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Original Article

Beyond the group: how food, mates, and group size influence intergroup encounters in wild bonobos

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In social-living animals, interactions between groups are frequently agonistic, but they can also be tolerant and even cooperative. Intergroup tolerance and cooperation are regarded as a crucial step in the formation of highly structured multilevel societies. Behavioral ecological theory suggests that intergroup tolerance and cooperation can emerge either when the costs of hostility outweigh the benefits of exclusive resource access or when both groups gain fitness benefits through their interactions. However, the factors promoting intergroup tolerance are still unclear due to the paucity of data on intergroup interactions in tolerant species. Here, we examine how social and ecological factors affect the onset and termination of intercommunity encounters in two neighboring communities of wild bonobos, a species exhibiting flexible patterns of intergroup interactions, at Kokolopori Bonobo Reserve, Democratic Republic of the Congo. We recorded the timing and location of intercommunity encounters and measured fruit abundance and distribution, groups' social characteristics, and space-use dynamics over a 19-month period. We found that intercommunity tolerance was facilitated by a decrease in feeding competition, with high fruit abundance increasing the likelihood of communities to encounter, and high clumpiness of fruit patches increasing the probability to terminate encounters likely due to increased contest. In addition, the possibility for extra-community mating, as well as the potential benefits of more efficient foraging in less familiar areas, reduced the probability that the communities terminated encounters. By investigating the factors involved in shaping relationships across groups, this study contributes to our understanding of how animal sociality can extend beyond the group level.

Lay Summary: Neighboring bonobo groups encounter each other more often when high abundance of fruits reduces feeding competition between them. When additional benefits, such as extra-group mating opportunities and potential improved foraging in less familiar areas emerge, even long-lasting intergroup associations can develop. By extending tolerant interactions beyond the group level, mechanisms such as those we describe in bonobos can lay the basis for the formation of complexly structured multilevel societies in animals.

Key words: **food distribution, foraging, fruit abundance, great apes, intercommunity encounter, intergroup tolerance.**

INTRODUCTION

Most intergroup relations in social-living animals are agonistic due to competition over access to resources, such as food (banded mongooses: Thompson et al. 2017; spotted hyenas: Boydston et al. 2001; nonhuman primates: Koenig 2002; Brown 2013) and mates (humpback whales: Clapham et al. 1992; red deer: Carranza et al. 1990; savannah baboons: Kitchen et al. 2004). However, intergroup interactions can also be tolerant and even cooperative (polydomous ants: Robinson and Barker 2017; humans and nonhuman great apes: Pisor and Surbeck 2019; monkeys: Grueter et al. 2012). Factors known to shape relations between groups include group differences in fighting abilities (which usually increase with group size [Adams 2003]) (lions: Mosser and Packer 2009; savannah baboons: Kitchen

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et al. 2004; wood ants: Tanner 2006), the relative value of a contestable resource to each group (banded mongooses: Furrer et al. 2011; sifakas: Koch et al. 2016; capuchin monkeys: Crofoot et al. 2008), and the groups' previous interaction history (which may result either in decreased aggressiveness ["dear enemy effect": Temeles 1994] or conversely in higher hostility toward neighbors than strangers ["nasty neighbor effect": Müller and Manser 2007] depending on the level of competition [Christensen and Radford 2018]). While extensive research has focused on group formation and the costs and benefits of social living (reviewed in Isbell and Young 2002; Koenig et al. 2013), less is known about the dynamics promoting tolerant relations extending beyond the group level (Koenig 2002; Grueter et al. 2012; Willems and van Schaik 2015; Robinson and Barker 2017; Pisor and Surbeck 2019). By promoting long-lasting associations between groups, intergroup tolerance may provide the basis for, or be the precursor of, social complexity and lead to the formation of multilevel societies (Rubenstein and Hack 2004; Grueter et al. 2012).

Economic defendability theory predicts that tolerant intergroup interactions develop when the costs of hostility outweigh the benefits of exclusive resource access (Brown 1964; Maher and Lott 2000). This occurs when 1) resources are so dispersed as to not be economically monopolizable by a group or 2) a group's access to resources is not hampered by the usage of such resources by other groups (Grant 1993). Furthermore, intergroup tolerance should emerge when interactions with extra-group members provide mutual fitness benefits to participants, thus promoting cooperation and prolonged intergroup associations (Robinson and Barker 2017). Proposed fitness benefits of intergroup associations include 1) defense from predation (polydomous ants: Van Wilgenburg and Elgar 2007; sperm whales: Whitehead et al. 2012; proboscis monkeys: Matsuda et al. 2010; coal tits: Brotons and Herrando 2003) and threat from conspecifics (plain zebras: Rubenstein and Hack 2004; colobine monkeys: Grueter and van Schaik 2010) as well as 2) improved resource access (polydomous ants: Ellis et al. 2014; killer whales: Tavares et al. 2017; humans and nonhuman great apes: Jaeggi et al. 2016; Pisor and Surbeck 2019). Tolerance between groups can improve a group's resource access by 1) allowing the group to buffer periods of local resource shortfall via accessing a neighbor's home range or via active sharing of resources (polydomous ants: Ellis et al. 2014; humans and potentially nonhuman great apes: Jaeggi et al. 2016; Pisor and Surbeck 2019), 2) providing access to nonlocal resources (humans: Robinson and Barker 2017; humans and nonhuman great apes: Pisor and Surbeck 2019), and 3) allowing more efficient foraging when individuals range in less familiar areas as they can follow out-group individuals more familiar with the location of food in such areas (fruit bats: Ratcliffe and Hofstede 2005; nonhuman primates: Isbell and Vuren 1996; humans: Cashdan et al. 1983; hooded crows: Sonerud et al. 2001). In addition to these socioecological factors, intergroup tolerance may be fostered by genetic relatedness between groups (polydomous ants: Ellis et al. 2014; plain zebras: Tong et al. 2015; African elephants: Archie et al. 2006; geladas: Snyder-Mackler et al. 2014; common eiders: McKinnon et al. 2006; western lowland gorillas: Bradley et al. 2004; Morrison et al. 2019) and by long-term relationships established via repeated interactions (humans: Robinson and Barker 2017; mammals and insects review: Temeles 1994; mountain gorillas: Mirville et al. 2018; western lowland gorillas: Forcina et al. 2019)

The respective roles of the abovementioned social and ecological factors in promoting tolerance between groups can be best examined in species that exhibit both tolerant and aggressive intergroup interactions. Bonobos (*Pan paniscus*) are a particularly suitable species in which to investigate these roles. Bonobos are hominoid primates that live in multimale multifemale groups generally called communities, which regularly fission into smaller parties of variable size and composition (Idani 1990; Mulavwa et al. 2008; Sakamaki et al. 2018). While males are phylopatric, females generally disperse from the natal community when reaching adolescence (Furuichi et al. 2012). Importantly, bonobos do not appear to defend territories (Hohmann and Fruth 2002), have extensive home range overlap with adjacent communities (Hashimoto et al. 1998), and exhibit variable forms of intercommunity interactions, ranging from brief aggressive encounters (where encounter refers to different communities coming into visual contact [Pisor and Surbeck 2019]) to peaceful intercommunity associations lasting several consecutive days (where association refers to different communities remaining in spatial proximity after an encounter has occurred [Pisor and Surbeck 2019]) (Idani 1990; Sakamaki et al. 2018). Recent findings provide tantalizing hints that bonobos' social networks may even extend beyond the community level (Fruth and Hohmann 2018; Sakamaki et al. 2018).

A number of ecological and social traits of the species have been suggested to reduce the fitness costs of intercommunity interactions, permitting the emergence of tolerance between communities. On the ecological level, it has been suggested that low fluctuation in food availability in bonobos' habitats (Malenky and Wrangham 1994; Furuichi 2009) increases tolerance by reducing feeding competition both within and between communities (*food availability hypothesis*), allowing the maintenance of stable and large mixed-sex parties (Furuichi 2009) and even the formation of intercommunity associations (Sakamaki et al. 2018). On the social level, it has been proposed that when parties from one community tend to be of similar size as parties from another community, the fighting abilities of the parties from these two communities will be similar (Pandit et al. 2016). This may discourage escalation of conflicts due to the potential high risk of injuries for both parties given that neither could easily overpower the other (*balanced competitive abilities hypothesis*) (Wilson et al. 2014; Pandit et al. 2016; but see Mirville et al. 2018 for discussion of how similarly matched fighting abilities may actually increase the likelihood of conflict escalation). Intercommunity tolerance may also be promoted by weak coalition formation among males and consequent reduction of collective male mate defense against out-group males (Ihobe 1992).

While reduced costs of intercommunity interactions may permit tolerant intercommunity encounters, fitness benefits to these encounters' participants may increase encounter frequency and promote long-lasting intercommunity associations (Pisor and Surbeck 2019). Communities would then remain together only as long as the benefits of association overweigh the costs, terminating associations when this condition is no longer met (Robinson and Barker 2017). On the ecological level, potential benefits of intercommunity associations include the possibility to locate and access resources occurring outside the home range or in less familiar areas of its periphery (Cashdan et al. 1983; Janmaat et al. 2009; Pisor and Surbeck 2019) and to buffer local resource shortfall (*food access hypothesis*) (Pisor and Surbeck 2019; Jaeggi et al. 2016). On the social level, individuals may acquire extra-community mating opportunities (*extra-community mating hypothesis*) (Sakamaki et al. 2018), which may benefit males by increasing their probability of siring offspring outside their own community and benefit females by increasing their potential for mate choice (Parish et al. 2000; but see Ishizuka et al. 2018).

Despite these proposed connections between socioecology and intercommunity dynamics in bonobos, field data assessing these connections are rare and limited to a single population (Idani 1990; Sakamaki et al. 2018). Having such data, we here test the validity of

the above-proposed hypotheses (the *food availability hypothesis*, the *food access hypothesis*, the *balanced competitive abilities hypothesis*, and the *extra-community mating hypothesis*). We do so by examining the relative influence of the predicted social and ecological factors on the timing of the onset and termination of intercommunity interactions between free-living bonobo communities. Under the *food availability hypothesis*, we predicted that intercommunity encounters are more likely to occur when high fruit availability compensates for the energetic costs of interaction (Sakamaki et al. 2018). Similarly, encounters will be more likely to occur when spatially localized resources force communities to simultaneously access the same resource, such as when fruit patches are clumped (Robbins and Sawyer 2007; Wilson et al. 2012). On the other hand, high clumpiness of food patches may also enhance contest and increase the likelihood that an encounter ends at a given time (Harris 2006). Moreover, we predicted encounters to be more likely when parties are small because larger parties suffer higher levels of feeding competition and, therefore, would tend to avoid the even higher costs of cofeeding with the other community. Under the *food access hypothesis*, we instead expected a community to be more likely to initiate an encounter when experiencing low fruit abundance in its home range (Robinson and Barker 2017; Pisor and Surbeck 2019). Furthermore, if encounters serve to enhance foraging efficiency in less familiar areas, we predicted that encounters would be less likely to terminate in areas unfamiliar to the focal community and to terminate more likely upon return to familiar areas in which resource locations are likely to be known by the focal community (Cashdan et al. 1983). Under the *balanced competitive abilities hypothesis*, we expected that small parties would avoid larger parties, lowering their probability of encounter (McComb et al. 1994). Furthermore, we predicted that when the party of one community was smaller than that of the other, there would be a higher chance that the smaller party would be outcompeted by the larger, increasing the likelihood of terminating an encounter (Pandit et al. 2016). Finally, under the *extra-community mating hypothesis*, we expected communities to be less likely to terminate encounters at times when the number of maximally tumescent females is high due to the benefits of potential extra-community mating (Sakamaki et al. 2018). In fact, maximally tumescent females seem to be more attractive to males than nonswollen females despite the decoupling of swelling tumescence from ovulation in bonobos (Paoli et al. 2006; Surbeck et al. 2012; Douglas et al. 2016).

METHODS

Field site and study subjects

The study was conducted from July 2016 to February 2018 on two neighboring communities of wild bonobos in the Kokolopori Bonobo Reserve, central Democratic Republic of the Congo (DRC) (Surbeck et al. 2017a). The habitat consists mainly of primary forest with small patches of secondary forest and inundated riverine forest. Two teams comprising trained international students and local field assistants simultaneously followed parties of the two communities from nest to nest on an average of 27.5 days per month. Interobserver reliability of data collection was ensured by weekly meetings of all students and field assistants with the same project data manager who checked all data collected and guaranteed its consistency. The smaller community, Ekalakala, consisted of 13 individuals (three adult males [≥15 years], three parous and three nulliparous adult females [≥15 years], and four immatures [<10 years]), and the larger community, Kokoalongo, comprised 45 individuals (eight adult males, two subadult males [10–15 years], 13 parous and four nulliparous adult females, and 18 immatures). All community members were habituated to researchers' presence before the onset of the study and were individually recognized via particular features of the genitals (shape of the sexual swellings for the females and shape and color of the testicles for the males) and individual facial and body features, such as missing digits and pigmentation marks.

Data collection and analysis

Ranging and behavioral data

We collected ranging data during daily party follows by recording the geographic location every minute via Global Positioning System (Garmin GPS 62). We determined party composition by recording the identities of all individuals present in the party every 30 min (Mulavwa et al. 2008) for a total of 8472 h of party composition for Ekalakala and 7170 h for Kokoalongo. In order to evaluate the visual cue of potential receptivity of females, we scored the tumescence of each female's sexual swelling on a scale from 1 to 4 at the first instance a female was observed on a given day (Hohmann and Fruth 2000). We recorded an intercommunity encounter (thereafter "encounter") when the same observer saw at least two adult individuals from the focal community with at least two adult individuals of the other community. We considered an encounter ended when no individuals of the other community were seen by the observer for 2 h. If a solitary individual was observed traveling with a community to which it did not belong, we scored this as a "temporary visit" and not as an encounter. We collected dietary information daily, recording all instances when members of the focal party fed on fruits, including the species name of the fruit consumed. All data except geographic location were collected using Android Smartphones and the CyberTracker software (version 3.486). Finally, we recorded copulations on an ad libitum basis.

Ecological variables

Fruit distribution. To quantify tree and liana species distribution, we applied a plot sampling method based on 50 × 50 m sampling quadrats (Bortolamiol et al. 2014). Since the bonobos of our study communities traveled an average of 6 km per day, we divided the study area into adjacent cells of 1 km^2 and randomly placed one sampling quadrat (thereafter "plot") within each cell for a total of 83 plots and a total sampled area of 20.75 ha. Within these plots, we identified, counted, and measured all trees with a dbh (i.e., diameter at 1.3 m above ground) of at least 20 cm and all lianas with a diameter of at least 5 cm at 1.3 m above the level of the ultimate rooting point (Gerwing et al. 2006). From the plot data, we then calculated Morisita's Index of dispersion (Morisita's I) (Amaral et al. 2015) for species that were observed as part of the bonobos' diet over the study period (number of species = 61), separately for each of the two communities' home ranges. This index measures the extent to which a species is spatially clumped. Index values of 1 indicate a random distribution, values smaller than 1 indicate a uniform distribution, and values larger than 1 indicate an aggregated distribution. To obtain monthly values of the index, we then averaged the species-specific Morisita's indices for each month weighted with the proportion of trees bearing fruits on the phenology trails (see below) and with the proportion of each species in the monthly diet.

Fruit abundance. To quantify fruit abundance, we conducted monthly phenology surveys on three transects spanning all forest types (totaling 12.4 km). Since 97% of all trees and 99% of all lianas the bonobos fed on over the study period met our criteria for measurement (see above), we identified all trees and lianas meeting

these criteria that were within 1 m of each side of the transect midline (955 trees, 118 species), and we scored them for presence/absence of fruits, leaves, and flowers. To assess temporal variation in overall fruit abundance, we calculated a monthly fruit abundance index (MFAI) (Potts et al. 2009) in each of the communities' home range integrating these phenology data with the plots' data as follows:

$$\mathrm{MFAI} = \sum_{i}^{S} P_{im} B_i$$

In this equation, P_{im} is the proportion of trees of species i in the phenology trail bearing ripe fruits in month m, B_i is the basal area of species i (i.e., the total cross-sectional area of tree trunks measured at 1.3 m above ground derived from the plots' data [see above]), and S is the total number of species included in the analysis. For this calculation, we again only considered trees that were part of the diet of the bonobos during the study period and weighted the index with their proportion in the monthly diet. We also determined values of fruit abundance for each grid cell (CFAI) after recalculating B_i as the average basal area of the trees found in the plot located in a given cell and the plots located in the eight directly adjacent cells, including in the analysis only the species found in these plots. This average is more representative of the local distribution of fruiting trees as it considers a larger area instead of a single point, thus suffering less from stochastic variation.

Statistical analysis

To examine the dynamics of intergroup encounters, we estimated the relative influence of fruit abundance, fruit distribution, and social variables (i.e., party size and number of maximally tumescent females) on the *occurrence* and *termination* of encounters between members of the two study communities. To this end, we used three statistical models: the first two models examined the relative roles of our set of ecological and social variables in influencing the probability of encounters to occur, while the third model examined their effect on the probability that a given encounter ended. To conduct our analysis, we determined 1) *fruit abundance* and *distribution* as described above (monthly averaged Morisita's Index, MFAI, and CFAI) for the focal community's home range, 2) the time spent in a given cell and whether a community was alone versus in association with the other, 3) the *party size* of the focal community in the cell (as average number of individuals in the party weighted by the party duration), and 4) the *number of maximally tumescent females* (i.e., females with swelling rated 4). In order to account for the different degree of utilization and familiarity a given community had with different areas of its home range, we used a kernel analysis to calculate a value of "*marginality*" for each cell using the package "adehabitatHR" (version 0.4.14; Calenge 2011) in R (R Core Team 2018). This method generates utilization distributions based on point density calculation (Worton 1989). Increased values of marginality for a given cell indicate a lower degree of utilization of the cell by the focal community. Because for some days the observations for the social predictors (party size and number of maximally tumescent females) were lacking, the estimation of the effect of these predictors on the probability of encounters to occur or terminate in such days was not possible, resulting in a different number of encounters included in the three models.

Probability of encounter occurrence (model 1)

To estimate the probability that an encounter occurred in a given cell, we used a generalized linear mixed model (GLMM; Baayen et al. 2008) with binomial error structure and logit link function (McCullagh and Nelder 1989). As binary response variable (yes/no), we scored whether an encounter began within a given cell once a party entered the cell (total sample size = 5266; yes = 36). As we aimed to estimate the probability that an encounter occurred, we excluded from the analysis all cells which parties from the two communities entered while already being in association. Because parties from both communities were followed simultaneously every day, there were instances in which the same encounter was scored twice, that is, when the followed party of one community encountered the followed party of the other community. To correct for this, we randomly chose one data point from each of these instances. We modeled the effects of our predictors of interest as fixed effects for *fruit abundance* (proxied by MFAI and CFAI) and *fruit distribution* (proxied by Morisita's *I*) in the home range of the focal community, for the *party size* of the focal community, and for the *number of maximally tumescent females* in the party of the focal community (Table 1). Because a longer time spent in a cell increased the probability of

Table 1

Expected direction of the influence of the various predictors on the response in the three models and their link to the hypotheses

Hypotheses	Predictors	Encounter occurrence probability (model 1)	Encounter occurrence probability within "potential encounter" (model 2)	Encounter termination probability (model 3)
Ecological hypotheses				
Food availability	Fruit abundance	+	+	−
	Fruit distribution (clumpiness)	+	+	+
	Party size	−		
Food access	Fruit abundance	−	−	
	Cell marginality			−
Social hypotheses				
Extra-community mating	No. maximally tumescent females	+		−
Balanced competitive abilities	Difference in party size		−	+

The table reports the expected direction of the effect of the predictors on the response for each model: + indicates a positive effect, − indicates a negative effect, and empty cells indicate predictors assumed not to have an effect on the response or whose effect on the response cannot be evaluated with the available data.

encountering the other community in that cell, we also included the time spent in a cell (log-transformed) as an offset term in the model (McCullagh and Nelder 1989). We included cell ID (number of levels = 81) as a random intercept effect, as we had multiple observations (across days and months) per cell. Because our analysis involved only two communities and their encounters with each other, an encounter for one automatically entails an encounter for the other; consequently, we did not include community ID into the model. To reduce model complexity, we did not include cell marginality as a predictor because correlation analysis showed that encounter probability did not depend on this measure of the degree of familiarity with a given area of the home range (see Results).

Probability of encounter occurrence when at "potential encounter distance" (model 2)

Due to methodological constraints, in the first model we analyzed encounter probability assuming the focal community had only knowledge of its own social characteristics but not of those of the other community. Therefore, in a second model, we additionally investigated the influence of the social characteristics of the other community on the probability of encounters to occur when the two communities were within potential auditory range (which is at least 700 m; Schamberg et al. 2016) and possibly aware of each other's presence and relative party size. To this end, we selected the parts of the focal community's daily tracklogs that were within 1 km distance of those of the other community and for which GPS locations for each community had been saved with at most 10-min time difference. Although we were not able to assess actual information transfer between communities, we deemed this distance threshold a reasonable proxy for the potential for information transfer (Schamberg et al. 2016). We scored as a binary response (yes/no) whether an encounter happened or not for each of these "potential encounter" instances when the communities where within 1 km of each other (total sample size = 96; yes = 57). We used a generalized linear model (GLM; McCullagh and Nelder 1989) with binomial error structure and a logit link function to evaluate the effects of our predictors of interest with fixed effects for *monthly fruit abundance* (proxied by MFAI) and *fruit distribution* (proxied by Morisita's *I*), for *fruit abundance per cell* (proxied by CFAI averaged across the cells visited while traveling within 1 km of distance and weighted by the time spent in them), and for the mean *difference in party size* between communities weighted by the party duration (Table 1). We did not include the number of maximally tumescent females as a predictor for two reasons: first, maximally tumescent females were present in the party of both communities in almost the entirety of the cases (92% of cases), thus not providing sufficient variation to investigate the effect of this variable on the response; second, because for a given party, assessing the number of maximally tumescent females in the party of the opposite community was likely not feasible before an encounter actually occurred. We included as an offset term in the model the duration of each potential encounter (log-transformed). We did not include cell ID as random effect because, in this model, for each potential encounter, the values of the predictors were averaged across all cells through which the two groups traveled while within 1 km of each other.

Probability of encounter termination (model 3)

While any given encounter certainly ends at some point, we analyzed which factors influenced the probability that an encounter terminated in a particular cell, namely the ecological conditions found in the cell and the social characteristics of the party entering the cell. Although the ecological characteristics of monthly fruit abundance and distribution did not change within the same encounter, these factors fluctuated across the year and across different encounters. If these factors influenced the overall duration of an encounter, they would influence the likelihood of an encounter to terminate in a given cell. In fact, since longer encounters encompass more cells (see Supplementary Table S1), the more cells are visited during an encounter, the smaller the probability that the encounter terminates in a certain cell. For the analysis, we used a GLMM with binomial error structure and a logit link function. As a binary response variable (yes/no), we scored whether, when the two communities entered a cell together while in association, their encounter ended in that cell (total sample size = 3158; yes = 50). We evaluated the effects on the probability of encounters to end in a cell of our predictors of interest with fixed effect for *fruit abundance* (proxied by MFAI and CFAI) and *fruit distribution* (proxied by Morisita's *I*) calculated for the area in which the two communities ranged together, for the *difference in party size* between the two communities, and for the total *number of maximally tumescent females* in both communities (Table 1). We included the time spent in a cell (log-transformed) as an offset term. Predicting that the focal community would remain in association with the other community if ranging in less familiar areas, hence reducing the probability of associations to end, we also included the maximum value of cell *marginality* of the two communities as a test predictor with fixed effect in the model. Finally, we included cell ID (number of levels = 38) and encounter ID (number of levels = 57) as random effects, the former because we had multiple observations for each cell across time, and the latter to account for the fact that the probability of encounters to end varies among encounters due to different factors.

Model implementation

All models were fitted in R (version 3.5.0; R Core Team 2018). For all models, we tested via likelihood ratio test (R function "anova" with argument test set to "Chisq"; Dobson 2002) whether our models significantly explained the variation in the response by comparing the full model including all predictors with a null model (Forstmeier and Schielzeth 2011) including only the random effects and the offset terms but none of the test predictors. Prior to fitting the models, to avoid influential cases, we log-transformed the fruit abundance in individual cells (CFAI), and we square root-transformed the distribution of the fruit patches (Morisita's *I*), the number of maximally tumescent females, and the difference in party size between communities to achieve roughly symmetrical distributions. To keep type I error rate at the nominal level of 5% (Schielzeth and Forstmeier 2009; Barr et al. 2013), we included random slopes for the predictors when applicable, allowing for the effects of the fixed-effects predictors to randomly vary among the levels of the random-effects variables. In model 1, we included random slopes for all predictors within cell ID; in model 3, we included random slopes for CFAI, MFAI, and Morisita's *I*, the difference in party size and the number of maximally tumescent females within cell ID, and the random slopes for CFAI, the difference in party size between communities, the number of maximally tumescent females, and cell marginality within encounter ID.

Model 1 and model 3 (GLMMs) were fitted using the function glmer of the R package lme4 (version 1.1–17) with the optimizer "bobyqa," and model 2 (GLM) was fitted using the R function glm. Confidence intervals (CIs) were derived using the function "bootMer" of the package lme4, using 1000 parametric bootstraps and bootstrapping also over the random effects (model 1 and model 3) or the

R-function confint (model 2). To check for the presence of influential cases, we assessed model stability for each model by comparing the estimates obtained from the models including all data with those obtained from models with the levels of the random effects (model 1 and model 3) or data points (model 2) excluded one at a time; no influential cases were found. In order to rule out collinearity, we derived variance inflation factors for each model (VIF; Field 2005) with the function "vif" of the R package car (Fox and Weisberg 2011); in case of model 1 and model 3, these were based on a standard linear model excluding the random effects. Among the three models, the largest VIF for a predictor was 3.5, indicating that collinearity was not a problem (Field 2005). After the square root- or log-transformation to the relevant predictors but prior to fitting the models, we z-transformed all predictors to a mean of 0 and a standard deviation (SD) of 1 to get comparable estimates (Schielzeth 2010). We tested the individual fixed effects in models 1 and 3 by comparing the respective full model with a reduced model lacking the effect, utilizing a likelihood ratio test (Barr et al. 2013). The means and SDs of the square root- and log-transformed predictors before the z-transformation are indicated in Supplementary Table S2.

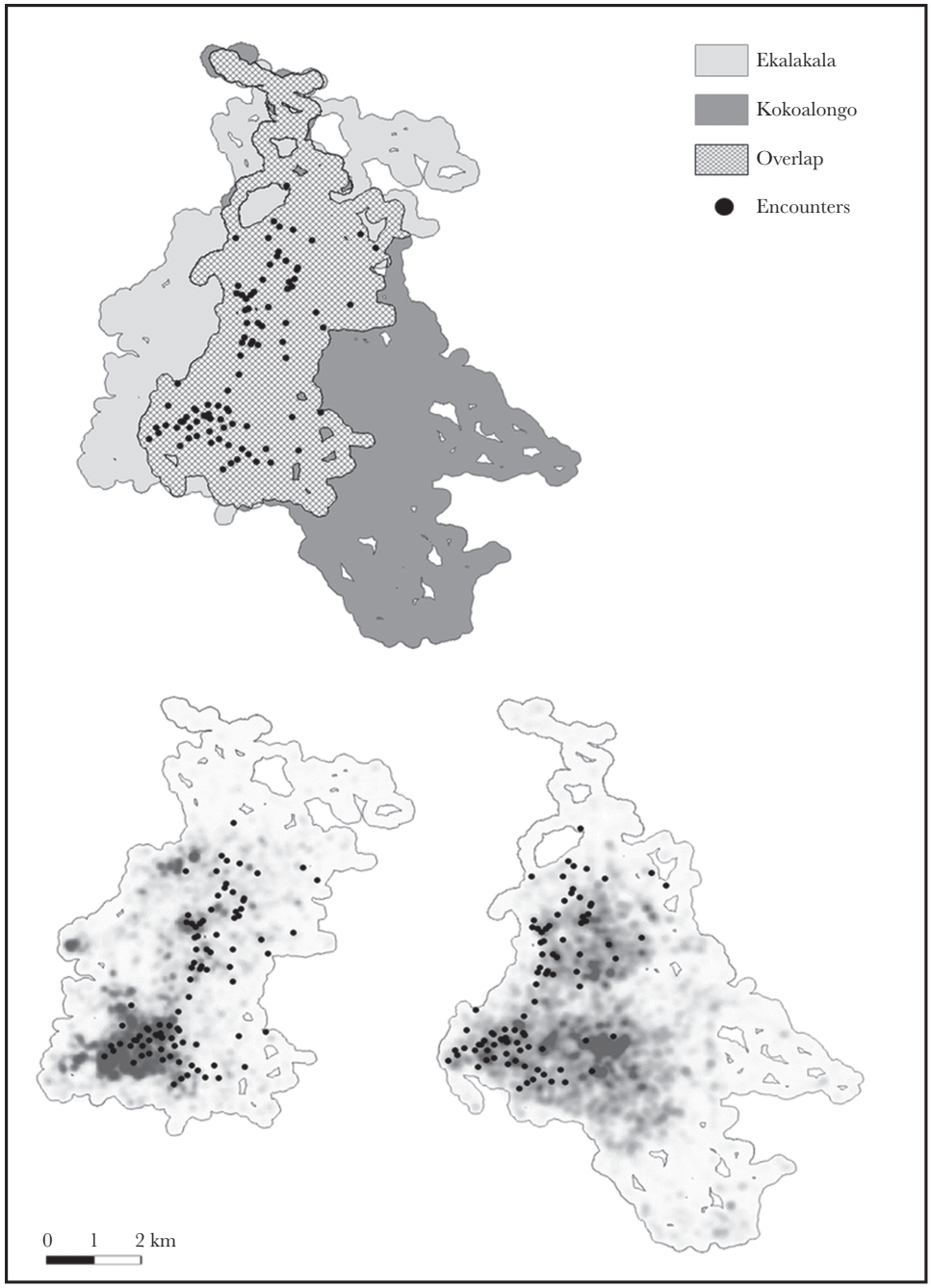

Figure 1
Top: the home ranges of Ekalakala, Kokoalongo, and their overlap, with the location of intercommunity encounters. Bottom: the separate home ranges of Ekalakala (left) and Kokoalongo (right) where darker color indicates a higher degree of utilization of an area.

RESULTS

During the study period, we followed the Ekalakala community for 415 days and the Kokoalongo community for 364 days, recording a total of 102 encounters between them. While Kokoalongo often fissioned in smaller parties, the members of Ekalakala were extremely cohesive, thus making us confident to have recorded the far majority of encounter events.

The probability of encountering the other community did not depend on the marginality of a particular area of the home ranges' overlap (Pearson correlation: $r = 0.08$, number of cells = 104, $P = 0.54$), with encounters occurring even in the most used area of the home range of each community (Figure 1). On a monthly basis, members of the two communities were in association 24% of the time on average but with considerable variation across months (range: 0–70%; Figure 2). Furthermore, encounter duration varied extensively, ranging from less than an hour to several consecutive days (monthly average: three consecutive days; range: 30 min to seven consecutive days). Both communities also encountered two other semihabituated communities to a lesser extent (27 days in total over the study period for Ekalakala and two for Kokoalongo); this lower frequency was probably due to the other two communities being less habituated and, thus, more wary of the researchers.

Ecological variables

Monthly fruit abundance varied during the course of the year (mean MFAI = 69, range: 16–171), peaking roughly from July to September (Figure 2a; see also Supplementary Materials for more details). Fruit abundance in individual cells varied considerably from cell to cell, as well as during the course of the year (mean CFAI = 1624, range: 20–16 983; see Supplementary Materials for details). The distribution of the species the bonobos fed on during the study period also varied on a monthly basis, whereby feeding species were on average more clumped than evenly distributed over the study site (monthly mean Morisita's $I = 2.8$, range: 0.1–7.2) (Figure 2b; see also Supplementary Materials for more details).

Social variables

The average daily *party size* (number of adult and subadult individuals) was 9 for Ekalakala (range: 8–9) and 15 for Kokoalongo (range: 4–26). At least one *maximally tumescent female* (swelling rated 4) was present in the followed party of each community 86% of the days the community was followed, with a daily mean of two maximally tumescent females for Ekalakala (range: 0–5) and three for Kokoalongo (range: 0–9). Copulations between individuals of different communities occurred during 88% of the encounters; an average of 66% of the copulations that occurred during encounters was between members of different communities (range: 0–30 intercommunity copulations per encounter).

Probability of encounter occurrence (model 1)

Consistent with the *food availability hypothesis*, the probability that the two communities encountered each other in a given cell significantly increased with an increase in the abundance of fruits in each community's home range (MFAI; Table 2; Figure 3a). Conversely, neither the clumpiness of fruit patches in the home range of a given community nor the fruit abundance in individual cells significantly influenced the probability of an encounter. Regarding the social variables, also consistent with the *food availability hypothesis*, an increase in the focal community party size significantly reduced the probability that an encounter occurred (Figure 3b).

Probability of encounter occurrence when at "potential encounter distance" (model 2)

Consistent with the *food availability hypothesis*, when the communities were within 1 km of each other, the probability that they met significantly increased with an increase in the fruit abundance in the visited cells (CFAI) and in the clumpiness of the fruit patches (Figures 4a,b). However, in contrast to the *balanced competitive abilities hypothesis*, differences in party size did not significantly influence the likelihood of an encounter (Table 2).

Probability of encounter termination (model 3)

Overall, both social and ecological factors played a significant role in the probability that the communities terminated an encounter in a particular cell after they entered that cell together (Table 2). Although the abundance of fruits over the whole area or in individual cells had no significant effect on the probability of encounters to end in a given cell, this probability increased with increased clumpiness of the fruit patches over the whole study site (Figure 5a), consistent with the *food availability hypothesis*. Additionally, consistent with the *food access hypothesis*, we found a decreased probability to terminate encounters in cells that were less familiar to one community (effect of cell marginality; Figure 5b). Regarding the social

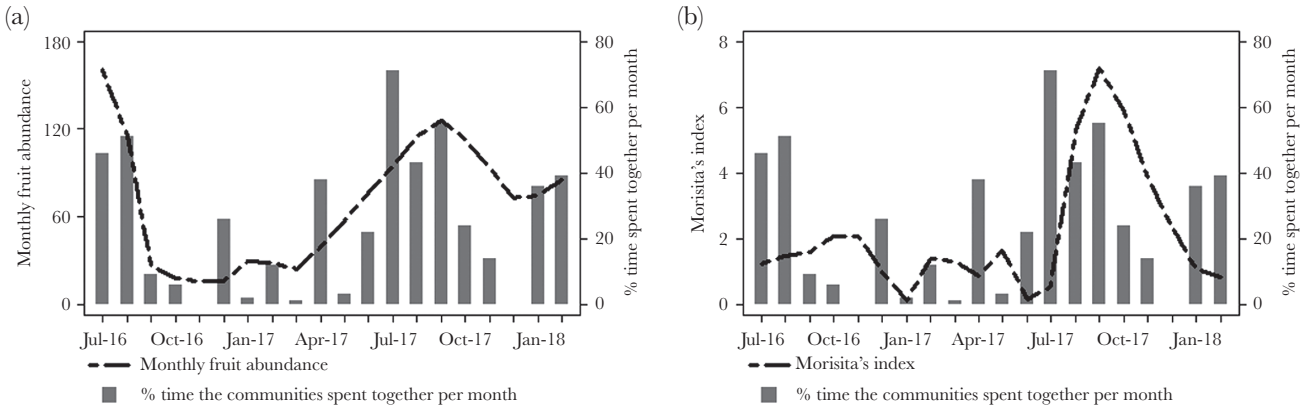

Figure 2
Percentage of time the two communities spent together, along with the monthly variation in (a) fruit abundance (MFAI) and in (b) the clumpiness of the fruiting patches (Morisita's index).

variables, consistent with the *balanced competitive abilities hypothesis*, the communities were more likely to terminate an encounter when they entered a cell with an increased difference in their party sizes (Figure 5c) but, consistent with the *extra-community mating hypothesis*, they were less likely to do so when the total number of maximally tumescent females was larger (Figure 5d).

DISCUSSION

We investigated which socioecological factors influenced the dynamics of association between two communities of bonobos. In accordance with the predictions of the *food availability hypothesis*, we found that intercommunity encounters were more likely to occur during times of high fruit abundance, when feeding competition was reduced, whereas encounters were more likely to end when feeding patches were clumped, increasing the potential for contest. Encounters were less likely to end when potential benefits from association arose, namely the possibility of extra-community mating (in accordance with the *extra-community mating hypothesis*) and more efficient foraging in less familiar areas (in accordance with the *food access hypothesis*). Furthermore, in accordance with the *balanced competitive abilities hypothesis*, encounters were more likely to end when there were larger differences in the party size of the interacting communities (Table 3).

Ecological factors affecting intercommunity encounters

Our findings suggest that, in Kokolopori, communities tended to encounter each other when the costs of association in terms of cofeeding were reduced by increased fruit abundance and by ranging in smaller parties. Similar results have been reported for the bonobo population of Wamba, in which encounters were most frequent during the annual peak in fruit abundance (Sakamaki et al. 2018), suggesting that this may be a general pattern in bonobos. Similar to what we observed in bonobos, resource abundance seems to influence groups' spatial partitioning in some other species (African elephants: Wittemyer et al. 2007; mountain gorillas: Seiler et al. 2017; capuchin monkeys: Di Bitetti 2001; mangabeys: Olupot et al. 1997), with increased group interconnectivity (killer whales: Foster et al. 2012) and the increased tendency of groups to coalesce into larger units (axis deer: Raman 1997; snub-nosed monkeys: Kirkpatrick and Grueter 2010) when food is abundant. However it is important to note that, although seemingly a precondition for encounters to occur, high fruit abundance may well not be the motive promoting encounters in the first place as it seems unlikely to us at this stage that additional nutritional benefits could be gained through encounters during times when fruits are already abundant (Pisor and Surbeck 2019).

Although fruit abundance influenced the probability of encounters to occur, fruit distribution did not obviously exert the same effect unless the communities were already ranging in close proximity to each other. This contrasts with observations in other species, where encounter frequency between groups often increases when food resources are patchily distributed (mountain gorillas: Robbins and Sawyer 2007) or occur in areas overlapping with neighbors' home ranges (banded mongooses: Gilchrist and Otali 2002; chimpanzees: Wilson et al. 2012). The fact that, in Kokolopori, the main constraint for encounters to occur was fruit abundance but not their overall distribution suggests that, on a large scale, virtually no fruit patches were only found in a single spot so as to drive both communities to simultaneously forage in a localized shared area.

Table 2
Summary of the results of the models investigating the probability of encounter occurrence/termination

Responseff	Encounter occurrence probability (model 1)					Encounter occurrence probability within "potential encounter" (model 2)					Encounter termination probability (model 3)				
Full-null model comparison	$\chi^2 = 17.37$, df = 5, $P = 0.003$					$\chi^2 = 34.04$, df = 4, $P < 0.001$					$\chi^2 = 23.17$, df = 6, $P < 0.001$				
Predictor[a]	Est	SE	P	Lower CI	Upper CI	Est	SE	P	Lower CI	Upper CI	Est	SE	P	Lower CI	Upper CI
Intercept	−7.076	0.740	[b]	−9.975	−6.406	−1.803	0.561	[b]	−3.056	−0.772	−2.494	0.286	[b]	−3.632	−2.112
CFAI	−0.097	0.415	0.815	−0.766	0.780	**1.481**	**0.711**	**0.037**	**0.130**	**2.989**	0.323	0.265	0.223	−0.219	0.840
MFAI	**1.426**	**0.463**	**0.002**	**0.385**	**2.485**	−0.109	1.009	0.914	−2.280	1.812	−0.272	0.242	0.262	−0.837	0.227
Morisita's I	−0.376	0.303	0.215	−1.146	0.261	**1.571**	**0.652**	**0.016**	**0.402**	**3.037**	**0.602**	**0.244**	**0.014**	**0.103**	**1.169**
Max marginality											**−0.569**	**0.254**	**0.025**	**−1.092**	**−0.063**
Party size	**−1.032**	**0.351**	**0.003**	**−1.878**	**−0.368**										
No. maximally tumescent females	−0.001	0.320	0.998	−0.548	0.691						**−0.934**	**0.227**	**<0.001**	**−1.383**	**−0.476**
Δ Party size						0.438	0.494	0.375	−0.553	1.436	**0.733**	**0.273**	**0.007**	**0.207**	**1.282**

For all three models, the full model explained significantly more of the variation in the response than the null model including only the offset term and the random effects but excluding the test predictors. Significant test predictors ($P < 0.05$) are indicated in bold. Empty cells indicate variables not included in a model. For the first model, the total sample size was 5266, for the second model it was 96, and for the third model it was 3158. df, degrees of freedom; SE, standard error.
[a]Most predictors were square root- or log-transformed and all were z-transformed; see Supplementary Table 2 for details.
[b]Not shown because of having a very limited interpretation.

Accordingly, when contest over clumped resources arose, it could be easily avoided via terminating an encounter. Since contest may also depend on the size of the fruit patches in addition to their distribution, with smaller patches enhancing contest, further research on fruit patch size may help to better understand the motives promoting encounter termination.

The finding that encounters were more likely to occur in periods of high fruit abundance and not of fruit scarcity also suggests that, in Kokolopori, potential resource buffering may not be the primary incentive for establishing intercommunity associations. In contrast, sharing between neighbors in conditions of asymmetric resource availability is documented to a certain extent in colonial insects (Ellis et al. 2014) and is regarded as one of the main factors promoting intercommunity cooperation in humans (Kelly 1995; Pisor and Gurven 2016; Pisor and Surbeck 2019).

Interestingly, our results raise the possibility that intercommunity interactions in Kokolopori may still play a role in increasing foraging efficiency in ways unrelated to resource buffering. The finding that the communities were less likely to terminate an encounter in areas that were less familiar to at least one of them suggests that individuals may be able to forage more efficiently in less familiar areas when associating with more knowledgeable extra-community members. This finding parallels observations in human foragers (Cashdan et al. 1983), in which lack of knowledge of resource location in unknown areas may even prevent exploration (Laden 1993). Following foraging routes of more knowledgeable out-group individuals is also believed to play an important role for dispersing primates (Janmaat et al. 2009), as well as for communally roosting birds (Sonerud et al. 2001) and bats (Ratcliffe and Hofstede 2005). Since our study covers a limited period of time, and home ranges can expand, shrink, or even shift over time (Furuichi et al. 2012), long-term following of the neighboring communities are needed to assess possible benefits of potential sharing of information about food location during intercommunity encounters. Moreover, data on the community membership of the individuals leading the ranging parties during associations would allow testing of whether one community tends to follow the other when ranging in areas more familiar to the latter (Amornbunchornvej et al. 2016).

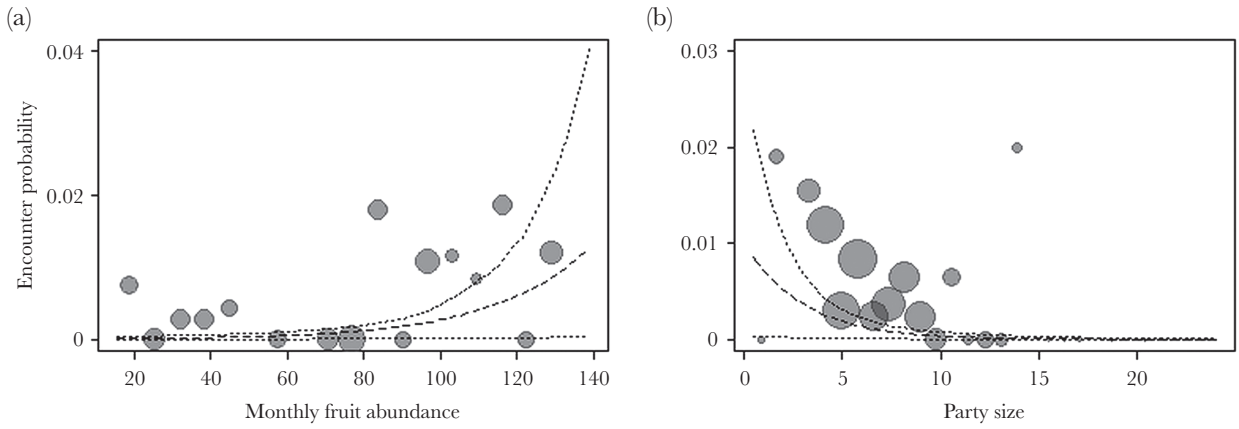

Figure 3
Encounter probability (model 1) as a function of (a) monthly fruit abundance and (b) party size. The dashed and dotted lines indicate the fitted influence of the predictor on the response and its 95% confidence intervals, respectively, with all other predictor variables in the model set to their average and the duration of stay in a cell set to its average. The area of the circles is proportionate to the number of observations (visits of a cell) that occurred given the binned value of the predictor [ranging from $N = 230$ to $N = 944$ in (a) and from $N = 9$ to $N = 1683$ in (b)].

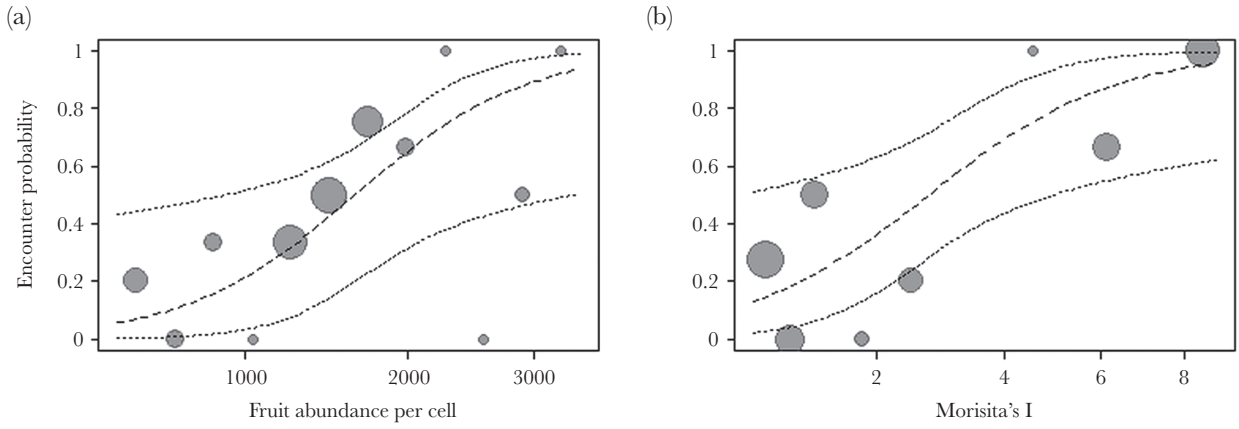

Figure 4
Encounter probability (model 2) as a function of (a) fruit abundance in visited cells and (b) clumpiness of fruit patches (Morisita's Index). The dashed and dotted lines indicate the fitted influence of the predictor on the response and its 95% confidence intervals, respectively, with all other predictor variables in the model set to their average and the duration of the potential encounter set to its average. The area of the circles is proportionate to the number of observations that occurred given the binned value of the predictor [ranging from $N = 1$ to $N = 24$ in (a) and from $N = 2$ to $N = 33$ in (b)].

Social factors affecting intercommunity encounters

In Kokolopori, imbalance in the number of individuals in potentially meeting parties did not affect the probability that encounters occurred, and a community was more likely to encounter the other when ranging in smaller parties. The fact that smaller parties did not avoid encounters suggests that the risk of severe aggression for smaller parties by larger parties was low and that within-community fission–fusion dynamics were a consequence of fluctuation in fruit abundance rather than of danger of intercommunity interactions (i.e., party size was not influenced by the potential for encounters to occur) (Mulavwa et al. 2008; Surbeck et al. 2015). In contrast, numerous studies have shown the importance of numeric assessment and groups' fighting abilities in the context of intergroup relations in other species. In general, if the disparity in numbers is high, larger groups face lower risks of lethal injuries than smaller ones ("imbalance of power"; Wrangham 1999), and they are, therefore, more likely to engage in and win contests (Adams 2003). For instance, lions (McComb et al. 1994), dogs (Bonanni et al. 2011), wolves (Cassidy et al. 2017), and chimpanzees (Wilson 2013) are more likely to engage in territory defense when largely outnumbering the opponents. Similarly, wood ants engage in aggression against out-group members when they recognize themselves as part of a larger group (Tanner 2006). On the other hand, similarly sized groups of mountain gorillas are more likely to engage in aggression because disputes cannot be settled by simple disparity in numbers (Mirville et al. 2018), and green woodhoopoes engage in longer territorial vocal displays when facing similarly sized groups (Radford and du Plessis 2004). The fact that encounters in Kokolopori were more likely to terminate when the difference in party size between communities was large hints at the possibility that numerical assessment and community membership played a role in determining when an encounter ended, although whether this is related to the risk of severe aggression is unclear. Detailed analyses of rates of intercommunity agonistic interactions are needed to explore the underlying mechanisms causing encounters to end when a community is outnumbered by the other (e.g., whether aggression rates depend on imbalance in party sizes). Importantly, although bonobos have been regarded as a highly xenophilic species (Idani 1990; Tan et al. 2017), our results suggest that the distinction between within-community versus extra-community members is not completely blurred during encounters.

Our result that communities were less likely to terminate an encounter when the number of maximally tumescent females in the party was high suggests a role of encounters in gaining *extra-community mating* opportunities. Similarly as what was reported for another bonobo population in Wamba (Furuichi 2011), intercommunity copulations were frequent during encounters in Kokolopori. In some species, possessive male mating strategies, such as the herding of females, may decrease the occurrence of intergroup encounters when potentially fertile females are present (savannah baboons: Kitchen et al. 2004; bottlenose dolphins: Connor et al. 1996). However, this does not appear to be true for bonobos due to the high dominance rank of females and their high potential for mate choice (Furuichi 2011; Surbeck and Hohmann 2013). Although intercommunity copulations in

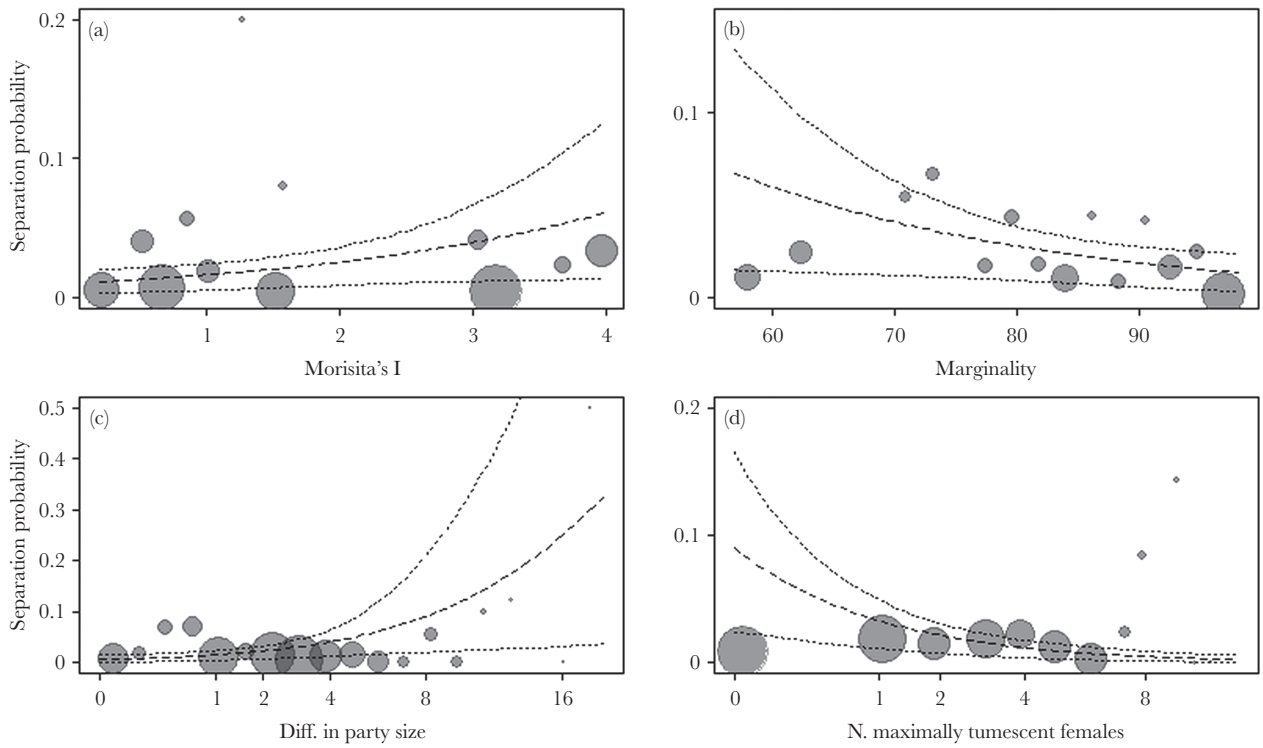

Figure 5

Probability of terminating an encounter (model 3) as a function of (a) clumpiness of fruit patches (Morisita's Index), (b) cell marginality, (c) difference in party size between communities, and (d) number of maximally tumescent females. The dashed and dotted lines indicate the fitted influence of the predictor on the response and its 95% confidence intervals, respectively, with all other predictor variables in the model set to their average and the duration of stay in a cell set to its average. The area of the circles is proportionate to the number of observations (visits of a cell) that occurred given the binned value of the predictor [$N = 11$ to $N = 920$ (a), $N = 161$ to $N = 1071$ (b), $N = 2$ to $N = 1269$ (c), and $N = 9$ to $N = 763$ (d)].

Table 3

Summarized results of the models and their support for the main hypotheses

Hypothesis	Food availability	Food access	Balanced competitive abilities	Extra-community mating
Model 1 (encounter occurrence probability)	Supported (MFAI, party size)	Not supported	—	Not supported
Model 2 (encounter occurrence probability during a "potential encounter")	Supported (CFAI, Morisita's *I*)	Not supported	Not supported	—
Model 3 (encounter termination probability)	Supported (Morisita's *I*)	Supported (cell marginality)	Supported (Δ in party size)	Supported (no. of maximally tumescent females)

Reported in brackets are the predictors for which a significant effect on the response (probability of encounters to occur/terminate) was found.

bonobos may not necessarily lead to conception (Surbeck et al. 2017b; Ishizuka et al. 2018), acquiring extra-community mating opportunities may be an incentive for males and females to seek intercommunity encounters or at least to delay the end of an encounter when such opportunities are numerous. Females may also indirectly benefit from, and thus actively prolong, encounters since remaining in association with the other community may increase the chances that their sons mate with out-community females (Surbeck et al. 2011, 2019).

Where do we draw group boundaries in bonobos?

According to the traditional definition of "community" in the bonobo literature (Idani 1990), Ekalakala and Kokoalongo can be defined as two separate communities despite the considerable amount of time they spent in association: local trackers have been following Ekalakala since 2005 and Kokoalongo since 2010, and the two communities are consistently different in membership and space use. A similar proportion of time spent in association has also been reported for neighboring communities in the bonobo population of Wamba (Sakamaki et al. 2018). Intercommunity relations in bonobos are complex, and interactions between parties from different communities can resemble interactions between parties of the same community (Fruth and Hohmann 2018; Sakamaki et al. 2018). This makes the validity of the traditional definition of "community" in bonobos contentious (Waller 2011).

Furthermore, in Kokolopori, the two study communities form part of a larger social network comprising at least two other semihabituated neighboring communities. Within this network, the degree of tolerance each community shows with each neighbor seems to differ. In a number of species, affiliative interactions result from close relatedness among dispersed individuals belonging to neighboring groups (African elephants: Archie et al. 2006; wood ants: Ellis et al. 2014; mountain gorillas: Mirville et al. 2018; western lowland gorillas: Bradley et al. 2004; plain zebras: Tong et al. 2015) and from individuals' social preferences (sperm whales: Cantor and Whitehead 2015; giraffes: Carter et al. 2013). The extent to which such mechanisms play a role in intercommunity dynamics in bonobos is still unclear. Detailed analyses on communities' ranging patterns, as well as genetic relatedness, frequency of interaction, and social preferences among individuals belonging to different communities will help to better define where the boundaries between social groups in bonobos can be drawn and whether the bonobo's social organization could even be defined as multilevel.

CONCLUSIONS

Adding to a growing body of evidence, our findings suggest that bonobos' relationships across communities are more complex than initially thought and that local socioecology plays a primary role in shaping them (Fruth and Hohmann 2018; Sakamaki et al. 2018). Broadening research to additional wild populations will allow researchers to better understand the behavioral breadth of the species and to evaluate whether the patterns we found in Kokolopori reflect a local adaptation or a more general behavioral trait of bonobos. Moreover, since cooperation between groups is a key and hallmark feature of human multilevel societies (Layton et al. 2012), investigating the factors affecting intercommunity relations in bonobos may help to shed light on the mechanisms involved in early hominins' social evolution (Boyd and Richerson 2009; Foley and Gamble 2009; Richter et al. 2011). The question of whether bonobo societies can be defined as multilevel is still premature, but examining the underlying mechanisms involved in shaping relationships across communities can be of crucial importance in the understanding of animals' sociality beyond the group level.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Lucchesi et al. (2019).

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REFERENCES

Adams ES. 2003. Lanchester's attrition models and fights among social animals. Behav Ecol. 14(5):719–723.

Amaral M, Pellico Netto S, Lingnau C, Figueiredo Filho A. 2015. Evaluation of the Morisita index for determination of the spatial distribution of species in a fragment of Araucaria forest. Appl Ecol Environ Res. 13(2):361–372.

Amornbunchornvej C, Brugere I, Strandburg-Peshkin A, Farine D, Crofoot MC, Berger-Wolf TY. 2016. FLICA: a framework for leader identification in coordinated activity. arXiv:1603.01570. Available from: http://arxiv.org/abs/1603.01570. Accessed 24 June 2019.

Archie EA, Moss CJ, Alberts SC. 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proc Biol Sci. 273:513–522.

Baayen R, Davidson D, Bates D. 2008. Mixed-effects modeling with crossed random effects for subjects and items. J Mem Lang. 59(4):390–412.

Barr D, Levy R, Scheepers C, Tily H. 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. J Mem Lang. 68(3):255–278.

Bonanni R, Natoli E, Cafazzo S, Valsecchi P. 2011. Free-ranging dogs assess the quantity of opponents in intergroup conflicts. Anim Cogn. 14:103–115.

Bortolamiol S, Cohen M, Potts K, Pennec F, Rwaburindore P, Kasenene J, Seguya A, Vignaud Q, Krief S. 2014. Suitable habitats for endangered frugivorous mammals: small-scale comparison, regeneration forest and chimpanzee density in Kibale National Park, Uganda. PLoS One. 9:e102177.

Boyd R, Richerson PJ. 2009. Culture and the evolution of human cooperation. Philos Trans R Soc Lond B Biol Sci. 364(1533):3281–3288.

Boydston EE, Morelli TL, Holekamp KE. 2001. Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). Ethology. 107(5):369–385.

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L. 2004. Dispersed male networks in western gorillas. Curr Biol. 14:510–513.

Brotons L, Herrando S. 2003. Effect of increased food abundance near forest edges on flocking patterns of Coal Tit *Parus ater* winter groups in mountain coniferous forests. Bird Study. 50(2):106–111.

Brown JL. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76(2):160–169.

Brown M. 2013. Food and range defence in group-living primates. Anim Behav. 85(4):807–816.

Calenge C. 2011. Home range estimation in R: the adehabitatHR package. Auffargis (France): Office National de la Classe et de la Faune Sauvage.

Cantor M, Whitehead H. 2015. How does social behavior differ among sperm whale clans? Mar Mamm Sci. 31(4):1275–1290.

Carranza J, Alvarez F, Redondo T. 1990. Territoriality as a mating strategy in red deer. Anim Behav. 40(1):79–88.

Carter KD, Seddon JM, Frère CH, Carter JK, Goldizen AW. 2013. Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. Anim Behav. 85(2):385–394.

Cashdan E, Barnard A, Bicchieri M, Bishop CA, Blundell V, Ehrenreich J, Guenther M, Hamilton A, Harpending H, Howell N, et al. 1983. Territoriality among human foragers: ecological models and an application to four bushman groups. Curr Anthropol. 24(1):47–66.

Cassidy KA, Mech LD, MacNulty DR, Stahler DR, Smith DW. 2017. Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups. Behav Processes. 136:64–72.

Christensen C, Radford AN. 2018. Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. Behav Ecol. 29(5):1004–1013.

Clapham PJ, Palsbøll PJ, Mattila DK, Vasquez O. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour. 122(3/4):182–194.

Connor RC, Richards AF, Smolker RA, Mann J. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour. 133(1/2):37–69.

Crofoot MC, Gilby IC, Wikelski MC, Kays RW. 2008. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proc Natl Acad Sci USA. 105:577–581.

Di Bitetti MS. 2001. Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. J Zool. 253(1):33–45.

Dobson A. 2002. An introduction to generalized linear models. Boca Raton FL: Chapman & Hall/CRC.

Douglas PH, 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.

Ellis S, Franks DW, Robinson EJ. 2014. Resource redistribution in polydomous ant nest networks: local or global? Behav Ecol. 25:1183–1191.

Field A. 2005. Discovering statistics using SPSS. London: Sage Publications London.

Foley R, Gamble C. 2009. The ecology of social transitions in human evolution. Philos Trans R Soc Lond B Biol Sci. 364:3267–3279.

Forcina G, Vallet D, Le Gouar PJ, Bernardo-Madrid R, Illera G, Molina-Vacas G, Dréano S, Revilla E, Rodríguez-Teijeiro JD, Ménard N, et al. 2019. From groups to communities in western lowland gorillas. Proc Biol Sci. 286:20182019.

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.

Foster EA, Franks DW, Morrell LJ, Balcomb KC, Parsons KM, van Ginneken A, Croft DP. 2012. Social network correlates of food availability in an endangered population of killer whales, Orcinus orca. Anim Behav. 83(3):731–736.

Fox J, Weisberg S. 2011. An R companion to applied regression. 2nd ed. Thousand Oaks (CA): Sage. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.2073.

Fruth B, Hohmann G. 2018. Food sharing across borders: first observation of intercommunity meat sharing by bonobos at luikotale, DRC. Hum Nat. 29:91–103.

Furrer RD, Kyabulima S, Willems EP, Cant MA, Manser MB. 2011. Location and group size influence decisions in simulated intergroup encounters in banded mongooses. Behav Ecol. 22(3):493–500.

Furuichi T, Idani G, Ihobe H, Hashimoto C, Tashiro Y, Sakamaki T, Mulavwa MN, Yangozene K, Kuroda S. 2012. Long-term studies on wild bonobos at wamba, luo scientific reserve, D. R. Congo: towards the understanding of female life history in a Male-Philopatric species. In: Kappeler PM, Watts DP, editors. Long-term field studies of primates. Berlin, Heidelberg (Germany): Springer. p. 413–433.

Furuichi T. 2009. Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates. 50:197–209.

Furuichi T. 2011. Female contributions to the peaceful nature of bonobo society. Evol Anthropol. 20:131–142.

Gerwing J, Schnitzer S, Burnham R, Bongers F, Chave J, DeWalt S, Ewango C, Foster R, Kenfack D, Martínez-Ramos M, et al. 2006. A standard protocol for liana censuses. Biotropica. 38(2):256–261.

Gilchrist JS, Otali E. 2002. The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. Can J Zool. 80(10):1795–1802.

Grant JWA. 1993. Whether or not to defend? The influence of resource distribution. Mar Behav Physiol. 23(1–4):137–153.

Grueter CC, Chapais B, Zinner D. 2012. Evolution of multilevel social systems in nonhuman primates and humans. Int J Primatol. 33:1002–1037.

Grueter CC, van Schaik CP. 2010. Evolutionary determinants of modular societies in colobines. Behav Ecol. 21(1):63–71.

Harris TR. 2006. Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behav Ecol Sociobiol. 61(2):317–329.

Hashimoto C, Tashiro Y, Kimura D, Enomoto T, Ingmanson EJ, Idani G, Furuichi T. 1998. Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. Int J Primatol. 19(6):1045–1060.

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 LF, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge, UK: Cambridge University Press. p. 138–150.

Idani G. 1990. Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. Afr Study Monogr. 11:153–186.

Ihobe H. 1992. Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire. Primates. 33(2):163–179.

Isbell LA, Vuren DV. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour. 133(1/2):1–36.

Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour. 139(2/3):177–202.

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.

Jaeggi A, Boose K, White F, 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(9–11):1015–1051.

Janmaat KR, Olupot W, Chancellor RL, Arlet ME, Waser PM. 2009. Long-term site fidelity and individual home range shifts in *Lophocebus albigena*. Int J Primatol. 30:443–466.

Kelly R. 1995. The lifeways of Hunter-Gatherers: the foraging spectrum. Cambridge, UK: Cambridge University Press.

Kirkpatrick RC, Grueter CC. 2010. Snub-nosed monkeys: multilevel societies across varied environments. Evol Anthropol. 19(3):98–113.

Kitchen D, Cheney D, Seyfarth R. 2004. Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour. 141(2):197–218.

Koch F, Signer J, Kappeler PM, Fichtel C. 2016. The role of the residence-effect on the outcome of intergroup encounters in Verreaux's sifakas. Sci Rep. 6:28457.

Koenig A. 2002. Competition for resources and its behavioral consequences among female primates. Int J Primatol. 23(4): 759–783.

Koenig A, Scarry CJ, Wheeler BC, Borries C. 2013. Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. Philos Trans R Soc Lond B Biol Sci. 368:20120348.

Laden G. 1993. Ethnoarchaeology and land use ecology of the Efe (Pygmies) of the Ituri Rain Forest, Zaire [doctoral dissertation]. Cambridge, MA: Harvard University.

Layton R, O'Hara S, Bilsborough A. 2012. Antiquity and social functions of multilevel social organization among human Hunter-Gatherers. Int J Primatol. 33(5):1215–1245.

Lucchesi S, Cheng L, Janmaat K, Mundry R, Pisor A, Surbeck M. 2019. Data from: beyond the group: how food, mates and group size influence inter-group encounters in wild bonobos. Behav Ecol. doi:10.5061/dryad.hqbzkh1bq.

Maher CR, Lott DF. 2000. A review of ecological determinants of territoriality within vertebrate species. Am Midl Nat. 143(1):1–29.

Malenky RK, Wrangham RW. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and Pan troglodytes in the Kibale Forest, Uganda. Am J Primatol. 32(1):1–12.

Matsuda I, Tuuga A, Higashi S. 2010. Effects of water level on sleeping-site selection and inter-group association in proboscis monkeys: why do they sleep alone inland on flooded days? Ecol Res. 25(2):475–482.

McComb K, Packer C, Pusey A. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Anim Behav. 47(2):379–387.

McCullagh P, Nelder JA. 1989. Generalized linear models. 2nd ed. London: Chapman & Hall.

McKinnon L, Gilchrist HG, Scribner KT. 2006. Genetic evidence for kin-based female social structure in common eiders (*Somateria mollissima*). Behav Ecol. 17(4):614–621.

Mirville MO, Ridley AR, Samedi JPM, Vecellio V, Ndagijimana F, Stoinski TS, Grueter CC. 2018. Low familiarity and similar "group strength" between opponents increase the intensity of intergroup interactions in mountain gorillas (*Gorilla beringei beringei*). Behav Ecol Sociobiol. 72(11):178.

Morrison RE, Groenenberg M, Breuer T, Manguette ML, Walsh PD. 2019. Hierarchical social modularity in gorillas. Proc Biol Sci. 286:20190681.

Mosser A, Packer C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Anim Behav. 78(2):359–370.

Mulavwa M, Furuichi T, Yangozene K, Yamba-Yamba M, Motema-Salo B, Idani G, Ihobe H, Hashimoto C, Tashiro Y, Mwanza N. 2008. Seasonal changes in fruit production and party size of bonobos at Wamba. In: Furuichi T, Thompson J, editors. The bonobos. New York: Springer. p. 121–134.

Müller CA, Manser MB. 2007. "Nasty neighbours" rather than "dear enemies" in a social carnivore. Proc Biol Sci. 274:959–965.

Olupot W, Chapman CA, Waser PM, Isabirye-Basuta G. 1997. Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. Am J Primatol. 43:65–78.

Pandit SA, Pradhan GR, Balashov H, Van Schaik CP. 2016. The conditions favoring between-community raiding in chimpanzees, bonobos, and human foragers. Hum Nat. 27:141–159.

Paoli T, Palagi E, Tacconi G, Tarli SB. 2006. Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos (*Pan paniscus*). Am J Primatol. 68:333–347.

Parish AR, De Waal F, Haig D. 2000. The other "Closest Living Relative": how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. Ann NY Acad Sci. 907(1):97–113.

Pisor AC, Gurven M. 2016. Risk buffering and resource access shape valuation of out-group strangers. Sci Rep. 6:30435.

Pisor AC, Surbeck M. 2019. The evolution of intergroup tolerance in non-human primates and humans. Evol Anthropol. 28:210–223.

Potts KB, Chapman CA, Lwanga JS. 2009. Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. J Anim Ecol. 78:1269–1277.

Radford AN, du Plessis MA. 2004. Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. Anim Behav. 68(4):803–810.

Raman TRS. 1997. Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. J Biosci. 22(2):203–218.

Ratcliffe JM, Ter Hofstede HM. 2005. Roosts as information centres: social learning of food preferences in bats. Biol Lett. 1:72–74.

R Core Team. 2018. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org.

Richter T, Garrard AN, Allock S, Maher LA. 2011. Interaction before agriculture: exchanging material and sharing knowledge in the final pleistocene levant. Cambridge Archaeol J. 21(01):95–114.

Robbins M, Sawyer S. 2007. Intergroup encounters in mountain gorillas of Bwindi Impenetrable National Park, Uganda. Behaviour. 144(12):1497–1519.

Robinson E, Barker J. 2017. Inter-group cooperation in humans and other animals. Biol Lett. 13(3):20160793.

Rubenstein D, Hack M. 2004. Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In: Kapeller PM, Schaik CV, editors. Sexual selection in primates: new and comparative perspectives. Cambridge, UK: Cambridge University Press. p. 266–279.

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(4):685–704.

Schamberg I, Cheney D, Clay Z, Hohmann G, Seyfarth R. 2016. Call combinations, vocal exchanges and interparty movement in wild bonobos. Anim Behav. 122:109–116.

Schielzeth H, Forstmeier W. 2009. Conclusions beyond support: overconfident estimates in mixed models. Behav Ecol. 20:416–420.

Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol. 1(2):103–113.

Seiler N, Boesch C, Mundry R, Stephens C, Robbins MM. 2017. Space partitioning in wild, non-territorial mountain gorillas: the impact of food and neighbours. R Soc Open Sci. 4:170720.

Snyder-Mackler N, Alberts SC, Bergman TJ. 2014. The socio-genetics of a complex society: female gelada relatedness patterns mirror association patterns in a multilevel society. Mol Ecol. 23:6179–6191.

Sonerud GA, Smedshaug CA, Bråthen O. 2001. Ignorant hooded crows follow knowledgeable roost-mates to food: support for the information centre hypothesis. Proc Biol Sci. 268:827–831.

Surbeck M, Boesch C, Crockford C, Thompson ME, Furuichi T, Fruth B, Hohmann G, Ishizuka S, Machanda Z, Muller MN, et al. 2019. Males with a mother living in their group have higher paternity success in bonobos but not chimpanzees. Curr Biol. 29:R354–R355.

Surbeck M, Coxe S, Lokasola A. 2017a. Lonoa: the establishment of a permanent field site for behavioural research on bonobos in the Kokolopori Bonobo Reserve. Pan Africa News. 24:13–15.

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.

Surbeck M, Deschner T, Schubert G, Weltring A, Hohmann G. 2012. Mate competition, testosterone and intersexual relationships in bonobos, Pan paniscus. Anim Behav. 83(3):659–669.

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(11):1767–1780.

Surbeck M, Langergraber K, Fruth B, Vigilant L, Hohmann G. 2017b. Male reproductive skew is higher in bonobos than chimpanzees. Curr Biol. 27(13): R640–R641.

Surbeck M, Mundry R, Hohmann G. 2011. Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). Proc Biol Sci. 278:590–598.

Tan J, Ariely D, Hare B. 2017. Bonobos respond prosocially toward members of other groups. Sci Rep. 7(1):14733.

Tanner CJ. 2006. Numerical assessment affects aggression and competitive ability: a team-fighting strategy for the ant *Formica xerophila*. Proc Biol Sci. 273:2737–2742.

Tavares SB, Samarra FIP, Miller PJO. 2017. A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol. 28(2):500–514.

Temeles EJ. 1994. The role of neighbours in territorial systems: when are they "dear enemies?" Anim Behav. 47(2):339–350.

Thompson FJ, Marshall HH, Vitikainen EIK, Cant MA. 2017. Causes and consequences of intergroup conflict in cooperative banded mongooses. Anim Behav. 126:31–40.

Tong W, Shapiro B, Rubenstein DI. 2015. Genetic relatedness in two-tiered plains zebra societies suggests that females choose to associate with kin. Behaviour. 152(15):2059–2078.

Van Wilgenburg E, Elgar MA. 2007. Colony characteristics influence the risk of nest predation of a polydomous ant by a monotreme: echidna predation on ant nests. Biol J Linn Soc. 92(1):1–8.

Waller M. 2011. The ranging behavior of bonobos in the Lomako forest (PhD thesis). Eugene, OR: University of Oregon.

Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? Int J Primatol. 33(5):1142–1164.

Willems E, van Schaik C. 2015. Collective action and the intensity of between-group competition in nonhuman primates. Behav Ecol. 26(2):625–631.

Wilson M, Boesch C, Fruth B, Furuichi T, Gilby I, Hashimoto C, Hobaiter C, Hohmann G, Itoh N, Koops K, et al. 2014. Lethal aggression in Pan is better explained by adaptive strategies than human impacts. Nature. 513(7518):414–417.

Wilson M, Kahlenberg S, Wells M, Wrangham R. 2012. Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. Anim Behav. 83(1):277–291.

Wilson ML. 2013. Chimpanzees, warfare, and the invention of peace. In: Fry D, editor. War, peace, and human nature: the convergence of evolutionary and cultural views. Oxford: Oxford University Press. p. 361–388.

Wittemyer G, Getz WM, Vollrath F, Douglas-Hamilton I. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. Behav Ecol Sociobiol. 61(12):1919–1931.

Worton B. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 70(1):164–168.

Wrangham RW. 1999. Evolution of coalitionary killing. Am J Phys Anthropol. 110(Suppl 29):1–30.