesis female–female coalitions should mainly target other females whereas collaborative aggression should mainly target males under the Cooperative Defense hypothesis. We found the latter prediction to be supported. In dyadic conflicts on the other hand, females did not target males more often than females. Thus, it is not the use of force in general that differs according to target sex, but specifically the collaborative element that characterizes conflicts with males. Another prediction that differentiates between the 2 hypotheses was that only under the Cooperative Defense hypothesis all contest effects should be weakened by female–female tolerance that is required for their cooperation against males. With both of these predictions being met, we conclude the Cooperative Defense hypothesis to be best supported by our data. This does not mean that cooperative defense of food sources against males is the only force promoting gregariousness in female bonobos. Females may associate to protect their offspring against males (e.g. lions, Packer et al. 1990), to defend the groups territory (e.g. spotted hyenas, Boydston et al. 2001), or to support close relatives (e.g. humans, Cant and Johnstone 2008) or to maintain autonomy in mating partner choice (Wrangham and Pilbeam 2001; Hare et al. 2012; Hare 2017). In bonobos, male infanticide has never been observed, but male aggression against immature individuals is likely to trigger agonistic aid among females (Surbeck and Hohmann 2013).

Other evidence in support of female bonobos counteracting aggressive male mating strategies includes extended periods and reduced precision of sexual signaling compared to chimpanzees (Douglas et al. 2016), and earlier maturation of females (Behringer et al. 2014) coupled with increased tolerance towards and early bonding with young immigrant females in bonobos versus delayed dispersal due to the resistance from residents in chimpanzees (Pusey 1990; Boesch and Boesch-Achermann 2000; Kahlenberg et al. 2008b). While gregariousness among female bonobos may derive multiple benefits, feeding competition remains a prominent factor that affects most or all resident females independent of their age, parity, and kinship. Ours and the published results discussed here are most congruent with the Cooperative Defense hypothesis.

More data on intra and intersexual conflicts, especially on polyadic conflicts, are needed and on other indicators of females excluding males from access to limiting resources. A more detailed understanding of female energy allocation to different functions (energy storage and maintenance functions versus investments in current reproduction) will be required until the Priority of Access hypothesis can be firmly rejected. Since another contrast between chimpanzees and bonobos concerns differences in male-male cooperation, one may also turn the argument around and, instead of asking why female bonobos exclude males from resources, ask why the highly cooperative male chimpanzees will never allow that. Thus, understanding the differences in female social relationships between bonobos and chimpanzees ultimately will require broadening the perspective to male-male and intersexual relationships.

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