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Variation in aggression rates and urinary cortisol levels indicates intergroup competition in wild bonobos

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ABSTRACT

Intergroup competition is a widespread phenomenon across taxa and groups typically compete over access to limited resources, such as food and mates. Such competition may be quantified by changes in individuals' behavioral and physiological status in response to intergroup encounters (IGEs). Bonobos, one of our closest living relatives, are often regarded as xenophilic and exhibit high tolerance towards out-group individuals. This tolerance between groups may still be accompanied by intergroup competition over resources. We hereby compared variation in aggression rates and urinary cortisol levels of bonobos during and outside contexts of IGEs in the Kokolopori Bonobo Reserve and investigated whether food and mate availability influenced males' and females' aggression and cortisol levels, when controlling for dominance rank and the number of individuals present. We found that although females had higher aggression rates and urinary cortisol levels during than outside contexts of IGEs, these increases were not related to food availability or changes in between-group dynamics when maximally tumescent females were present, rather than absent. Furthermore, males showed higher aggression rates and urinary cortisol levels during than outside contexts of IGEs. However, males' responses during IGEs were not related to the presence of maximally tumescent females and food availability. Taken together, while competition intensified during seemingly tolerant IGEs in bonobos, such competition was unrelated to short-term changes in food and mate availability. Despite physical and physiological costs of aggression, bonobos associate with out-group individuals frequently and for extended periods. This suggests potential benefits of bonobo intergroup associations.

1. Introduction

Competition between social groups is ubiquitous in group-living animals. Such competition can be costly to individuals as it can be energetically demanding (Amsler, 2010; Jaeggi et al., 2018; Schoof and Jack, 2013) and interactions between groups can escalate into physical fights, resulting in severe injuries or even fatality (Clutton-Brock et al., 1982; Dyble et al., 2019; Mitani et al., 2010; Rosenbaum et al., 2016). Sometimes, groups may avoid physical contact in order to minimize costs associated with intergroup competition (Furuichi, 2020; Robbins and Sawyer, 2007). Competition over resources such as food and mates is identified as the underlying primary cause of fights between groups in many nonhuman animals (Arseneau-Robar et al., 2017; Grant, 1997; Scarry, 2017; Thompson et al., 2017). Owing to differences in

reproductive strategies, males' and females' response towards out-groups may vary with the type of resources at stake (Clutton-Brock and Huchard, 2013). Since female reproductive success is mainly constrained by access to food resources, females tend to react more aggressively towards intruders or during intergroup encounters when food abundance is low or when intergroup interactions occur in feeding sites that are more frequently used by group members (Brown, 2013; Fedy and Stutchbury, 2005; Ostfeld, 1990; but see Crofoot, 2007). Conversely, male fitness is mostly restricted by direct access to mating opportunities, but sometimes also by access to resources that can attract or benefit mates (Fashing, 2001; Kitchen and Beehner, 2007). Hence, males are often more aggressive towards intruders or out-groups when sexually receptive females are present and/or when food is scarce (lizards: Stamps, 1977; banded mongooses: Cant et al., 2002; black and

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white colobus monkeys: Harris, 2010; savannah baboons: Kitchen et al., 2004). Taken together, the availability of fitness-limiting resources, such as food and mates, may determine the participation and competitive strategies of males and females during intergroup encounters (Cooper et al., 2004; Fashing, 2001; Kitchen and Beehner, 2007; Koch et al., 2016a; Majolo et al., 2005; Mirville et al., 2018; van Schaik et al., 1992).

To better understand the evolutionary selection pressures favoring different strategies of intergroup interactions in humans, many researchers have turned to the chimpanzees as a referential model. Chimpanzees are a territorial species, in which males, and sometimes females, collectively defend their territory through border patrols and intergroup encounters (Langergraber et al., 2017; Mitani and Watts, 2005; Samuni et al., 2017). An increase in territory size at the expense of the out-group can improve access to food sources and increase female reproductive success in chimpanzees (Mitani et al., 2010; Williams et al., 2004; Wilson et al., 2012). Given the potential benefits resulting from intergroup competition, chimpanzees are motivated to expel and sometimes even kill out-group individuals (Wilson et al., 2014). A lesser known, but equally relevant referential model for the evolution of male and female strategies in intergroup encounters in humans is the bonobo (*Pan paniscus*). Alongside chimpanzees, bonobos are our closest living relatives that live in male-philopatric societies with fission-fusion dynamics. Physical intergroup encounters in bonobos vary greatly in duration, ranging from less than an hour to more than 10 consecutive days (Lucchesi et al., 2020a; Sakamaki et al., 2018). During bonobo intergroup encounters, males and females of different groups may interact in both aggressive and non-aggressive ways (Furuichi, 2020; Hill et al., 2014; Hohmann and Fruth, 2002; Samuni et al., 2020; Tokuyama et al., 2019). The highly varied intergroup interactions of male and female bonobos are in striking contrast to the largely hostile, male-dominated intergroup interactions in chimpanzees (Boesch et al., 2008; Hashimoto et al., 2020; Samuni et al., 2017). While lethal attacks on out-group individuals have been documented in 15 of the 18 long-term chimpanzee study sites, there is no clear evidence for the occurrence of such killing in bonobos (Wilson et al., 2014). On rare occasions, lone male bonobos may even make voluntary visits to neighboring groups for a few days, without receiving any severe attacks by out-group individuals (Toda et al., 2018; Cheng & Samuni personal observations). However, even in the absence of severe attacks, bonobo intergroup encounters involve aggressive interactions between groups (Tokuyama et al., 2019), which may lead to social tension and uncertainty. Yet, most studies have focused on the amicable intergroup relations in bonobos (Fruth and Hohmann, 2018; Sakamaki et al., 2018; Tan et al., 2017), with an emphasis on the contribution of females to the peaceful nature of bonobo societies (Furuichi, 2011; Tokuyama et al., 2019). To date, little is known about the potential competitive aspect of bonobo intergroup encounters.

It has been suggested that feeding competition is more relaxed in bonobos than in chimpanzees owing to reduced seasonal variation in fruit abundance and larger fruit patch sizes in bonobo habitat (Chapman et al., 1994; Furuichi, 2009). As a result, different groups can associate peacefully for extended periods without incurring significant feeding costs (Lucchesi et al., 2021; Sakamaki et al., 2018). However, there are indications that male bonobos may incur some feeding costs, as females often collectively defend food access against males within group (Nurmi et al., 2018; Surbeck et al., 2015). Furthermore, even though male bonobos were more aggressive than female bonobos during intergroup encounters (Tokuyama et al., 2019), whether males of different groups directly compete over mates is still unclear. While copulations between individuals of different groups are relatively common in bonobos as compared to chimpanzees, extra-group paternity is rare in bonobos (Gerloff et al., 1999; Ishizuka et al., 2018). Female bonobos cycle more frequently and for longer periods than female chimpanzees (Douglas et al., 2016; Jaeggi et al., 2016). Given that there can be several sexually receptive females present at a given time and that female sexual swellings are not reliable indicators of fecundity in bonobos (Douglas et al.,

2016), it may be difficult for male bonobos to monopolize and defend their mates in both within- and between-group contexts. In contrast to the vast literature on intergroup relationships in chimpanzees, detailed behavioral accounts of intergroup relations and competition in bonobos mainly emerge from one bonobo population, Wamba (Idani, 1990; Sakamaki et al., 2018; Tokuyama et al., 2019). Here, to better understand the nature and diversity of intergroup relations in bonobos, we explore proximate measures of intergroup competition in another bonobo population.

When an animal is exposed to an unpredicted or aversive stimulus in its physical and/or social environment, the hypothalamic-pituitary-adrenal (HPA) axis is activated (Beehner and Bergman, 2017; Goymann and Wingfield, 2004). Cortisol is then released from the adrenal gland, enters systemic circulation via the bloodstream, and binds to receptors throughout the brain and body. This physiological reactivity leads to an inhibition of non-essential metabolic functions and allows energy to be mobilized temporarily to support immediate energetically demanding activities. Thus, cortisol reactivity is an indicator of increased metabolic demands, regardless of whether or not the event or stimulus is stressful (MacDougall-Shackleton et al., 2019). An acute rise in cortisol is adaptive as long as the mobilized energy helps increase fitness (McEwen and Wingfield, 2003). Due to practical constraints, most studies of wild animals cannot measure cortisol directly and rely on measuring metabolites of cortisol in urine or feces (i.e., glucocorticoid metabolites/GCs; Gesquiere et al., 2008; Preis et al., 2019; Sapolsky, 1993; Wessling et al., 2018). Elevated GC levels have also been linked to territorial behavior and intergroup competition in birds (van Duyse et al., 2004; Landys et al., 2010; Gill et al., 2008; Lobato et al., 2010), nonhuman primates (Amsler, 2010; Jaeggi et al., 2018; Samuni et al., 2019b; Schoof and Jack, 2013; Sobolewski, 2012; Wittig et al., 2016), and humans (Edwards et al., 2006; Salvador et al., 2003; Wagner et al., 2002). The association between higher GC levels and intergroup competition is evident in both sexes among chimpanzees and humans (Edwards and Kurlander, 2010; Oxford et al., 2010; Wittig et al., 2016), with higher GC levels observed in more intensified intergroup competition (e.g., contact aggression between groups versus vocal encounters; Samuni et al., 2019b). Cortisol can therefore be a useful tool to indicate competition that occurs in between-group contexts. However, to better identify competitive situations during intergroup encounters, it is beneficial to complement endocrinological measures with behavioral correlates of intergroup competition.

In this study, we monitored variation in rates of aggression during intergroup encounters (i.e., between-group settings) and outside contexts of intergroup encounters (i.e., within-group settings) alongside changes in urinary cortisol levels from two neighboring bonobo groups in the Kokolopori Bonobo Reserve, Democratic Republic of Congo. Here, we use higher aggression rates and urinary cortisol levels in between-group settings, while controlling for the number of potential competitors, as indicators of contest competition between groups. To explore the role of food and mate availability on intergroup competition within each sex, we tested the following non-mutually exclusive hypotheses (see also

Table 1
Hypotheses and predictions.

Hypotheses	Predictions
Contest competition between groups arises as members of different groups compete over food	Higher aggression rates and cortisol levels in between-group than within-group settings during periods of low fruit abundance
Contest competition between groups arises as members of different groups compete over mates	Higher aggression rates and cortisol levels in between-group than within-group settings when maximally tumescent females are present
Groups compete to maintain or expand access to food resources in the long run	Higher aggression rates and cortisol levels in between-group than within-group settings, regardless of changes in fruit and mate availability

Table 1):

1.1. Female intergroup competition hypothesis

If female bonobos engage in contest competition over food resources during intergroup encounters (i.e., competition arises when food access is limited and can be monopolized), we expect females to act more aggressively and show higher urinary cortisol levels in between-group than within-group settings (Isbell, 1991; Vogel and Janson, 2011), during periods of low fruit abundance, and as the number of individuals in the association party increases (i.e., more potential competitors present). Besides competition over food resources, male-male competition over sexually receptive females may also influence females' response to intergroup competition and should be accounted for when testing the female intergroup competition hypothesis. Given that female bonobos can intervene in male competition and that coalitions may form in response to male aggressions, variation in female aggressiveness (i.e., the number of aggressions given) and cortisol response may not be driven by female resource competition, but occur as a side effect of male competition (Surbeck and Hohmann, 2013; Tokuyama and Furuichi, 2016). Females may therefore be more aggressive and have higher urinary cortisol levels in between-group settings when maximally tumescent females are present, rather than absent.

1.2. Male intergroup competition hypothesis

If male bonobos engage in contest competition over mates and/or food resources during intergroup encounters, we predict higher male aggression rates and urinary cortisol levels in between-group than within-group settings. Specifically, if males compete over access to mates during intergroup encounters, we expect higher aggression rates and urinary cortisol levels in between-group settings when maximally tumescent females are present, rather than absent. In bonobos, males' access to food is not only limited by food availability, but also by females' priority of access to food over males (Nurmi et al., 2018; Surbeck et al., 2015). As a result, males may react strongly towards fluctuations in fruit abundance during intergroup encounters, as feeding pressure likely increases with the presence of out-group females. Under this assumption, we expect higher male aggression rates and urinary cortisol levels in between-group settings during periods of low fruit abundance.

Alternatively, bonobo groups may compete to maintain or expand access to food resources in the long run, rather than competing directly for resource access within the course of intergroup encounter (Crofoot and Wrangham, 2010). In this case, we expect higher aggression rates and urinary cortisol levels in between-group than within-group settings despite short-term changes in fruit abundance and mate availability.

2. Methods

2.1. Study site and subjects

We collected behavioral data and urine samples non-invasively from two neighboring bonobo groups, Ekalakala and Kokoalongo, in the Kokolopori Bonobo Reserve, Democratic Republic of Congo (N 0.41716°, E 22.97552°; Surbeck et al., 2017), from October 2016 to August 2018. We included a total of 13 males and 25 females in this study (see Table S1 for group composition and age estimates). All individuals were mature individuals of age 10 years or above and were fully habituated to human observers.

2.2. Data collection

We conducted full-day party follows and 30-minute focal animal sampling of individuals present in the party (Altmann, 1974), resulting in a total of 1320 observation hours of Ekalakala alone and 1326 h of Kokoalongo alone. Due to the fission-fusion dynamics of bonobo groups,

individuals of the same group do not all associate permanently, but rather range in smaller parties of varying sizes and composition. Thus, during party follows, we prioritized the observation of the largest party. Throughout the day, we collected party composition data, all occurrences of agonistic interactions and data on feeding behavior. Specifically, we recorded accumulatively all individuals that were observed in the followed party during 30-minute intervals. We also recorded all directed contact (attacks; e.g., bites, hits, kicks, clashes) and non-contact (e.g., chases, charges, branch displays, arm waves) agonistic interactions between two or more individuals. We considered all agonistic interactions that occurred within and between groups when investigating individuals' competitiveness in between-group settings because physical activity (increased energetic demands) may elicit cortisol secretion regardless of the identity of the partner. Additionally, we conducted group activity scans at 10-minute intervals and recorded the feeding activity of the followed party, as well as the species of food individuals in the party were feeding on. We also collected monthly phenology data and rated female sexual swellings daily (see below). We recorded every observed occurrence of intergroup encounters during party and focal follows ($N = 92$), with a total of 1325 observation hours of intergroup encounters (of which 169.5 h involved a third, semi-habituated, neighboring group that comprised 4 adult males and 3 adult females at the time of the study).

2.2.1. Definition of group membership and intergroup encounter

The fission-fusion dynamics of bonobos and large home range overlap between adjacent groups can make the distinction of bonobo groups difficult. Here, we assign group memberships based on individual familiarity with each other, whereby individuals of Ekalakala spend the majority of time associating with other individuals of Ekalakala rather than with individuals of Kokoalongo; and likewise for Kokoalongo individuals (Lucchesi et al., 2020). By this definition of group membership, Ekalakala and Kokoalongo each have their exclusive ranging areas, in which members of the other group do not range in (Lucchesi et al., 2020). We consequently defined the start of an intergroup encounter as when a followed party of two or more individuals came into visual contact with two or more individuals of another group and the end of an intergroup encounter as when the groups were no longer in visual and vocal contact. Although most encounters included in this study occurred between our two study groups, some encounters involved more than two groups (see above).

2.2.2. Dominance rank

We assessed dominance relationships among group members based on the outcomes of all directed, dyadic agonistic interactions. While pant grunts serve as a signal of submission in chimpanzees (Bygott, 1979), fleeing and jumping aside upon aggression is typically taken as a measure of submission in bonobos (Surbeck et al., 2012). Following this measure, we treated individuals showing submission in response to aggression as subordinate. Based on a total of 628 within-group agonistic interactions (Ekalakala $N = 261$; Kokoalongo $N = 367$), we calculated individual dominance rank separately for the two study groups using the randomized Elo-rating method (Sánchez-Tójar et al., 2018). We used the function *elo_scores* of the R package aniDom (version 0.1.4). We specified the speed at which elo scores change ("K") as 100, the starting score ("init.score") as 1000 and the number of randomizations to be performed ("n.rands") as 1000. We then standardized individual elo scores between 0 and 1 for each group, with 1 being the highest rank. Given that males mostly compete with each other during mate competition, we assessed male dominance ranks separately based on outcomes of male-male dyadic agonistic interactions. Subsequently in the analyses that examined intergroup competition among males, we accounted for the effect of dominance hierarchy among males by incorporating the elo scores of males, standardized between 0 and 1 for each group.

2.2.3. Food availability

To examine the effects of feeding competition during intergroup encounters, we determined a monthly fruit abundance index (hereafter FAI) using a previously established index (Anderson et al., 2005) that has been implemented in the same bonobo population (Lucchesi et al., 2020). The FAI was determined separately for each bonobo group, based on the phenology of fruiting trees bonobos fed on and the corresponding trees' basal areas, which was derived from averaging the basal area of the respective tree species found in floristic plots placed across the home range of each group. Specifically, the index was defined as follows:

$$FAI_m = \sum_i^S N_{im} B_i$$

where FAI_m is the FAI in a given month and home range; N_{im} denotes the proportion of trees of species i bearing ripe fruits in the phenology trail in month m ; B_i represents the basal area of species i (i.e., total cross-sectional area of tree trunks measured at 1.3 m above ground), and S is the total number of tree species. When calculating the FAI, we considered only tree species that were in the diet of the two bonobo groups during the study period and we weighted the proportion of fruiting trees based on the frequency of a given tree species that were fed by the group in a given month (which was obtained from the group activity scans conducted during party follows).

2.2.4. Mate availability

To explore the effect of mate competition, we scored genital swellings of females that were present in the followed party at any point during the day. We scored swelling stages on a scale of 1 (minimal tumescence) to 4 (maximal tumescence), based on the firmness and skin surface structure of the swelling (Hohmann and Fruth, 2000). We then used the presence of (in- and out-group) maximally tumescent females on a given day to quantify potential mate competition.

2.3. Urine collection and analysis

We opportunistically and non-invasively collected urine samples from identified individuals (13 males and 15 cycling females that were not pregnant nor in the period of "early lactation" at the time of sample collection; Douglas et al., 2016) during party and focal follows (range: 11–39 samples/individual; see Table S1). We transferred the samples into liquid nitrogen within 12 h of collection. All samples were shipped frozen on dry ice to the Endocrinology Laboratory at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and stored at $-20\text{ }^{\circ}\text{C}$ until analysis. We managed to get urine samples in 76 of the 92 intergroup encounters observed and we had to exclude one sample due to incomplete behavioral observations during the respective intergroup encounter. To obtain a balanced dataset for analysis, we selected 684 urine samples that were matched across individuals and sample collection days between the two group settings (i.e., within-group and between-group settings).

We extracted the selected samples and measured urinary cortisol using liquid chromatography-tandem mass spectrometry (LC-MS/MS) based on a method adapted from Hauser et al. (2008; see SI). To correct for the variation in urine volume and concentration, we also measured the specific gravity (SG) of each sample with a digital handheld refractometer (TEC, Ober-Ramstadt, Germany) and determined cortisol levels corrected for SG as described in Miller et al. (2004). The population mean of SG for bonobos at Kokolopori was 1.0135. We excluded 9 samples with SG below 1.002 from the analyses because the low SG did not allow for a reliable correction for urine concentration (Löhrich et al., 2018). The clearance of steroids into urine after an event is estimated to be approximately 2 to 4 h in nonhuman primates (Bahr et al., 2000). To capture the beginning and end of the peak cortisol level expressed after the event (i.e., intergroup encounter), we adopted a more conservative measure and extended the time window for the classification of encounter samples to at least 1 h after the start of intergroup encounter

and at most 5 h after the end of encounter. Using this criterion, we had a total of 357 samples in between-group settings (males $N = 146$; females $N = 211$) and 318 samples in within-group settings (male $N = 151$; female $N = 167$). The mean sample collection time (expressed in hours) was 8.65 ± 3.03 for within-group samples and 11.8 ± 2.45 for between-group samples (Fig. S1). To account for different sampling time and the effect of sample collection time on cortisol levels (Muller and Lipson, 2003), we included the time of sample collection in all cortisol analyses (see below).

2.4. Statistical analyses

To test our hypotheses, we fitted two Generalized Linear Mixed Models (GLMMs; Baayen, 2008) with Poisson error structure and log link function (McCullagh and Nelder, 1989) and two Linear Mixed Models (LMMs) with Gaussian error structure and identity link function in the statistical program R (version 3.6.3; R Core Team 2020) using the function *glmer* and *lmer* of the R package *lme4* (version 1.1–21; Bates et al., 2015b). The response for the GLMMs (model 1 and 3) was the total number of aggressions given per individual towards in- and out-group individuals on a given day (controlling for individual observation time per day; see below for more details), whereas the response for the LMMs (model 2 and 4) was log-transformed (base e) urinary cortisol level, which was expressed as ng/ml SG. The models differed regarding the hypotheses addressed and the datasets used (see below). In model 1 and 2, we tested the female intergroup competition hypothesis by examining whether female aggressiveness (i.e., total number of aggressions given towards in- and out-group individuals; model 1) and urinary cortisol levels (model 2) varied in relation to intergroup encounter, fruit abundance, and the presence of maximally tumescent females. In model 3 and 4, we tested the male intergroup competition hypothesis and examined variation in male aggressiveness (model 3) and urinary cortisol levels (model 4) in relation to intergroup encounter, fruit abundance, and the presence of maximally tumescent females. Since the main goal of this study was to explore the role of food and mate availability on intergroup competition within each sex, we tested the effects of fruit abundance and mate availability on individual competitiveness (i.e., aggression rates and urinary cortisol levels) as separate models for the two sexes. Consequently, we cannot directly compare aggression rates and cortisol patterns we found for each sex and infer sex differences in competitiveness during bonobo intergroup encounters (Nieuwenhuis et al., 2011).

2.4.1. Model 1: Female aggression model

In the first model, we included all observation days for each mature female in within- and between-group settings ($N = 5600$, 485 days, 24 individuals). To test the influence of intergroup encounter, food availability and the presence of maximally tumescent females on female aggressiveness, we included the two-way interactions between intergroup encounter (i.e., observation made during an intergroup encounter; yes/no) and FAI, and intergroup encounter and the presence of maximally tumescent females as fixed effects. We controlled for any group-related differences in individual competitiveness and accounted for a potential increase in competition due to more individuals present at a given point of time by including group identity (Ekalakala/Kokoalongo) and the average number of individuals (in- and out-group) present per 30-minute interval on a given day as further fixed effects. We also included individuals' observation time per day (total number of 30-minute observation scans on a given day; log-transformed) as an offset term (McCullagh and Nelder, 1989). See below for the additional fixed and random effects included into this and the other models.

2.4.2. Model 2: Female cortisol model

In the second model, we included urine samples collected from females in within- and between-group settings ($N = 378$, 226 days, 15 individuals). For the predictors of female urinary cortisol levels, we

included the same two-way interactions and accounted for group identity, as we did in model 1. We also included the total number of individuals (in- and out-group) present during the day and sample collection time as fixed effects in order to account for potential influence of daily association size and the diurnal patterns of urinary cortisol excretion (Muller and Lipson, 2003; Samuni et al., 2019b).

2.4.3. Model 3: Male aggression model

In the third model, we included all observation days for each mature male in within- and between-group settings ($N = 2990$, 482 days, 13 individuals). We included test and control variables identical to model 1 as fixed effects in this model. We also included individuals' observation time per day as an offset term.

2.4.4. Model 4: Male cortisol model

In the fourth model, we included urine samples collected from males in within- and between-group settings ($N = 297$, 181 days, 13 individuals). We included test and control variables identical to model 2 as fixed effects in this model.

2.5. Additional fixed and random effects

We could not simultaneously account for the effects of dominance rank and age (adult/subadult; subadults were individuals of age 10 to 15 years; see Table S1) in the abovementioned models because there was nearly complete separation between the two variables (i.e. dominant individuals were all adults and subordinate individuals were mostly subadults; Fig. S2). Therefore, for each respective response variable, we compared results obtained from a model that included dominance rank, but not age, as a fixed effect control variable and vice versa. As both models yielded comparable results, we reported below the models with the lower AIC (i.e., models that better explained variation in the respective response variable; Bumham and Anderson, 2002; AIC of: female aggression model with rank = 3662.0; female cortisol model with rank = 797.3; male aggression model with rank = 3318.1; male cortisol model with age = 591.7). We showed results for the models with the higher AIC in the supplementary information (AIC of: female aggression model with age = 3677.7, Table S4; female cortisol model with age = 799.0; Table S6; male aggression model with age = 3355.5; Table S8; male cortisol model with rank = 602.9; Table S10). As we had multiple observations for each individual and each observation day, we included individual identity and date as random intercept effects in all models to avoid pseudoreplication and to account for variability across individuals and observation days (Zuur and Ieno, 2016). We also included in each model all theoretically identifiable random slopes (see Table S2), but not the correlation parameters among random intercepts and random slope terms in order to reduce model complexity (Barr et al., 2013; Bates et al., 2015a). Here, we prioritized optimal model structure (i.e., accounting for all quantifiable control predictors) over model power in our statistical approach. Thus, given the rather complex random effect structure of our statistical analyses and relatively small sample size, we do not present results regarding the random effects, which would have informed us about potential inter-individual differences.

2.6. Model implementation

We centered all fixed effect covariates by z-transforming them to a mean of zero and standard deviation of one for the sake of estimate comparability and to ease model convergence. We tested the significance of each full model (Forstmeier and Schielzeth, 2011) by comparing it to a respective null model, which was identical with the exception that it lacked the test predictors (see Table S2 for full and null model structure), using a likelihood ratio test (Dobson and Barnett, 2008; R function *anova* with argument test set to "Chisq"). To allow for a likelihood ratio test, we fitted the models using Maximum Likelihood. We used the optimizing function "bobyqa" and determined P values of

individual terms by dropping them from the model one at a time (Barr et al., 2013). When an interaction term was not significant, but the full-null model comparison was, we removed the interaction from the model to test the effect of the main effects it comprised. For all the models fitted, we checked for model stability (i.e., excluding each level of the random effects one at a time and comparing the estimates to the full dataset), potential collinearity problems among fixed effects, and the distribution and homogeneity of residuals in case of LMMs (see SI for details). We also confirmed the absence of overdispersion in all GLMMs (model 1: dispersion parameter = 0.753; model 3: dispersion parameter = 0.794). Finally, we determined confidence intervals of estimates and the fitted model by means of a parametric bootstrap (function *bootMer* of the package lme4).

3. Results

3.1. Nature and duration of intergroup encounters in Kokolopori

We observed a total of 92 visual intergroup encounters, together spanning 175 days (35.9% of observation days). The median duration of intergroup encounters was 51.96 h (interquartile range; IQR = 23.76–79.00 h). Of the 92 encounters, 78 occurred between the two main study groups and 14 involved a third neighboring group. Eight out of these 14 encounters involved all three groups. In total, we observed 1469 agonistic events throughout the study period and 61.6% of the agonistic events occurred during intergroup encounters. Of all the aggressions given during intergroup encounters ($N = 905$), 53.0% were directed towards out-group individuals, 42.4% were towards in-group individuals, and 4.5% were instances of aggression in which two or more individuals from different groups formed a coalition to attack another individual. The mean hourly rates of aggression per female were 0.02 ± 0.02 (mean \pm sd) in within-group settings and 0.04 ± 0.02 in between-group settings (Fig. 1). The mean hourly rates of aggression per male were 0.05 ± 0.04 in within-group settings and 0.09 ± 0.07 in between-group settings. The hourly rates of intra-group aggression were comparable between within- and between-group settings (Fig. S3). The hourly rates of aggression also varied across encounters (mean \pm sd =

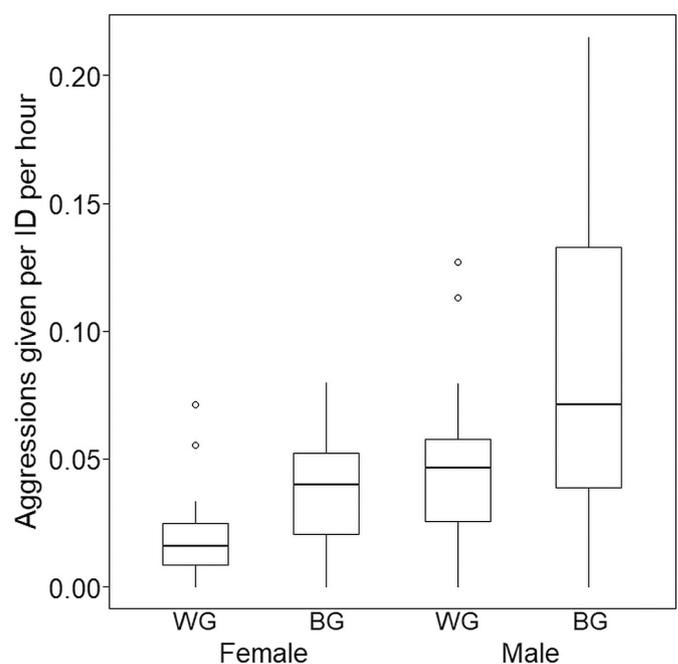


Fig. 1. The number of aggressions given by males and females per hour in within-group (WG) and between-group (BG) settings. Depicted are the raw data medians (horizontal lines), quartiles (boxes) and range of values that are within 1.5 inter-quartile range (whiskers).

0.07 ± 0.06, range = 0–0.41). We observed 25 cases of physical injuries (10 female injuries and 15 male injuries), ranging from small cuts to serious bite wounds, but no killings during intergroup encounters. The median urinary cortisol levels of females were 3.26 ng/ml SG in within-group settings (IQR: 2.04–5.70 ng/ml SG) and 3.28 ng/ml SG in between-group settings (IQR: 1.91–6.29 ng/ml SG), whereas the median urinary cortisol levels of males were 6.89 ng/ml SG in within-group settings (IQR: 3.50–14.00 ng/ml SG) and 7.65 ng/ml SG in between-group settings (IQR: 4.18–12.03 ng/ml SG).

3.2. Female aggression model (model 1)

While females had higher aggression rates in between-group than within-group settings (Fig. 1), the difference did not reach significance at the 0.05 alpha level (estimate = 0.414, SE = 0.213, $P = 0.058$; Table 2). In contrast to our expectations, neither fruit abundance (two-way interaction between encounter and FAI: estimate = -0.156, SE = 0.125, $P = 0.216$; Table S3) nor the presence of maximally tumescent females (two-way interaction between encounter and presence of maximally tumescent females: estimate = 0.140, SE = 0.472, $P = 0.766$) significantly explained the increase in females' aggressive response in between-group settings. After removing the non-significant interactions, we found that, independent of intergroup encounter occurrence, females were more aggressive in the presence of maximally tumescent females (estimate = 0.703, SE = 0.218, $P = 0.001$). Further, females were more aggressive when the number of individuals in the party increased (estimate = 0.220, SE = 0.073, $P = 0.003$), as well as when females' dominance rank (estimate = 0.318, SE = 0.061, $P < 0.001$) and age increased (adult as the reference category; estimate = -0.573, SE = 0.246, $P = 0.023$; Table S4).

3.3. Female cortisol model (model 2)

Females had significantly higher urinary cortisol levels in between-

Table 2

Reduced model investigating the number of aggressions given by females in relation to intergroup encounter, fruit abundance, and the presence of maximally tumescent females (model 1; see Table S3 for results of the full model).

Term	Estimate	SE	CI lower	CI upper	χ^2 #	P
Intercept	-5.684	0.237	-6.208	-5.299	-	-
Test predictors						
Intergroup encounter (yes)	0.414	0.213	-0.010	0.805	3.586	0.058
Fruit Abundance Index ^a	0.122	0.067	-0.020	0.253	3.202	0.074
Presence of maximally tumescent females (yes)	0.703	0.218	0.307	1.180	11.089	0.001
Control predictors:						
Dominance rank ^b	0.318	0.061	0.209	0.437	20.745	<0.001
Average number of individuals ^c	0.220	0.073	0.073	0.356	8.866	0.003
Group (Kokoalongo)	0.362	0.129	0.119	0.613	6.811	0.009

Statistically significant terms are displayed in bold. The coded levels are shown in parenthesis. ^a-z-transformed, original mean ± sd: ^a50.60 ± 41.99, ^b0.71 ± 0.19 (range from 0 to 1 with 1 being the highest ranking), ^c7.42 ± 2.58. #df of all $\chi^2 = 1$. Full model comprising interactions of test predictors explained more of the variation in female aggressiveness than null model, which lacked all test predictors (full-null model comparison likelihood ratio test: $\chi^2 = 22.538$, $df = 5$, $P < 0.001$). Reduced model lacked all non-significant interactions to allow for the interpretation of terms that were included in the interactions.

group than within-group settings (estimate = 0.608, SE = 0.138, $P < 0.001$; Table 3, Fig. 2a). However, the elevated female urinary cortisol levels in between-group settings were not related to fruit abundance (two-way interaction between intergroup encounter and FAI: estimate = -0.164, SE = 0.100, $P = 0.112$) or the presence of maximally tumescent females (two-way interaction between intergroup encounter and presence of maximally tumescent females: estimate = 0.052, SE = 0.296, $P = 0.863$; Table S5). Although fruit abundance did not elicit a differentiated response in female urinary cortisol levels depending on the group setting, high fruit abundance was associated with overall higher female urinary cortisol levels across days (estimate = 0.123, SE = 0.052, $P = 0.043$). Neither dominance rank nor age had a significant effect on female urinary cortisol levels (dominance rank: estimate = 0.101, SE = 0.059, $P = 0.103$; Table 3; age: estimate = -0.167, SE = 0.157, $P = 0.307$; Table S6).

3.4. Male aggression model (model 3)

Males had higher aggression rates in between-group than within-group settings (Fig. 1). After controlling for observation time and other covariates (see Methods), the number of aggressions given by males varied with fruit abundance only in within-group settings. Specifically, males were more aggressive in within-group settings when fruit abundance was high, but the number of aggressions given by males remained unchanged in between-group settings despite changes in fruit abundance (interaction between encounter and FAI: estimate = -0.233, SE = 0.110, $P = 0.040$; Table 4, Fig. 3). Independent of the group setting, the presence of maximally tumescent females (estimate = 0.853, SE = 0.216, $P < 0.001$) and high dominance rank (estimate = 0.750, SE = 0.061, $P < 0.001$) were associated with higher number of aggressions in males.

Table 3

Reduced model investigating female urinary cortisol levels (log-transformed) in relation to intergroup encounter, fruit abundance, and the presence of maximally tumescent females (model 2; see Table S5 for results of the full model).

Term	Estimate	SE	CI lower	CI upper	χ^2 #	P
Intercept	0.917	0.152	0.630	1.224	-	-
Test predictors						
Intergroup encounter (yes)	0.608	0.138	0.334	0.877	14.548	<0.001
Fruit Abundance Index ^a	0.123	0.052	0.014	0.222	4.093	0.043
Presence of maximally tumescent females (yes)	0.116	0.118	-0.100	0.341	0.935	0.334
Control predictors						
Dominance rank ^b	0.101	0.059	-0.019	0.218	2.657	0.103
Total number of individuals ^c	-0.121	0.061	-0.233	0.004	3.312	0.069
Group (Kokoalongo)	-0.249	0.125	-0.486	-0.008	3.481	0.062
Sample collection time ^d	-0.430	0.050	-0.529	-0.332	28.426	<0.001

Statistically significant terms are displayed in bold. The coded levels are shown in parenthesis. ^a-z-transformed, original mean ± sd: ^a42.93 ± 34.91, ^b0.66 ± 0.22 (range from 0 to 1 with 1 being the highest ranking), ^c17.77 ± 8.10, ^d10.44 ± 3.18. #df of all $\chi^2 = 1$. Full model comprising interactions of test predictors explained more of the variation in female cortisol than null model, which lacked all test predictors (full-null model comparison likelihood ratio test: $\chi^2 = 24.588$, $df = 5$, $P < 0.001$). Reduced model lacked all non-significant interactions to allow for the interpretation of terms that were included in the interactions.

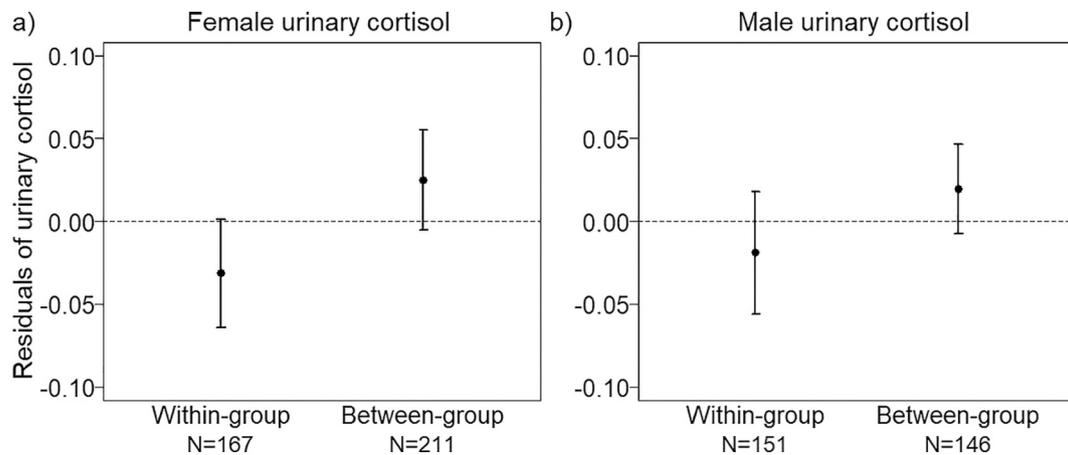


Fig. 2. The effect of intergroup encounter on urinary cortisol levels of a) females and b) males. The y axis represents the residuals of log-transformed urinary cortisol levels obtained from models identical to the a) female and b) male cortisol models, which account for changes in fruit abundance, the presence of maximally tumescent females, and all other control variables, but lack the term ‘intergroup encounter’. Depicted are the mean cortisol (circles) and SE (error bars) in within- and between-group settings.

Table 4

Reduced model investigating the number of aggressions given by males in relation to intergroup encounter, fruit abundance, and the presence of maximally tumescent females (model 3; see Table S7 for results of the full model).

Term	Estimate	SE	CI lower	CI upper	χ^2 #	P
Intercept	-4.636	0.232	-5.088	-4.244	-	-
Test predictors						
Intergroup encounter (yes) x Fruit Abundance Index ^a	-0.233	0.110	-0.444	-0.010	4.239	0.040
Intergroup encounter (yes)	0.361	0.205	-0.049	0.752	-	-
Fruit Abundance Index ^a	0.261	0.107	0.038	0.470	-	-
Presence of maximally tumescent females (yes)	0.853	0.216	0.485	1.263	13.350	< 0.001
Control predictors						
Male dominance rank ^b	0.750	0.061	0.634	0.865	40.812	< 0.001
Average number of individuals ^c	0.099	0.070	-0.039	0.238	2.008	0.156
Group (Kokoalongo)	-0.026	0.109	-0.219	0.164	0.058	0.810

Statistically significant terms are displayed in bold. The coded levels are shown in parenthesis. ^ac-z-transformed, original mean \pm sd: ^a52.93 \pm 43.42, ^b0.49 \pm 0.36 (range from 0 to 1 with 1 being the highest ranking), ^c7.53 \pm 2.57. # df of all $\chi^2 = 1$. Full model comprising interactions of test predictors explained more of the variation in male aggressiveness than null model, which lacked all test predictors (full-null model comparison likelihood ratio test: $\chi^2 = 24.016$, $df = 5$, $P < 0.001$). Reduced model lacked the non-significant interaction between intergroup encounter and presence of maximally tumescent females to allow for the interpretation of the main effect of presence of maximally tumescent females.

3.5. Male cortisol model (model 4)

Males had higher urinary cortisol levels in between-group than within-group settings (Fig. 2b). However, fruit abundance only predicted variation in male urinary cortisol levels in within-group, but not

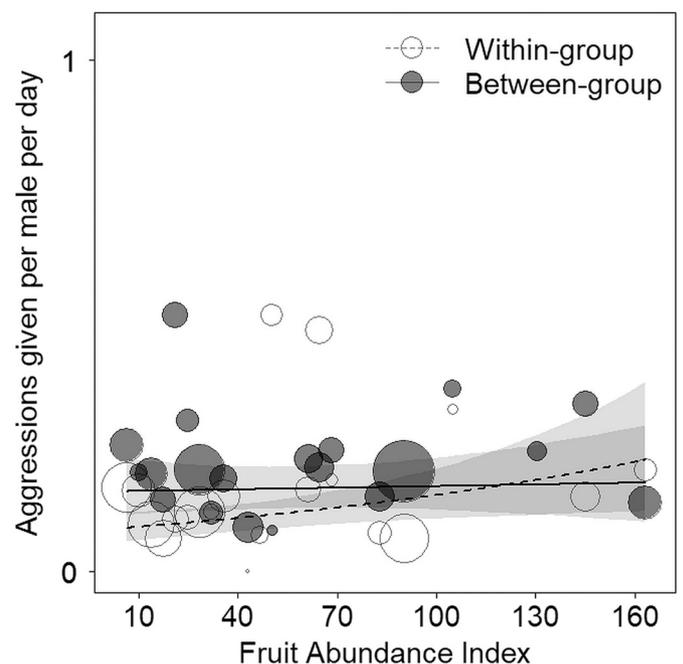


Fig. 3. The number of aggressions given by males in within- and between-group settings in relation to fruit abundance (higher values in Fruit Abundance Index represent higher fruit abundance). The dashed and solid lines depict variation in the number of aggressions given by males in within- and between-group settings, respectively, with all other fixed effects centered to a mean of zero. The shaded area surrounding the lines represents the 95% confidence interval of the fitted model (model 3). Open and filled circles represent aggressions given in within- and between-group settings, respectively, averaged per bin of the predictor. The area of the circles depicts the sample size per bin (total N: within-group $N = 1421$; between-group $N = 1485$).

between-group settings (two-way interaction between intergroup encounter and FAI: estimate = -0.254 , SE = 0.094 , $P = 0.015$; Table 5). Similar to patterns of male aggression, male urinary cortisol levels were higher in within-group settings when fruit abundance was high, but the levels were similar in between-group settings despite changes in fruit abundance (Fig. 4). Different from what we expected, male urinary cortisol levels did not significantly vary with the presence of maximally tumescent females (estimate = 0.634 , SE = 0.132 , $P = 0.426$) or males' dominance rank (estimate = 0.080 , SE = 0.068 , $P = 0.254$; Table S10).

Table 5

Reduced model investigating male urinary cortisol levels (log-transformed) in relation to intergroup encounter, fruit abundance, and the presence of maximally tumescent females (model 4; see Table S9 for results of the full model).

Term	Estimate	SE	CI lower	CI upper	χ^2 #	P
Intercept	1.811	0.167	1.492	2.142	–	–
Test predictors						
Intergroup encounter (yes) x Fruit Abundance Index ^a	-0.254	0.094	-0.440	-0.079	5.928	0.015
Intergroup encounter (yes)	0.453	0.147	0.161	0.722	–	–
Fruit Abundance Index ^a	0.298	0.075	0.160	0.432	–	–
Presence of maximally tumescent females (yes)	0.109	0.132	-0.149	0.361	0.634	0.426
Control predictors						
Age (subadult)	-0.553	0.125	-0.785	-0.297	12.518	<0.001
Total number of individuals ^b	0.001	0.082	-0.166	0.160	0.000	0.989
Group (Kokolongo)	-0.110	0.112	-0.342	0.120	0.917	0.338
Sample collection time ^c	-0.565	0.042	-0.653	-0.481	37.557	<0.001

Statistically significant terms are displayed in bold. The coded levels are shown in parenthesis. ^az-transformed, original mean \pm sd: ^a50.78 \pm 43.32, ^b18.45 \pm 8.66, ^c10.16 \pm 3.14. #df of all χ^2 = 1. Full model comprising interactions of test predictors explained more of the variation in male cortisol than null model, which lacked all test predictors (full-null model comparison likelihood ratio test: χ^2 = 21.966, *df* = 5, *P* < 0.001). Reduced model lacked the non-significant interaction between intergroup encounter and presence of maximally tumescent females to allow for the interpretation of the main effect of presence of maximally tumescent females.

Overall, adult males had higher urinary cortisol levels than subadult males (estimate = -0.553, SE = 0.125, *P* < 0.001).

4. Discussion

In this study, we tested whether male and female bonobos competed over access to food and mates during intergroup encounters in Kokolopori by examining aggression rates and urinary cortisol levels of each sex in within- and between-group settings. Despite the prolonged and relatively peaceful nature of bonobo intergroup encounters, we found that within each sex these encounters were associated with higher aggression rates and urinary cortisol levels. Given that patterns of urinary cortisol varied in parallel with individual aggressiveness (i.e., the number of aggressions given), the elevation in urinary cortisol levels is unlikely just a consequence of emotional excitement of associating with less familiar conspecifics. As hourly rates of intra-group aggression were comparable in within- and between-group settings (Fig. S3), the increase in aggressiveness in between-group settings represents aggressions towards outgroup individuals. Furthermore, the higher aggression rates and urinary cortisol levels cannot be solely explained by a higher number of individuals present in between-group than within-group settings, as we have accounted for the number of individuals in our analyses. In the case of females, the increase in competitiveness in between-group settings was neither related to fruit abundance nor the presence of maximally tumescent females, suggesting that female competitiveness during intergroup encounters is not related to changes in food availability or between-group dynamics when maximally tumescent females are

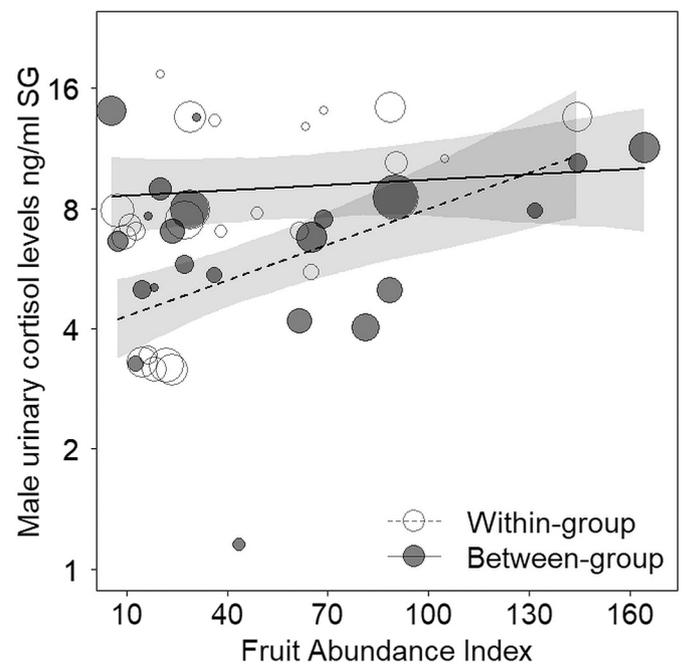


Fig. 4. Male urinary cortisol levels (log-transformed) in within- and between-group settings in relation to fruit abundance (higher values in Fruit Abundance Index represent higher fruit abundance). The dashed and solid lines depict variation in male urinary cortisol levels in within- and between-group settings, respectively, with all other fixed effects centered to a mean of zero. The shaded area surrounding the lines represents the 95% confidence interval of the fitted model (model 4). Open and filled circles represent cortisol levels in within- and between-group settings, respectively, averaged per bin of the predictor. The area of the circles depicts the sample size per bin (total N: within-group *N* = 151; between-group *N* = 146).

present. In the case of males, the presence of maximally tumescent females did not explain the higher number of aggressions given and cortisol levels during intergroup encounters, implying that contest over mates may not be the primary form of competition among males during intergroup encounters. Also, male aggression and urinary cortisol levels did not strongly vary with fruit abundance in between-group settings. Overall, our results emphasize the competitive nature of bonobo intergroup encounters and reveal that bonobo intergroup competition is not directly related to short-term changes in the availability of food and mates.

The intergroup encounters observed in Kokolopori sometimes lasted for extended periods (35.9% of total observation days, encounter duration ranging from 1.62 h to 13 days). The frequency and duration of intergroup encounters in Kokolopori was comparable to that reported in a nearby bonobo population, Wamba (31% of total observation days, duration ranging from less than a day to 12 days; Sakamaki et al., 2018). Another similarity between intergroup encounters in Kokolopori and Wamba is the active participation of both males and females (Furuichi, 2020; Tokuyama et al., 2019). Given that active participation of both sexes in territorial defense or intergroup conflicts is also common in other nonhuman primates (Arseneau-Robar et al., 2016; Boesch et al., 2008; Fashing, 2001; Koch et al., 2016a; Samuni et al., 2017; Van Belle and Scarry, 2015), sex differences in competitive strategies during intergroup encounters may be a widespread phenomenon. For example, participation in competitive intergroup interactions may be biased towards the philopatric sex (Manson and Wrangham, 1991) or the dominant sex (Markham et al., 2012), which varies in different species and is typically related to the degree of sexual dimorphism in body size and other physical traits. In bonobo societies, males are philopatric and co-dominant with females. However, the missing direct comparison of male and female competitiveness in our study precludes us from inferring

potential sex differences in bonobos' competitive strategies during intergroup encounters.

Female bonobos in Kokolopori had higher aggression rates and urinary cortisol levels in between-group than within-group settings, independent of variation in fruit abundance. Additionally, female urinary cortisol levels were generally higher when fruit abundance was high, which was the opposite pattern to what we hypothesized if females engaged in direct contest over food. The motivation to intensely compete against neighboring groups for food resources may be comparatively lower in bonobos than chimpanzees as fruits appear to be more readily available throughout the year and food patches are overall larger in the habitat of bonobos (Chapman et al., 1994; Furuichi, 2009). While competitiveness of female bonobos in response to intergroup encounters was not determined by fruit abundance, we cannot entirely rule out the occurrence of feeding competition between groups in female bonobos. Given that females were more aggressive when they were in larger parties and that older, high-ranking females were more aggressive than younger, low-ranking females, it is possible that females, especially those of high ranks, compete to exclude others in the party from a prime feeding spot in a fruit patch during intergroup encounters, as they do in within-group settings (Nurmi et al., 2018). In addition, female bonobos may compete with out-group individuals over food resources that are highly valued and/or food patches that are clumped in space. In fact, ecological measures that we did not consider in our study, including food preference, as well as food distribution and defensibility, have been shown to drive patterns of intergroup behavior in various species (lions: Spong, 2002; vervet monkeys: Arseneau-Robar et al., 2017; grey-cheeked mangabeys: Brown, 2013; chacma baboons: Noser and Byrne, 2009; mountain gorillas: Robbins and Sawyer, 2007; chimpanzees: Wilson et al., 2012). As previously shown in Kokolopori, encounters between our two study groups are more likely to end when fruits are clumped in space (Lucchesi et al., 2020), suggesting that groups either split upon intense fights over clumped resources, or that groups avoid prolonged encounters to mitigate costs of feeding competition. In humans, groups tend to defend clumped resources because such resources are economically defensible (Cashdan et al., 1983). Improved access to clumped and valuable food resources in the context of intergroup conflicts may have ultimate fitness benefits in bonobos, as in the case of chimpanzees and human foragers (Allen et al., 2016; Cashdan et al., 1983; Mitani et al., 2010; Williams et al., 2004).

In Wamba, males are more aggressive towards out-group individuals than females (Tokuyama et al., 2019). The authors inferred this sex difference in aggressiveness towards out-groups as indicative of mate competition between groups. Here in Kokolopori, male bonobos responded to intergroup encounters with higher aggression rates and urinary cortisol levels. However, such increase in male aggression rates and urinary cortisol levels was independent of the presence of maximally tumescent females. Both during and outside intergroup encounter contexts, males showed higher aggression rates in the presence of maximally tumescent females and high-ranking males were more aggressive than low-ranking males (cf. Surbeck et al., 2012). Despite the frequent occurrence of between-group copulations, extra-group paternity is extremely rare in bonobos (Gerloff et al., 1999; Ishizuka et al., 2018). It remains controversial how well male bonobos can infer the fecundity of females because sexual swellings do not serve as reliable indicators of ovulation in female bonobos (Douglas et al., 2016). To overcome this, males may use additional cues, such as behavioral or olfactory signals, to infer female fecundity. This may lead to males also competing for females that are not in maximal tumescence. For example, males of different groups may compete to increase future mating opportunities and/or to recruit females from the other group (especially young females that are ready to disperse). Indeed, young female bonobos often use intergroup encounters as a platform to explore transfer opportunities (Sakamaki et al., 2015). To better understand the role of male-male competition as a mating strategy during intergroup encounters in male bonobos, a promising avenue is to include measurements of

male testosterone.

The variation in aggression and urinary cortisol levels in response to intergroup encounters was linked to fruit abundance in males. Specifically, the increase in male aggressions given and urinary cortisol levels in between-group than within-group settings was larger when fruit abundance was low. An alternative explanation for this larger increase in male competitiveness during times of low fruit abundance is that rates of intergroup encounters were particularly high during times when fruit was scarce as groups increased foraging. However, bonobo groups in Kokolopori and Wamba are more likely to encounter and tend to spend more time together when fruit abundance is high, rather than low (Lucchesi et al., 2020; Sakamaki et al., 2018; Fig. S4). Moreover, male aggressions given and urinary cortisol levels remained high in between-group settings despite variation in fruit abundance. Therefore, the increase in male competitiveness associated with intergroup encounters is unlikely just a result of higher encounter rates when fruit was abundant. Altogether, the heightened behavioral and physiological responses of males in between-group settings cannot be fully explained by short-term changes in food and mate availability. Instead, other parameters specific to intergroup encounters, such as encounter location, may better explain males' behavioral and physiological responses during these encounters. In various mammalian and primate species, the location of intergroup encounters has a strong impact on individuals' intergroup behavior, which may in turn determine the outcome (Crofoot et al., 2007; Crofoot and Gilby, 2012; Furrer et al., 2011; Koch et al., 2016b; Markham et al., 2012). For instance, individuals are more likely to confront out-groups and win in intergroup contests when encounters occur in the core, exclusive, or intensively used areas of their group's home range. While the occurrence of encounters between our two study groups does not depend on groups' utilization of the area (Lucchesi et al., 2020), members of different groups may still show stronger stress responses and/or compete more intensely when intergroup encounters occur in highly valued areas of their home range. These areas can be areas that are clumped with certain key resources at a given time (Wilson et al., 2012). Additional data on the location in which agonistic interactions between bonobo groups occur will allow us to explore this possibility. Finally, bonobo groups may also compete to strive for dominance over neighboring groups to improve future access to resources (food and females). Indeed, competition for group dominance may be adaptive in many primates because dominant groups have been shown to benefit from increased long-term fitness (Crofoot and Wrangham, 2010). The drive for intergroup dominance may have evolved as a proximate means to achieve reproductive prospects in humans (Gat, 2010).

The close link between patterns of aggression and urinary cortisol in relation to intergroup encounters illustrates that urinary cortisol responses of bonobos in intergroup contexts likely reflect physiological costs of increased energetic demands due to the competitive interactions during intergroup encounters. Conflicts and tension are often intensified when interacting with less familiar conspecifics due to uncertainties arising from such interactions. Even though bonobos spend extended periods of time interacting with out-group individuals, they still spend most of their time (~70%) interacting with their group members in within-group settings. It is thus plausible that social tension (as reflected by higher urinary cortisol levels) and competition increase when bonobos encounter these less familiar, less predictable individuals from the out-group. Despite direct intergroup competition, the anticipation of attacks from out-group individuals during intergroup encounters may also be additional stressor to individuals. The anticipation of competitive interactions has been shown to result in elevated cortisol levels in various nonhuman primates (Hohmann et al., 2009; Jaeggi et al., 2018; Sobolewski, 2012; Wobber et al., 2010). In humans, anticipation of intergroup interactions and participation in intergroup competition are associated with heightened cortisol responses in men (Bijleveld et al., 2012; Wagner et al., 2002). Unfortunately, endocrine studies on cortisol levels during intergroup competition in humans are mostly limited to experimental settings and are often conducted on individuals of the

same sex (Edwards and Kurlander, 2010; Oxford et al., 2010), making it difficult to draw parallels between humans and non-human primates.

The patterns of HPA axis activity in bonobos during prolonged intergroup encounters were comparable to those elicited during relatively short and predominantly aggressive intergroup encounters in chimpanzees and monkey species (Jaeggi et al., 2018; Samuni et al., 2019b; Schoof and Jack, 2013; Wittig et al., 2016). The similar physiological patterns in bonobos and chimpanzees are unexpected given the differences in the intensity of intergroup aggression between the two species (Tokuyama et al., 2019; Watts et al., 2006). Despite the absence of lethal intergroup aggression, bonobos showed higher urinary cortisol levels during intergroup encounters, similar to male and female chimpanzees (Samuni et al., 2019b). This reveals that low-risk intergroup encounters (i.e., without lethal consequences) can also elicit HPA axis activity. Observations of bonobo and chimpanzee intergroup behavior, especially with regard to territoriality, suggest fundamental interspecific differences in groups' incentives to meet or compete (Furuichi, 2020). Chimpanzees actively patrol and collectively defend their territories (Mitani et al., 2010; Samuni et al., 2019a, 2017), whereas bonobos do not engage in border patrols (Waller, 2011) and often tolerate or even actively affiliate with out-group individuals (Furuichi, 2020; Hohmann and Fruth, 2002). Nevertheless, our findings on bonobos' behavioral and physiological responses in between-group settings reflect competitive aspects of these tolerant intergroup encounters.

Despite potential costs of aggression, bonobos appear to be attracted to members of out-groups, given the frequent occurrence of intergroup encounters. According to classic game theory, group-living organisms should only interact peacefully with out-groups when the benefits of such behavior likely outweigh its costs (Parker, 1974; Smith and Parker, 1976). While individuals may incur costs when participating in intergroup encounters, such costs are diminished in bonobos when compared to chimpanzees, because of the absence of lethal raiding and reduced male aggression towards females (Hare et al., 2012; Wilson et al., 2014). The absence of strong male alliances, together with the presence of strong female coalitions within group, may have rendered the escalation of intergroup aggression difficult in bonobos as compared to chimpanzees (Wrangham, 1999). Another plausible explanation for these tolerant intergroup encounters of bonobos is that the costs for groups to tolerate each other may simply be lower than the costs of excluding each other. In black howler monkeys and chimpanzees, groups sometimes meet because they are attracted to the same food resources (Van Belle and Estrada, 2020; Wilson et al., 2012). Attraction to food source locations is unlikely the only proximate cause of bonobo intergroup encounters, as members of different groups frequently interact in non-feeding contexts. Besides co-feeding in the same food patches, bonobos of different groups also travel in the same association party, groom each other, rest in proximity, and even share sleeping sites and food (Fruth and Hohmann, 2018; Samuni et al., 2020). Furthermore, we found in another study that bonobos at Kokolopori incurred costs of longer travel distances during intergroup encounters, possibly due to a faster rate of resource depletion as more individuals were co-feeding in the same food patch (Lucchesi et al., 2021). Instead of separating, members of both groups adjusted their foraging behavior accordingly (e.g., by increasing their time spent feeding on fruits during intergroup encounters) to offset the higher travel costs during intergroup encounters (Lucchesi et al., 2021). The largely null findings of the influence of food and mate availability on intergroup competition in this study further suggest that there may be other underlying drivers promoting bonobo intergroup encounters. For instance, prolonged, non-violent intergroup encounters may provide a platform for males and females to gain access to additional social partners, particularly allowing young females to gain information about future migration opportunities (Pisor and Surbeck, 2019; Sakamaki et al., 2018). In humans, prolonged, non-violent intergroup encounters can have important consequences including access to non-local resources and resource exchange (Pisor and Gurven, 2016; Robinson and Barker, 2017), as well as information

transfer and evolution of cumulative culture (Hill et al., 2014). Taken together, it is likely that there are benefits for bonobo groups to remain together over extended periods despite costs of intergroup competition. We encourage future studies to explore potential short- and long-term benefits associated with intergroup encounters in wild bonobos.

5. Conclusions

In this study, we demonstrated through behavioral and physiological markers, aggression and urinary cortisol, that competition between groups persists in bonobos, a species in which intergroup encounters are prolonged and lethal intergroup aggression seems absent. These competitive interactions between bonobo groups are not restricted to periods of low fruit abundance or the presence of potential mates. Instead, groups may compete to establish and exert dominance over each other in order to improve future access to food and mates in the long run (Crofoot and Wrangham, 2010). While intergroup encounters elicit similar patterns of physiological reactivity in bonobos and chimpanzees, interactions between groups are generally more varied and peaceful in the former. Combining our findings on the occurrence of competition during prolonged intergroup encounters in bonobos with patterns of intergroup interactions in chimpanzee and hunter-gatherer societies (Boehm, 2013; Boesch et al., 2008; Wilson and Wrangham, 2003), it is likely that the ability to use violence and compete peacefully between groups has a long evolutionary history and that the two intergroup strategies can be used interchangeably and conjointly as a response to changes in ecological and/or social conditions (Gat, 2019). By being tolerant towards each other, members of different groups can interact and remain together over extended periods of time, and this may have eventually promoted the evolution of multilevel societies in humans (Grueter et al., 2012).

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Appendix A. Supplementary data

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References

- Allen, M.W., Bettinger, R.L., Codding, B.F., Jones, T.L., Schwitalla, A.W., 2016. Resource scarcity drives lethal aggression among prehistoric hunter-gatherers in central California. *Proc. Natl. Acad. Sci.* 113, 12120–12125. <https://doi.org/10.1073/pnas.1607996113>.
- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–266. <https://doi.org/10.1163/156853974X00534>.
- Amsler, S.J., 2010. Energetic costs of territorial boundary patrols by wild chimpanzees. *Am. J. Primatol.* 72, 93–103. <https://doi.org/10.1002/ajp.20757>.
- Anderson, D.P., Nordheim, E.V., Moermond, T.C., Bi, Z.B.G., Boesch, C., 2005. Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. *Biotropica* 37, 631–640. <https://doi.org/10.1111/j.1744-7429.2005.00080.x>.

- Arseneau-Robar, T.J.M., Taucher, A.L., Müller, E., van Schaik, C., Bshary, R., Willems, E. P., 2016. Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. *Proc. R. Soc. B Biol. Sci.* 283, 20161817 <https://doi.org/10.1098/rspb.2016.1817>.
- Arseneau-Robar, T.J.M., Taucher, A.L., Schneider, A.B., van Schaik, C.P., Willems, E.P., 2017. Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. *Anim. Behav.* 123, 129–137. <https://doi.org/10.1016/j.anbehav.2016.10.034>.
- Baayen, R.H., 2008. *Analyzing Linguistic Data: A Practical Introduction to Statistics Using R*. Cambridge University Press.
- Bahr, N.I., Palme, R., Möhle, U., Hodges, J.K., Heistermann, M., 2000. Comparative aspects of the metabolism and excretion of cortisol in three individual nonhuman primates. *Gen. Comp. Endocrinol.* 117, 427–438. <https://doi.org/10.1006/gcen.1999.7431>.
- Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. *J. Mem. Lang.* 68, 255–278. <https://doi.org/10.1016/j.jml.2012.11.001>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015a. Fitting linear mixed-effects models using *lme4*. *J. Stat. Softw.* 67 <https://doi.org/10.18637/jss.v067.i01>.
- Bates, D., Kliegl, R., Vasishth, S., Baayen, H., 2015b. *Parsimonious Mixed Models*.
- Beehner, J.C., Bergman, T.J., 2017. The next step for stress research in primates: to identify relationships between glucocorticoid secretion and fitness. *Horm. Behav., Field endocrinology of nonhuman primates and humans* 91, 68–83. <https://doi.org/10.1016/j.yhbeh.2017.03.003>.
- Bjellelev, E., Scheepers, D., Ellemers, N., 2012. The cortisol response to anticipated intergroup interactions predicts self-reported prejudice. *PLoS One* 7, e33681. <https://doi.org/10.1371/journal.pone.0033681>.
- Boehm, C., 2013. *The Biocultural Evolution of Conflict Resolution between Groups*. Oxford University Press.
- Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., Normand, E., 2008. Intergroup conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective. *Am. J. Primatol.* 70, 519–532. <https://doi.org/10.1002/ajp.20524>.
- Brown, M., 2013. Food and range defence in group-living primates. *Anim. Behav.* 85, 807–816. <https://doi.org/10.1016/j.anbehav.2013.01.027>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference*, 2nd ed. Springer, Berlin.
- Bygott, J.D., 1979. Agonistic behaviour, dominance, and social structure in wild chimpanzees of the Gombe National Park. In: Hamburg, D.A., McCown, E.R. (Eds.), *The Great Apes*. Benjamin/Cummings, Menlo Park, CA, pp. 405–428.
- Cant, M.A., Otsali, E., Mwanguhya, F., 2002. Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. *Ethology* 108, 541–555. <https://doi.org/10.1046/j.1439-0310.2002.00795.x>.
- Cashdan, E., Barnard, A., Bicchieri, M.C., Bishop, C.A., Blundell, V., Ehrenreich, J., Guenther, M., Hamilton, A., Harpending, H.C., Howell, N., Smith, E.A., Terashima, H., Wiessner, P., 1983. Territoriality among human foragers: ecological models and an application to four bushman groups [and comments and reply]. *Curr. Anthropol.* 24, 47–66.
- Chapman, C.A., White, F.J., Wrangham, R.W., 1994. Party size in chimpanzees and bonobos. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Helme, P.G. (Eds.), *Chimpanzee Cultures*. Harvard University Press, Cambridge, pp. 41–57.
- Clutton-Brock, T.H., Huchard, E., 2013. Social competition and selection in males and females. *Philos. Trans. R. Soc. B Biol. Sci.* 368, 20130074. <https://doi.org/10.1098/rstb.2013.0074>.
- Clutton-Brock, T.H., Guinness, F.E., Albon, S.D. (Eds.), 1982. *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.
- Cooper, M.A., Aureli, F., Singh, M., 2004. Between-group encounters among bonnet macaques (*Macaca radiata*). *Behav. Ecol. Sociobiol.* 56, 217–227. <https://doi.org/10.1007/s00265-004-0779-4>.
- Crofoot, M.C., 2007. Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. *Behaviour* 144, 1473–1495. <https://doi.org/10.1163/156853907782512119>.
- Crofoot, M.C., Gilby, L.C., 2012. Cheating monkeys undermine group strength in enemy territory. *Proc. Natl. Acad. Sci.* 109, 501–505. <https://doi.org/10.1073/pnas.1115937109>.
- Crofoot, M.C., Wrangham, R.W., 2010. Intergroup aggression in primates and humans: The case for a unified theory. In: Kappeler, P.M., Silk, J. (Eds.), *Mind the Gap*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 171–195. https://doi.org/10.1007/978-3-642-02725-3_8.
- Crofoot, M.C., Gilby, L.C., Wikelski, M.C., Kays, R.W., 2007. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proc. Natl. Acad. Sci.* 105, 577–581. <https://doi.org/10.1073/pnas.0707749105>.
- Dobson, A.J., Barnett, A., 2008. *An Introduction to Generalized Linear Models*. CRC Press, Philadelphia, PA.
- Douglas, P.H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., Deschner, T., 2016. Mixed messages: wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. *BMC Evol. Biol.* 16, 140 <https://doi.org/10.1186/s12862-016-0691-3>.
- Dyble, M., Houslay, T., Manser, M., Clutton-Brock, T., 2019. Intergroup aggression in meerkats. *Proc. R. Soc. B Biol. Sci.* <https://doi.org/10.1098/rspb.2019.1993>.
- Edwards, D.A., Kurlander, L.S., 2010. Women's intercollegiate volleyball and tennis: effects of warm-up, competition, and practice on saliva levels of cortisol and testosterone. *Horm. Behav.* 58, 606–613. <https://doi.org/10.1016/j.yhbeh.2010.06.015>.
- Edwards, D.A., Wetzel, K., Wyner, D.R., 2006. Intercollegiate soccer: saliva cortisol and testosterone are elevated during competition, and testosterone is related to status and social connectedness with teammates. *Physiol. Behav.* 87, 135–143. <https://doi.org/10.1016/j.physbeh.2005.09.007>.
- Fashing, P.J., 2001. Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. *Behav. Ecol. Sociobiol.* 50, 219–230. <https://doi.org/10.1007/s002650100358>.
- Fedy, B.C., Stutchbury, B.J.M., 2005. Territory defence in tropical birds: are females as aggressive as males? *Behav. Ecol. Sociobiol.* 58, 414–422. <https://doi.org/10.1007/s00265-005-0928-4>.
- Forstmeier, W., Schielzeth, H., 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* 65, 47–55. <https://doi.org/10.1007/s00265-010-1038-5>.
- Fruth, B., Hohmann, G., 2018. Food sharing across borders. *Hum. Nat.* 29, 91–103. <https://doi.org/10.1007/s12110-018-9311-9>.
- Furrer, R.D., Kyabulima, S., Willems, E.P., Cant, M.A., Manser, M.B., 2011. Location and group size influence decisions in simulated intergroup encounters in banded mongooses. *Behav. Ecol.* 22, 493–500. <https://doi.org/10.1093/beheco/arr010>.
- Furuichi, T., 2009. Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. *Primates* 50, 197–209. <https://doi.org/10.1007/s10329-009-0141-6>.
- Furuichi, T., 2011. Female contributions to the peaceful nature of bonobo society. *Evol. Anthropol. Issues News Rev.* 20, 131–142. <https://doi.org/10.1002/evan.20308>.
- Furuichi, T., 2020. Variation in intergroup relationships among species and among and within local populations of African apes. *Int. J. Primatol.* 41, 203–223. <https://doi.org/10.1007/s10764-020-00134-x>.
- Gat, A., 2010. Why war? Motivations for fighting in the human state of nature. In: Kappeler, P.M., Silk, J. (Eds.), *Mind the Gap*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 197–220. https://doi.org/10.1007/978-3-642-02725-3_9.
- Gat, A., 2019. Is war in our nature? *Hum. Nat.* 30, 149–154. <https://doi.org/10.1007/s12110-019-09342-8>.
- Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., Tautz, D., 1999. Intra-community relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc. R. Soc. B Biol. Sci.* 266, 1189–1195.
- Gesquiere, L.R., Khan, M., Shek, L., Wango, T.L., Wango, E.O., Alberts, S.C., Altmann, J., 2008. Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). *Horm. Behav.* 54, 410–416. <https://doi.org/10.1016/j.yhbeh.2008.04.007>.
- Gill, S.A., Costa, L.M., Hau, M., 2008. Males of a single-brooded tropical bird species do not show increases in testosterone during social challenges. *Horm. Behav.* 54, 115–124. <https://doi.org/10.1016/j.yhbeh.2008.02.003>.
- Goymann, W., Wingfield, J.C., 2004. Allostatic load, social status and stress hormones: the costs of social status matter. *Anim. Behav.* 67, 591–602. <https://doi.org/10.1016/j.anbehav.2003.08.007>.
- Grant, J.W.A., 1997. Territoriality. In: Godin, J.-G.J. (Ed.), *Behavioural Ecology of Teleost Fishes*. Oxford University Press, Oxford, pp. 81–103.
- Grueter, C.C., Chapais, B., Zinner, D., 2012. Evolution of multilevel social systems in nonhuman primates and humans. *Int. J. Primatol.* 33, 1002–1037. <https://doi.org/10.1007/s10764-012-9618-z>.
- Hare, B., Wobber, V., Wrangham, R., 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Anim. Behav.* 83, 573–585. <https://doi.org/10.1016/j.anbehav.2011.12.007>.
- Harris, T.R., 2010. Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). *Anim. Behav.* 79, 89–98. <https://doi.org/10.1016/j.anbehav.2009.10.007>.
- Hashimoto, C., Isaji, M., Mouri, K., Takemoto, H., 2020. Intergroup encounters of chimpanzees (*Pan troglodytes*) from the female perspective. *Int. J. Primatol.* <https://doi.org/10.1007/s10764-020-00145-8> s10764-020-00145-8.
- Hauser, B., Deschner, T., Boesch, C., 2008. Development of a liquid chromatography–tandem mass spectrometry method for the determination of 23 endogenous steroids in small quantities of primate urine. *J. Chromatogr. B* 862, 100–112. <https://doi.org/10.1016/j.jchromb.2007.11.009>.
- Hill, K.R., Wood, B.M., Baggio, J., Hurtado, A.M., Boyd, R.T., 2014. Hunter-gatherer inter-band interaction rates: implications for cumulative culture. *PLoS One* 9, e102806. <https://doi.org/10.1371/journal.pone.0102806>.
- Hohmann, G., Fruth, B., 2000. Use and function of genital contacts among female bonobos. *Anim. Behav.* 60, 107–120.
- Hohmann, G., Fruth, B., 2002. Dynamics in social organization of bonobos (*Pan paniscus*). In: Boesch, C., Hohmann, G., Marchant, L. (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp. 138–150.
- Hohmann, G., Mundry, R., Deschner, T., 2009. The relationship between socio-sexual behavior and salivary cortisol in bonobos: tests of the tension regulation hypothesis. *Am. J. Primatol.* 71, 223–232. <https://doi.org/10.1002/ajp.20640>.
- Idani, G., 1990. Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. *African Study Monographs* 11 (3), 153–186. <https://doi.org/10.14989/68066>.
- Isbell, L.A., 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav. Ecol.* 2, 143–155. <https://doi.org/10.1093/beheco/2.2.143>.
- Ishizuka, S., Kawamoto, Y., Sakamaki, T., Tokuyama, N., Toda, K., Okamura, H., Furuichi, T., 2018. Paternity and kin structure among neighbouring groups in wild bonobos at Wamba. *R. Soc. Open Sci.* 5, 171006 <https://doi.org/10.1098/rsos.171006>.

- Jaeggi, A.V., Boose, K.J., White, F.J., Gurven, M., 2016. Obstacles and catalysts of cooperation in humans, bonobos, and chimpanzees: behavioural reaction norms can help explain variation in sex roles, inequality, war and peace. *Behaviour* 153, 1015–1051. <https://doi.org/10.1163/1568539X-00003347>.
- Jaeggi, A.V., Trumble, B.C., Brown, M., 2018. Group-level competition influences urinary steroid hormones among wild red-tailed monkeys, indicating energetic costs. *Am. J. Primatol.* 80, e22757 <https://doi.org/10.1002/ajp.22757>.
- Kitchen, D.M., Beehner, J.C., 2007. Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour* 144, 1551–1581. <https://doi.org/10.1163/156853907782512074>.
- Kitchen, D.M., Cheney, D.L., Seyfarth, R.M., 2004. Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). *Behaviour* 141, 197–218. <https://doi.org/10.1163/156853904322890816>.
- Koch, F., Signer, J., Kappeler, P.M., Fichtel, C., 2016a. Intergroup encounters in Verreaux's sifakas (*Propithecus verreauxi*): who fights and why? *Behav. Ecol. Sociobiol.* 70, 797–808. <https://doi.org/10.1007/s00265-016-2105-3>.
- Koch, F., Signer, J., Kappeler, P.M., Fichtel, C., 2016b. The role of the residence-effect on the outcome of intergroup encounters in Verreaux's sifakas. *Sci. Rep.* 6, 28457 <https://doi.org/10.1038/srep28457>.
- Landys, M.M., Goymann, W., Schwabl, I., Trapschuh, M., Slagsvold, T., 2010. Impact of season and social challenge on testosterone and corticosterone levels in a year-round territorial bird. *Horm. Behav.* 58, 317–325. <https://doi.org/10.1016/j.yhbeh.2010.02.013>.
- Langergraber, K.E., Watts, D.P., Vigilant, L., Mitani, J.C., 2017. Group augmentation, collective action, and territorial boundary patrols by male chimpanzees. *Proc. Natl. Acad. Sci.* 114, 7337–7342. <https://doi.org/10.1073/pnas.1701582114>.
- Lobato, E., Moreno, J., Merino, S., Morales, J., Tomás, G., Martínez, J., Vázquez, R.A., Kuchar, A., Möstl, E., Osorno, J.L., 2010. Arrival date and territorial behavior are associated with corticosterone metabolite levels in a migratory bird. *J. Ornithol.* 151, 587–597. <https://doi.org/10.1007/s10336-009-0488-x>.
- Löhrich, T., Behringer, V., Wittig, R.M., Deschner, T., Leendertz, F.H., 2018. The use of neopterin as a noninvasive marker in monitoring diseases in wild chimpanzees. *EcoHealth* 15, 792–803. <https://doi.org/10.1007/s10393-018-1357-y>.
- Lucchesi, S., Cheng, L., Deschner, T., Mundry, R., Wessling, E.G., Surbeck, M., 2021. Better together? How intergroup associations affect energy balance and feeding behavior in wild bonobos. *Behav. Ecol. Sociobiol.* 75, 2 <https://doi.org/10.1007/s00265-020-02943-9>.
- Lucchesi, S., Cheng, L., Janmaat, K., Mundry, R., Pisor, A., Surbeck, M., 2020. Beyond the group: how food, mates, and group size influence intergroup encounters in wild bonobos. *Behav. Ecol.* <https://doi.org/10.1093/beheco/arz214>.
- MacDougall-Shackleton, S.A., Bonier, F., Romero, L.M., Moore, L.T., 2019. Glucocorticoids and “stress” are not synonymous. *Integr. Org. Biol.* 1, obz017 <https://doi.org/10.1093/iob/obz017>.
- Majolo, B., Ventura, R., Koyama, N.F., 2005. Sex, rank and age differences in the Japanese Macaque (*Macaca fuscata yakui*) participation in inter-group encounters. *Ethology* 111, 455–468. <https://doi.org/10.1111/j.1439-0310.2005.01087.x>.
- Manson, J.H., Wrangham, R.W., 1991. Intergroup aggression in chimpanzees and humans. *Curr. Anthropol.* 32, 369–390. <https://doi.org/10.1086/203974>.
- Markham, A.C., Alberts, S.C., Altmann, J., 2012. Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population. *Anim. Behav.* 84, 399–403. <https://doi.org/10.1016/j.anbehav.2012.05.009>.
- McCullagh, P., Nelder, J.A. (Eds.), 1989. *Generalized Linear Models*, 2nd edition. Chapman and Hall, London.
- McEwen, B.S., Wingfield, J.C., 2003. The concept of allostasis in biology and biomedicine. *Horm. Behav.* 43, 2–15. [https://doi.org/10.1016/S0018-506X\(02\)00024-7](https://doi.org/10.1016/S0018-506X(02)00024-7).
- Miller, R.C., Brindle, E., Holman, D.J., Shofer, J., Klein, N.A., Soules, M.R., O'Connor, K.A., 2004. Comparison of specific gravity and creatinine for normalizing urinary reproductive hormone concentrations. *Clin. Chem.* 50, 924–932. <https://doi.org/10.1373/clinchem.2004.032292>.
- Mirville, M.O., Ridley, A.R., Samedí, J.P.M., Vecellio, V., Ndagijimana, F., Stoinski, T.S., Grueter, C.C., 2018. Factors influencing individual participation during intergroup interactions in mountain gorillas. *Anim. Behav.* 144, 75–86. <https://doi.org/10.1016/j.anbehav.2018.08.003>.
- Mitani, J.C., Watts, D.P., 2005. Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Anim. Behav.* 70, 1079–1086. <https://doi.org/10.1016/j.anbehav.2005.02.012>.
- Mitani, J.C., Watts, D.P., Amsler, S.J., 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Curr. Biol.* 20, R507–R508. <https://doi.org/10.1016/j.cub.2010.04.021>.
- Muller, M.N., Lipson, S.F., 2003. Diurnal patterns of urinary steroid excretion in wild chimpanzees. *Am. J. Primatol.* 60, 161–166. <https://doi.org/10.1002/ajp.10103>.
- Nieuwenhuis, S., Forstmann, B.U., Wagenmakers, E.-J., 2011. Erroneous analyses of interactions in neuroscience: a problem of significance. *Nat. Neurosci.* 14, 1105–1107. <https://doi.org/10.1038/nn.2886>.
- Noser, R., Byrne, R.W., 2009. How do wild baboons (*Papio ursinus*) plan their routes? Travel among multiple high-quality food sources with inter-group competition. *Anim. Cogn.* 13, 145. <https://doi.org/10.1007/s10071-009-0254-8>.
- Nurmi, N.O., Hohmann, G., Goldstone, L.G., Deschner, T., Schülke, O., 2018. The “tolerant chimpanzee”—towards the costs and benefits of sociality in female bonobos. *Behav. Ecol.* 29, 1325–1339. <https://doi.org/10.1093/beheco/ary118>.
- Ostfeld, R.S., 1990. The ecology of territoriality in small mammals. *Trends Ecol. Evol.* 5, 411–415. [https://doi.org/10.1016/0169-5347\(90\)90026-A](https://doi.org/10.1016/0169-5347(90)90026-A).
- Oxford, J., Ponzi, D., Geary, D.C., 2010. Hormonal responses differ when playing violent video games against an ingroup and outgroup. *Evol. Hum. Behav.* 31, 201–209. <https://doi.org/10.1016/j.evolhumbehav.2009.07.002>.
- Parker, G.A., 1974. Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* 47, 223–243. [https://doi.org/10.1016/0022-5193\(74\)90111-8](https://doi.org/10.1016/0022-5193(74)90111-8).
- Pisor, A.C., Gurven, M., 2016. Risk buffering and resource access shape valuation of out-group strangers. *Sci. Rep.* 6 <https://doi.org/10.1038/srep30435>.
- Pisor, A.C., Surbeck, M., 2019. The evolution of intergroup tolerance in nonhuman primates and humans. *Evol. Anthropol.* 28 (4), 210–223. <https://doi.org/10.1002/evan.21793>.
- Preis, A., Samuni, L., Deschner, T., Crockford, C., Wittig, R.M., 2019. Urinary cortisol, aggression, dominance and competition in wild, west African male chimpanzees. *Front. Ecol. Evol.* 7 <https://doi.org/10.3389/fevo.2019.00107>.
- Robbins, M.M., Sawyer, S.C., 2007. Intergroup encounters in mountain gorillas of Bwindi Impenetrable National Park, Uganda. *Behaviour* 144, 1497–1519. <https://doi.org/10.1163/156853907782512146>.
- Robinson, E.J.H., Barker, J.L., 2017. Inter-group cooperation in humans and other animals. *Biol. Lett.* 13, 20160793 <https://doi.org/10.1098/rsbl.2016.0793>.
- Rosenbaum, S., Vecellio, V., Stoinski, T., 2016. Observations of severe and lethal coalitionary attacks in wild mountain gorillas. *Sci. Rep.* 6, 37018 <https://doi.org/10.1038/srep37018>.
- Sakamaki, T., Behncke, I., Laporte, M., Mulavva, M., Ryu, H., Takemoto, H., Tokuyama, N., Yamamoto, S., Furuichi, T., 2015. Intergroup transfer of females and social relationships between immigrants and residents in bonobo (*Pan paniscus*) societies. In: Furuichi, T., Yamagiwa, J., Aureli, F. (Eds.), *Dispersing Primate Females*, Primatology Monographs. Springer Japan, pp. 127–164. https://doi.org/10.1007/978-4-431-55480-6_6.
- Sakamaki, T., Ryu, H., Toda, K., Tokuyama, N., Furuichi, T., 2018. Increased frequency of intergroup encounters in wild bonobos (*Pan paniscus*) around the yearly peak in fruit abundance at Wamba. *Int. J. Primatol.* 39, 685–704. <https://doi.org/10.1007/s10764-018-0058-2>.
- Salvador, A., Suay, F., González-Bono, E., Serrano, M.A., 2003. Anticipatory cortisol, testosterone and psychological responses to judo competition in young men. *Psychoneuroendocrinology* 28, 364–375. [https://doi.org/10.1016/S0306-4530\(02\)00028-8](https://doi.org/10.1016/S0306-4530(02)00028-8).
- Samuni, L., Preis, A., Mundry, R., Deschner, T., Crockford, C., Wittig, R.M., 2017. Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proc. Natl. Acad. Sci.* 114, 268–273. <https://doi.org/10.1073/pnas.1616812114>.
- Samuni, L., Mielke, A., Preis, A., Crockford, C., Wittig, R.M., 2019a. Intergroup competition enhances chimpanzee (*Pan troglodytes verus*) in-group cohesion. *Int. J. Primatol.* <https://doi.org/10.1007/s10764-019-00112-y>.
- Samuni, L., Preis, A., Wittig, R.M., Crockford, C., 2019b. Cortisol and oxytocin show independent activity during chimpanzee intergroup conflict. *Psychoneuroendocrinology* 104, 165–173. <https://doi.org/10.1016/j.psyneuen.2019.02.007>.
- Samuni, L., Wegdell, F., Surbeck, M., 2020. Behavioural diversity of bonobo prey preference as a potential cultural trait. *eLife* 9, e59191. <https://doi.org/10.7554/eLife.59191>.
- Sánchez-Tójar, A., Schroeder, J., Farine, D.R., 2018. A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *J. Anim. Ecol.* 87, 594–608. <https://doi.org/10.1111/1365-2656.12776>.
- Sapolsky, R.M., 1993. The physiology of dominance in stable versus unstable social hierarchies. In: Mason, W., Mendoza, S. (Eds.), *Primate Social Conflict*. SUNY Press, New York, pp. 171–204.
- Scarry, C.J., 2017. Male resource defence during intergroup aggression among tufted capuchin monkeys. *Anim. Behav.* 123, 169–178. <https://doi.org/10.1016/j.anbehav.2016.10.015>.
- Schoof, V.A.M., Jack, K.M., 2013. The association of intergroup encounters, dominance status, and fecal androgen and glucocorticoid profiles in wild male white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* 75, 107–115. <https://doi.org/10.1002/ajp.22089>.
- Smith, J.M., Parker, G.A., 1976. The logic of asymmetric contests. *Anim. Behav.* 24, 159–175. [https://doi.org/10.1016/S0003-3472\(76\)80110-8](https://doi.org/10.1016/S0003-3472(76)80110-8).
- Sobolewski, M.E., 2012. *The Hormonal Correlates of Male Chimpanzee Social Behavior*. PhD. Thesis. University of Michigan.
- Spong, G., 2002. Space use in lions, *Panthera leo*, in the Selous game reserve: social and ecological factors. *Behav. Ecol. Sociobiol.* 52, 303–307. <https://doi.org/10.1007/s00265-002-0515-x>.
- Stamps, J.A., 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. *Ecology* 58, 349–358. <https://doi.org/10.2307/1935609>.
- Surbeck, M., Hohmann, G., 2013. Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behav. Ecol. Sociobiol.* 67, 1767–1780. <https://doi.org/10.1007/s00265-013-1584-8>.
- Surbeck, M., Deschner, T., Schubert, G., Weltring, A., Hohmann, G., 2012. Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Anim. Behav.* 83, 659–669. <https://doi.org/10.1016/j.anbehav.2011.12.010>.
- Surbeck, M., Deschner, T., Behringer, V., Hohmann, G., 2015. Urinary C-peptide levels in male bonobos (*Pan paniscus*) are related to party size and rank but not to mate competition. *Horm. Behav.* 71, 22–30. <https://doi.org/10.1016/j.yhbeh.2015.03.007>.
- Surbeck, M., Coxé, S., Lokasola, A.L., 2017. Lonoa: the establishment of a permanent field site for behavioural research on bonobos in the Kokolopori Bonobo Reserve. *Pan Afr. News* 24, 13–15.
- Tan, J., Arieli, D., Hare, B., 2017. Bonobos respond prosocially toward members of other groups. *Sci. Rep.* 7, 14733 <https://doi.org/10.1038/s41598-017-15320-w>.
- Thompson, F.J., Marshall, H.H., Vitikainen, E.L.K., Cant, M.A., 2017. Causes and consequences of intergroup conflict in cooperative banded mongooses. *Anim. Behav.* 126, 31–40. <https://doi.org/10.1016/j.anbehav.2017.01.017>.

- Toda, K., Tokuyama, N., Ishizuka, S., Furuichi, T., 2018. A short-term visit of an adult male bonobo from the neighboring unit-group at Wamba. *Pan Afr. News* 25, 22–24. <https://doi.org/10.5134/236291>.
- Tokuyama, N., Furuichi, T., 2016. Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Anim. Behav.* 119, 27–35. <https://doi.org/10.1016/j.anbehav.2016.06.021>.
- Tokuyama, N., Sakamaki, T., Furuichi, T., 2019. Inter-group aggressive interaction patterns indicate male mate defense and female cooperation across bonobo groups at Wamba, Democratic Republic of the Congo. *Am. J. Phys. Anthropol.* 170, 535–550. <https://doi.org/10.1002/ajpa.23929>.
- Van Belle, S., Estrada, A., 2020. The influence of loud calls on intergroup spacing mechanism in black howler monkeys (*Alouatta pigra*). *Int. J. Primatol.* 41, 265–286. <https://doi.org/10.1007/s10764-019-00121-x>.
- Van Belle, S., Scarry, C.J., 2015. Individual participation in intergroup contests is mediated by numerical assessment strategies in black howler and tufted capuchin monkeys. *Philos. Trans. R. Soc. B Biol. Sci* 370, 20150007. <https://doi.org/10.1098/rstb.2015.0007>.
- van Duyse, E., Pinxten, R., Arckens, L., Eens, M., Darras, V., 2004. Opposite changes in plasma testosterone and corticosterone levels following a simulated territorial challenge in male great tits. *Behaviour* 141, 451–467. <https://doi.org/10.1163/156853904323066739>.
- van Schaik, C.P., Assink, P.R., Salafsky, N., 1992. Territorial behavior in southeast Asian langurs: resource defense or mate defense? *Am. J. Primatol.* 26, 233–242. <https://doi.org/10.1002/ajp.1350260402>.
- Vogel, E.R., Janson, C.H., 2011. Quantifying primate food distribution and abundance for socioecological studies: an objective consumer-centered method. *Int. J. Primatol.* 32, 737–754. <https://doi.org/10.1007/s10764-011-9498-7>.
- Wagner, J.D., Flinn, M.V., England, B.G., 2002. Hormonal response to competition among male coalitions. *Evol. Hum. Behav.* 23, 437–442. [https://doi.org/10.1016/S1090-5138\(02\)00100-9](https://doi.org/10.1016/S1090-5138(02)00100-9).
- Waller, M.T., 2011. *The Ranging Behavior of Bonobos in the Lomako Forest*. PhD. Thesis. University of Oregon.
- Watts, D.P., Muller, M.N., Amsler, S.J., Mbabazi, G., Mitani, J.C., 2006. Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *Am. J. Primatol.* 68, 161–180. <https://doi.org/10.1002/ajp.20214>.
- Wessling, E.G., Deschner, T., Mundry, R., Pruett, J.D., Wittig, R.M., Kühl, H.S., 2018. Seasonal variation in physiology challenges the notion of chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. *Front. Ecol. Evol.* 6 <https://doi.org/10.3389/fevo.2018.00060>.
- Williams, J.M., Oehlert, G.W., Carlis, J.V., Pusey, A.E., 2004. Why do male chimpanzees defend a group range? *Anim. Behav.* 68, 523–532. <https://doi.org/10.1016/j.anbehav.2003.09.015>.
- Wilson, M.L., Wrangham, R.W., 2003. Intergroup relations in chimpanzees. *Annu. Rev. Anthropol.* 32, 363–392. <https://doi.org/10.1146/annurev.anthro.32.061002.120046>.
- Wilson, M.L., Kahlenberg, S.M., Wells, M., Wrangham, R.W., 2012. Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Anim. Behav.* 83, 277–291. <https://doi.org/10.1016/j.anbehav.2011.11.004>.
- Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L., Hohmann, G., Itoh, N., Koops, K., Lloyd, J.N., Matsuzawa, T., Mitani, J.C., Mjungu, D.C., Morgan, D., Muller, M.N., Mundry, R., Nakamura, M., Pruett, J., Pusey, A.E., Riedel, J., Sanz, C., Schel, A.M., Simmons, N., Waller, M., Watts, D.P., White, F., Wittig, R.M., Zuberbühler, K., Wrangham, R.W., 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature* 513, 414–417. <https://doi.org/10.1038/nature13727>.
- Wittig, R.M., Crockford, C., Weltring, A., Langergraber, K.E., Deschner, T., Zuberbühler, K., 2016. Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nat. Commun.* 7 <https://doi.org/10.1038/ncomms13361>.
- Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R.W., Ellison, P.T., 2010. Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proc. Natl. Acad. Sci.* 107, 12457–12462. <https://doi.org/10.1073/pnas.1007411107>.
- Wrangham, R.W., 1999. Evolution of coalitionary killing. *Am. J. Phys. Anthropol.* 110, 1–30. [https://doi.org/10.1002/\(SICI\)1096-8644\(1999\)110:29+<1::AID-AJPA2>3.0.CO;2-E](https://doi.org/10.1002/(SICI)1096-8644(1999)110:29+<1::AID-AJPA2>3.0.CO;2-E).
- Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.* 7, 636–645. <https://doi.org/10.1111/2041-210X.12577>.