



Dominance or Tolerance? Causes and consequences of a period of increased intercommunity encounters among bonobos (*Pan paniscus*) at LuiKotale

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Abstract

Group-living primates exhibit variable reactions to intergroup encounters (or IGEs), reflecting species-specific strategies and individual motivations. In chimpanzees (*Pan troglodytes*), dominating in IGEs provides fitness benefits. Less is known about responses to IGEs in bonobos (*Pan paniscus*) despite their equal relevance for understanding the origins of human intergroup relations. We observed the Bompusa West (WBp) bonobo community at LuiKotale during a 2-month shift in ranging resulting in frequent IGEs with the smaller Bompusa East (EBp) community. We tested whether incursions provided ecological benefits, and whether responses to IGEs were consistent with inter-community dominance or tolerance. We measured fruit availability and collected activity scans from 26 mature WBp community members when in their core ranging area, during incursions into the EBp ranging area, and during IGEs. We collected data on sexual interactions and aggression with in-group and out-group members during 19 independent IGEs. During their shift in ranging, fruit availability was greater in the EBp ranging area, and WBp bonobos consumed more fruit during incursions than when in their core ranging area. Coalitionary intergroup aggression occurred during nine IGEs, and outcomes were consistent with imbalances in fighting power, in that larger WBp parties supplanted smaller EBp parties from the immediate area. However, communities reformed associations following 70% of coalitionary conflicts, and prolonged IGEs facilitated out-group sexual interactions and female transfers. The WBp community shift in ranging was likely motivated by ecological factors and responses to increased IGEs reflected a mixture of competitive and tolerant strategies.

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Introduction

Intergroup encounters (or IGEs) are a universal aspect of group-living, whether animals defend strict territories or use more flexible home ranges (Christensen & Radford, 2018). Responses to IGEs determine intergroup relations, which in turn influence communal range use, access to resources, and dispersal patterns (Mitani et al., 2010; Robinson & Barker, 2017; Willems et al., 2013). Across many primate species, group-level responses to IGEs are characterized as mainly competitive (e.g., chimpanzees (*Pan troglodytes*): Crofoot & Wrangham, 2010; spider monkeys (*Ateles geoffroyi yucatanensis*): Aureli et al., 2006; tufted capuchin monkeys (*Sapajus nigritus*): Scarry, 2013; red-tailed monkeys (*Cercopithecus ascanius*): Jaeggi et al., 2018). However, there also is evidence that socioecological factors, including food abundance and degree of intergroup familiarity, can promote more tolerant responses to IGEs (e.g., mountain gorillas (*Gorilla beringei beringei*): Mirville et al., 2018; bonobos (*Pan paniscus*): Sakamaki et al., 2018). Within primate groups as well, individuals often differ in their propensities towards more aggressive or more tolerant responses to IGEs based on attributes, such as sex, age, and rank (reviewed in Kitchen & Beehner, 2007).

Humans by far exhibit the greatest range in intergroup relations, including unprecedented scales of conflict (Bowles, 2009; Keeley, 1996; Shaw, 2003), but also examples of out-group cooperation and peace-keeping mechanisms, such as trade, reciprocal land use, and the exchange of marriage partners, which strengthen out-group alliances and decrease intergroup aggression (Chapais, 2013; Fry, 2013). Thus, intergroup relations in humans are by nature flexible, reflecting the relative fitness benefits resulting from competition or cooperation in their current environment (Dyson-Hudson & Smith, 1978; Jaeggi et al., 2016; Majolo, 2019; Pisor & Surbeck, 2019; Robinson & Barker, 2017).

Our two closest living relatives, chimpanzees and bonobos, share several similarities in social structure and ecology (reviewed in: Fruth et al., 1999; Gruber & Clay, 2016), but a comparison of intergroup relations suggests biases toward predominantly competitive relations for chimpanzees and more tolerant relations for bonobos. Chimpanzees patrol and aggressively defend their home ranges (Herbinger et al., 2001) and subgroups (or parties) also travel into areas more frequently used by neighboring communities to access preferred foods that are not locally abundant (Wilson et al., 2012), to coerce copulations with fertile out-group females (Boesch et al., 2008), or to launch coordinated and sometimes lethal attacks on out-group members (reviewed in: Wilson et al., 2014). Responses to IGEs in chimpanzees are largely consistent with the *intergroup dominance hypothesis* (Crofoot & Wrangham, 2010; Sobolweski et al., 2012), which proposes that members of a group will form coalitions to aggressively compete against out-groups, and that outcomes of these conflicts will be decided by imbalances in fighting power, with groups with greater relative fighting ability (usually determined by the difference in the number of

mature individuals in each group) aggressively excluding smaller groups from preferred areas (Crofoot & Wrangham, 2010; Majolo et al., 2020). The potential risks associated with IGEs for chimpanzees are reflected physiologically by increased concentrations of the glucocorticoid hormone cortisol, which is commonly associated with energetic or psychological stress, during IGEs (Samuni et al., 2019; Wittig et al., 2016).

Evidence from bonobo IGEs is more variable, but generally consistent with more tolerant intergroup relations relative to chimpanzees, especially concerning interactions among females (Furuichi, 2011; Jaeggi et al., 2016; White et al., 2013). Bonobo communities exhibit a greater degree of home range overlap than chimpanzees (Grueter, 2015) and little evidence for territoriality (Lucchesi et al., 2020; White et al., 2013). Several studies describe prolonged and largely peaceful mixed-community associations, even including some instances of out-group cooperation in food sharing (LuiKotale: Fruth & Hohmann, 2018) and coalitions (Wamba: Tokuyama et al., 2019). Several hypotheses relate the more tolerant intergroup relations in bonobos to reduced seasonality in fruit availability in bonobo habitats (Oelze et al., 2016) and reduced reliance on fruit relative to chimpanzees (Hohmann et al., 2010; Nurmi et al., 2018), both of which are likely to reduce direct conflicts (or contest competition) over access to resources. However, there also is evidence that bonobos experience increased competition and conflict during IGEs. At Kokolopori, DRC, IGEs are associated with longer daily travel distances, which require modifications in feeding behavior to offset the associated energetic costs (Lucchesi et al., 2021). Across field sites, IGEs are associated with increases in aggression specifically directed at out-group members (LuiKotale: Hohmann & Fruth, 2002; Wamba: Tokuyama et al., 2019; Kokolopori: Cheng et al., 2021), and a recent study at Kokolopori suggests that bonobos have increased urinary cortisol concentrations associated with IGEs (Cheng et al., 2021), similar to chimpanzees.

While there is increasing evidence that bonobos experience energetic and physiological costs associated with IGEs, less attention has been paid to the potential benefits that may accrue through tolerant responses to IGEs and prolonged intergroup associations (but see: Pisor & Surbeck, 2019; Robinson & Barker, 2017). Such benefits are likely to be social, including opportunities for out-group mating (Lucchesi et al., 2020; Sakamaki et al., 2018). Considering females' high social status (Furuichi, 2011) and their less reliable indicators of ovulation compared with chimpanzees (Douglas et al., 2016), out-group mating is more likely to result from tolerant interactions than from male coercion. Nonreproductive sexual interactions, such as same-sex genital contacts, have been linked to within-group cooperation among females (Hohmann & Fruth, 2000; Moscovice et al., 2017, 2019) and also may promote female out-group cooperation (Tokuyama et al., 2019), and facilitate female intergroup transfers, which have been observed during IGEs at other bonobo study sites (Wamba: Sakamaki et al., 2015).

At the individual level, there is evidence that male bonobos participate more than females in intercommunity aggression (Kokolopori: Cheng et al., 2021; Wamba: Tokuyama et al., 2019), and at Wamba, high-ranking males engage in the most out-group aggression (Tokuyama et al., 2019), which may represent a form of mate defense (Tokuyama et al., 2019). However, since high-ranking male bonobos

monopolize mating opportunities and paternity within their own groups (Surbeck et al., 2010, 2017), they may also stand to benefit more than low-ranking males from tolerant out-group associations, if such associations facilitate out-group mating opportunities. As members of the dispersing sex, female bonobos of all ranks may benefit through more tolerant and prolonged IGEs. For young, low-ranking females, tolerant IGEs may help to reduce the risks associated with dispersal into novel habitats containing unfamiliar and potentially hostile groups (Kahlenberg et al., 2008; Lee & Strier, 2015). For older and higher-ranking females, tolerant IGEs provide opportunities to maintain out-group social networks that facilitate female out-group cooperation (Tokuyama et al., 2019) and provide indirect fitness benefits when social networks involve relatives (Ishizuka et al., 2018, reviewed in Pisor & Surbeck, 2019).

We conducted a detailed analysis on a period of frequent IGEs between two habituated bonobo communities at the LuiKotale field site, Democratic Republic of the Congo (DRC). The Bompusa West community (WBp) has been fully habituated since 2007 and has an annual ranging area (or home range) of $\sim 30 \text{ km}^2$, which includes habitat on both sides of the Bompusa stream (Fruth & Hohmann, 2018). However, the WBp bonobos spend the majority of their time (97%, or 159/163 observation days in the 10 months leading up to this study) in the area to the West of the Bompusa stream, which we subsequently refer to as the WBp core ranging area. The neighboring Bompusa East community (EBp) has been habituated since 2015 and has an annual home range of $\sim 20 \text{ km}^2$ primarily to the East of the Bompusa stream (Fruth & Hohmann, 2018). In the 10 months before this study, the community spent 100% of their time (out of 241 observation days) in ranging areas to the East of the Bompusa stream, which we subsequently refer to as the EBp core ranging area. The IGEs were triggered by a shift in the ranging patterns of the WBp community members, who were the focus of this study, to overlap with the core ranging area of the EBp community (Fig. 1). Although our analysis is based on a short time period, we consider this an important case study to investigate the different factors that influence shifts in ranging, as well as individual responses during heightened frequencies of encounters with out-group members, for one bonobo community at LuiKotale.

We first test whether the shift in ranging patterns of the WBp community was driven by ecological factors (*Ecological needs (ECO) hypothesis*). If so, we predict that during incursions into the core ranging area of the EBp community: ECO 1) the WBp core ranging area will contain less fruit of confirmed bonobo foods compared to the EBp core ranging area, ECO 2) the WBp bonobos will consume more fruit when in the EBp core ranging area than when in their own core ranging area, and ECO 3) the WBp bonobos will spend less time feeding and traveling and more time resting when in the EBp core ranging area than when in their own core ranging area, since their energetic needs can be met faster, due to their increased access to higher quality foods (Doran, 1997).

We then test two hypotheses to explain responses of the WBp community to encounters with the EBp community: The *intercommunity dominance (ICD)* and the *intercommunity tolerance (ICT) hypotheses* (Table 1). Under the ICD hypothesis, we predict that: ICD 1) During IGEs, WBp bonobos will bias aggression towards

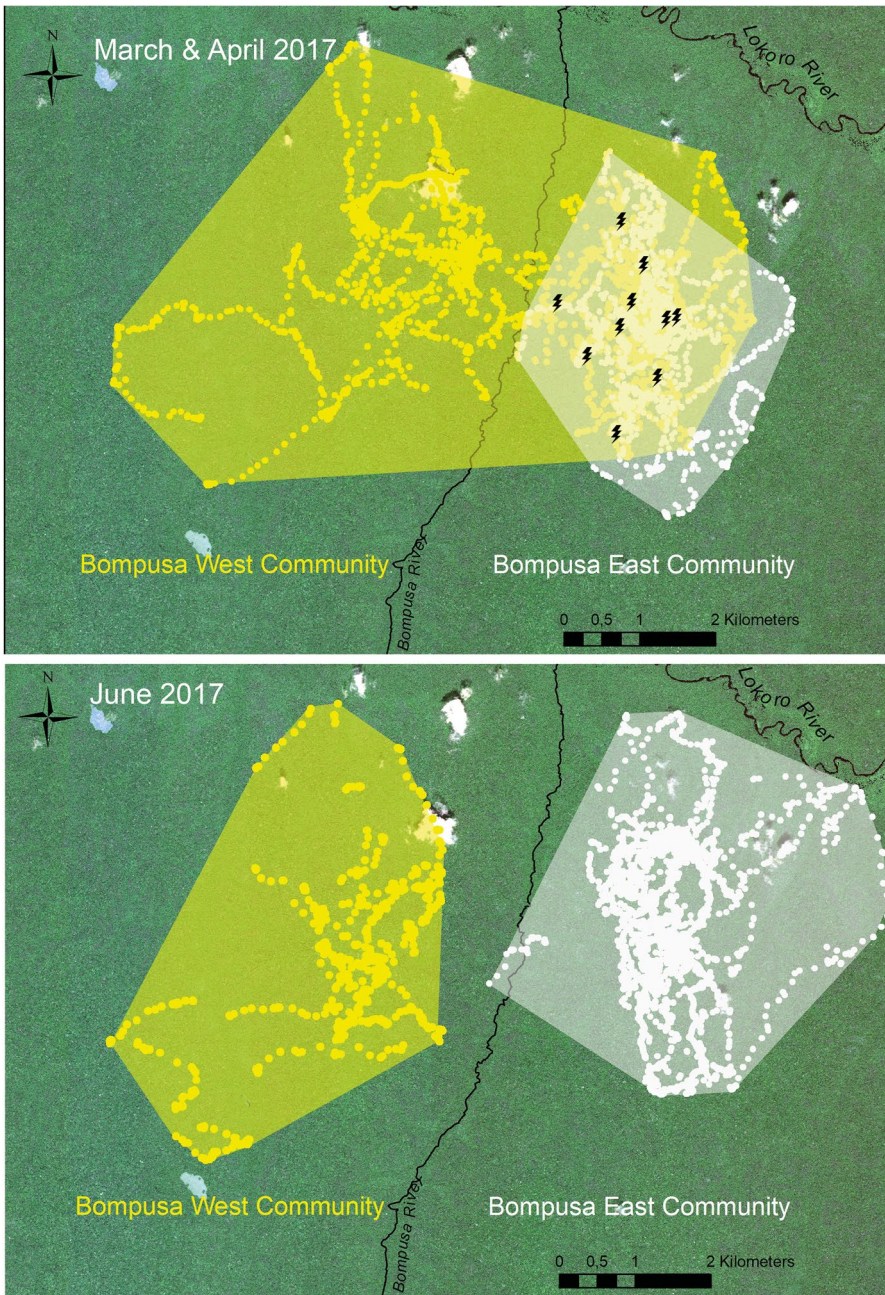


Fig. 1 Monthly track logs and Minimum Convex Polygon (MCP) ranging estimates of the Bompusa West (WBp, in yellow) and the Bompusa East (EBp, in white) bonobo communities at the LuiKotale field site, DRC. Ranging estimates are from March 15th to April 2017 (top panel), during a shift in the WBp ranging area, and June 2017 (bottom panel), when the WBp community returned to their core ranging area. The locations of intercommunity coalitional conflicts are indicated by black lightning bolts

Table 1 Comparison of predictions under the intercommunity dominance (ICD) and intercommunity tolerance (ICT) hypotheses to explain bonobo responses to intergroup encounters (IGEs). Numbers indicate predictions as referred to in the text. The direction of support received for each prediction is indicated

Predictions	Inter-community dominance (ICD)	Inter-community tolerance (ICT)	Support
Responses to IGEs	Aggression will be biased towards out-group compared to in-group members, and will be more intense when directed at out-group members (<i>ICD 1</i>)	Tolerant interactions will be biased towards out-group compared to in-group members (<i>ICT 1</i>)	ICD
Immediate outcomes of intergroup aggressive conflicts	Decided by differences in group fighting power, with the smaller group being displaced from the conflict area (<i>ICD 2</i>)	Decided by differences in dominance relations between the individuals involved, and unrelated to relative group fighting power (<i>ICT 2</i>)	ICD
Impacts of inter-group aggression on inter-group associations	Following inter-group aggression, members of the two communities will fission, ending the IGE (<i>ICD 3</i>)	Following inter-group aggression, some members of both communities will continue to associate together (<i>ICT 3</i>)	ICT
Comparison of activity patterns during IGEs relative to incursions	No changes in time spent feeding and moving for the dominant group, due to competitive exclusion of the subordinate group from the area (<i>ICD 4</i>)	Larger combined party sizes during tolerant IGEs will increase scramble competition, leading to more time spent moving and feeding during IGEs relative to incursions (<i>ICT 4</i>)	ICD (no changes in time spent moving during IGEs) & ICT (larger combined party sizes and more time spent feeding during IGEs)

out-group compared to in-group members, and out-group aggression will be more intense in form than in-group aggression, including more large-scale coalitions and contact aggression. ICD 2) Immediate outcomes of out-group aggression will be determined by differences in fighting power, with larger groups aggressively displacing smaller groups from the conflict area. ICD 3) Following intercommunity aggression, the two communities will fission and avoid further associations, and ICD 4) For the dominant community, time spent feeding will not differ between incursions and IGEs, since they will competitively exclude members of the smaller community from preferred resources. Support for the ICD hypothesis would suggest that bonobos benefit by competing with out-group members during IGEs.

Under the intercommunity tolerance (ICT) hypothesis, we predict that: ICT 1) Wbp individuals will respond to IGEs by seeking out affiliative interactions with out-group members, resulting in a greater likelihood of tolerant associations with members of fusing parties following fusions with out-group compared to in-group members. ICT 2) Out-group aggression will primarily occur between dyads or small coalitions (similar to in-group aggression) and will be determined by differences in dominance relations between the specific individuals involved. As a result, group size before out-group aggression will not predict the outcome of the aggression. ICT 3) Members of both communities will continue to associate together following out-group aggression, and ICT 4) Prolonged IGEs will result in larger combined party sizes of Wbp and Ebp bonobos compared with Wbp party sizes during incursions without IGEs. While associating in larger parties, Wbp bonobos will experience increased scramble competition over access to food, resulting in more time spent feeding and moving during IGEs compared to incursions. Support for the ICT hypothesis would suggest that bonobos gain benefits by behaving tolerantly towards out-group members during IGEs.

Methods

Study site and subjects

The LuiKotale study site is situated in an area of continuous equatorial lowland rainforest near the southern sector of Salonga National Park (2°47'S, 20° 21'E). The study site contains a network of ~80 km of transects that cover the core ranging areas of the Bompusa West and East communities. The Bompusa stream is in most places too deep for bonobos to cross directly and thus acts as a natural barrier reducing contact between the two communities. However, members of both communities sometimes use natural bridges, such as fallen logs or overhanging vegetation, to cross the stream and spend from hours to days in the core ranging area of the other community. Our analyses focus on data collected by LRM and assistants over 92 observation days between March and June 2017, covering half or full day follows of the Wbp community. This short time period involved a major shift in the typical ranging patterns of the Wbp community to overlap extensively with the core ranging area of the neighboring Ebp community (Fig. 1), resulting in frequent IGEs (Table S1). During the study period, the Wbp community consisted of 18

female and 8 male mature individuals (estimated to be > 10 years of age) who were the focus of data collection, along with 8 juveniles (aged between 6–9 years) and 11 infants (< 6 years of age; Table 2). In comparison, the EBp community had fewer members across age categories (Table 2).

Ethical note

All research adhered to the legal requirements of the DRC and the Institut Congolais pour la Conservation de la Nature (ICCN). Methods for data collection were non-invasive and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Determining fruit availability

We established forty 10 m² phenological plots (total area=0.4 ha) at 100-m intervals located parallel to each other and bisecting the core ranging area of each community, from north to south. Within plots, we measured diameter at breast height (DBH) for all trees with > 5 cm DBH, and taxonomically identified all trees with > 10 cm DBH. For the subset of identified trees that were bonobo feeding trees (Table S2), we measured fruit availability using a 0–4 scale where 0=little to no visible fruit, 1=approximately 25% of the canopy fruiting, 2=approximately 50% of the canopy fruiting, 3=approximately 75% of the canopy fruiting, 4=> 75% of the canopy fruiting. For simplification, we included all visible fruit, regardless of their degree of ripeness. We measured fruit availability on the 40 plots in each ranging area over four days coinciding with a period when the WBp community was ranging exclusively in the EBp ranging area. We then calculated a Fruit Availability Index (FAI) for each tree by multiplying the fruit production score by the tree basal area, which is positively correlated with crop size at other field sites (Chapman et al., 1992; Hawes & Peres, 2016). We summed this value for all fruit-bearing trees of a given species per habitat, resulting in a density estimate of fruit availability per species (FAI/ha) during the incursion period (Table S2). As a measure of more general food availability outside of the incursion period, we also compared the

Table 2 Demographics of two bonobo communities at LuiKotale, DRC from March–June 2017. Numbers in parentheses refer to the subset of females who made primary or secondary transfers during the study period

	Bompusa West community		Bompusa East community	
	Females	Males	Females	Males
Mature individuals (<i>subset of these who transferred</i>)	18 (-1)	8	10	6
Juveniles (<i>subset of these who transferred</i>)	6 (-3)	2	2	2
Infants	5	6	5	3
Total	29	16	17	11

density and basal area of bonobo feeding trees between ranging areas independent of whether or not they had fruit.

Behavioral data

We assigned behavioral data to one of three broad contexts: I) “Baseline” when the WBP focal party was in its core ranging area; II) “Incursion” when the WBP focal party was within the EBP core ranging area, but not in visible contact with members of the EBP community; III) “IGE” when at least some members of the WBP focal party had visual contact with members of the EBP community. Similar to other authors (Cheng et al., 2021), we considered an IGE to end when bonobos were no longer in visual or auditory contact with members of other communities. We considered IGE events to be independent when there was no visual or auditory contact between different communities for at least one hour. We used Garmin GPS devices (GPSMAP® 62) to georeference focal parties of the WBP community every 5 min. We recorded cumulative WBP party size at 30-min intervals, including all mature individuals observed in the previous 29 min. Whenever additional researchers observed the EBP community, we obtained corresponding data on their party size during encounters. We recorded activity (moving, feeding, resting, social interaction) of each mature individual using fifteen-minute instantaneous scans ($N=4,299$ scans, $\text{Mean} \pm \text{SD} = 165.35 \pm 82.93$ per individual). For feeding scans ($N=1,824$, $\text{Mean} \pm \text{SD} = 70.10 \pm 35.90$ per individual), we recorded food type (fruit, seeds, leaves, piths, insects, meat, other) and species. For scans with social interactions ($N=409$, $\text{Mean} \pm \text{SD} = 17.04 \pm 10.39$ per individual), we recorded the group identity (in-group or out-group) of partners. During all scans, we also recorded the group identity (in-group or out-group) of every individual within close proximity (5 m) of the instantaneous scan subject.

In addition to the scan sampling, we recorded all observed occurrences of the following social behaviors with in-group or out-group partners: 1) Same- and opposite-sex sexual behavior including copulations, female genito-genital (GG) rubbing, and other genital contacts. We considered sexual interactions to be independent when they were separated by an interval of ≥ 1 min between events involving the same dyad; 2) Grooming, measured as the number of observation minutes that partners groomed each other; 3) Food sharing, defined as the passive or active transfer of a potentially monopolizeable food from a food possessor to a bystander; and 4) Aggression, defined as displays, chases, hitting, or biting, directed by one or more individuals toward one or more target individuals, with coalitionary aggression involving joint aggression by two or more individuals. We considered aggressive events to be independent if they were separated by an interval of ≥ 10 min without any aggressive interactions between the same individuals. In the case of intercommunity coalitionary aggression, we calculated “relative fighting power” for each community based on all mature individuals present during the encounter. We categorized the outcome of out-group coalitionary aggression as a win for the WBP community if EBP individuals retreated, a loss if WBP individuals retreated, or a

tie if some members of both communities remained in close proximity immediately after the conflict. To maximize our chances of observing important social behaviors, two to three observers recorded data on WBp individuals in different areas during each IGE. However, WBp community members were sometimes spread out over large areas, and visibility was sometimes poor during IGEs, making it difficult to observe all interactions. As a result, our data should be considered representative rather than comprehensive.

We assigned dominance ranks to mature members of the WBp community based on all occurrences of independent in-group aggressive events ($N = 243$) over a 9-month period from Mar–Nov 2017, using the Elo-rating method (Neumann et al., 2011) in the R package “EloRating” (Neumann & Kulik, 2020). Because we wanted to test how dominance rank influenced responses to IGEs for each sex separately, we standardized Elo ratings between 0–1 for each sex, with higher scores indicating a greater proportion of same-sex individuals dominated.

Statistical analyses

We analyzed scan data using linear and generalized linear mixed-effects models fit and interpreted within a Bayesian framework. Bayesian models were implemented in Stan (Carpenter et al., 2017) through the *brms* R package (Bürkner, 2017). In all models, continuous predictors were log- or square-root transformed when necessary to achieve normal distributions and then standardized, such that the mean is 0 and units are standard deviations. In each model, we included random effects of subject and random slopes for all fixed effects that varied within levels of a random factor (Barr et al., 2013). To improve convergence and guard against overfitting, we specified mildly regularizing priors (for regression slopes: Gaussian with mean 0 and SD 5. For variance components: Half-Cauchy, with location 0 and scale 2). Convergence was good in all models as R_{hat} values were 1 and effective sample sizes $> 1,000$ in all cases. Bayesian models produce a posterior probability distribution for each estimated parameter. We present the means and 95% credible intervals (CI) of this distribution for each parameter, as well as the proportion of the distribution that supports a given association (e.g., $P_{Baseline>East}$, or $P_{odds\ ratio>1}$). By presenting quantitative support for predictions instead of relying on arbitrary significance thresholds we encourage probabilistic rather than dichotomous inference and avoid the pitfalls of p-hacking. Readers who prefer binary thresholds may refer to the 95% CIs.

To measure local fruit availability during the study period (ECO 1), we tested for differences in the number of trees and the cumulative FAI per plot for species of confirmed bonobo fruits in the WBp core ranging areas and in the EBp core ranging area. In the models, each row of data represents the number of trees, or the cumulative FAI score, for bonobo feeding trees within one plot in the WBp ($N = 40$ plots with 125 trees, cumulative FAI = 8.2/ha) or EBp core ranging area ($N = 40$ plots with 120 trees, cumulative FAI = 39.2/ha). To test for influences of shifts in ranging on feeding behavior (ECO 2), we compared the proportion of each

bonobo's daily feeding scans that they spent feeding on fruit when WBp bonobos were on the west side of the Bompusa stream, in their core ranging area or on the East side of the Bompusa stream, in the EBp core ranging area. Each row of data in the model represents the proportion of a subject's daily feeding scans that they spent feeding on fruit when in their core ranging area ($N=312$ daily proportional fruit scores, 12.48 ± 3.99 per subject) or when in the EBp core ranging area ($N=468$ daily proportional fruit scores, 19.50 ± 8.56 per subject). We included an offset term to account for the different number of feeding scans per subject. To determine whether activity patterns were consistent with increased access to high quality foods during incursions (ECO 3) and competitive exclusion (ICD 4) or increased scramble competition (ICT 4) during IGEs, we used multinomial models (Koster & McElreath, 2017) to compare the proportion of scans that each individual spent feeding, moving, resting, and socializing during baseline ($N=1,830$ scans, 70.38 ± 34.83 per subject), incursion ($N=1,922$ scans, 76.88 ± 41.90 per subject), and IGE ($N=547$ scans, 23.78 ± 14.43 per subject) contexts. Each row of data in this model represents one 15-min activity scan for one individual. We included sex, rank, and WBp party size as control predictors, all of which may additionally influence access to resources or the intensity of scramble competition.

As a measure of out-group social tolerance (ICT 1), we compared responses of WBp focal party members toward members of joining parties during the first hour following fusions. We used a binomial model to compare the likelihood that WBp focal party individuals fed, rested, or groomed while members of joining parties were within close proximity when joining parties consisted of only in-group members ($N=75$ scans following 10 fusion events) or only out-group members ($N=110$ scans following 12 fusion events). Each row of data in this model represents for each individual present at each fusion event, the proportion of their relaxed scans (while feeding, resting, or grooming) that they spent in close proximity to members of joining parties in the hour following fusion events with either in-group or out-group members.

The data on aggression were too sparse for modeling and did not meet the criteria for *t*-tests (Shapiro–Wilk test, $W=0.90$, $P=0.026$). We used a Wilcoxon Signed-Ranks test to determine whether WBp bonobos directed more aggression at out-group vs. in-group members during IGEs (ICD 1). We used descriptive statistics to examine the immediate outcomes of intergroup aggressive conflicts (ICD/ICT 2) and the impacts of aggression on intergroup associations (ICD/ICT 3).

To compare individual responses to IGEs, we used Pearson correlations to examine the relationship between out-group aggressive interactions, sexual interactions and dominance rank for males and females separately. We also compared occurrences of female out-group transfer during and outside of the study period to examine whether frequent IGEs may help females to assess dispersal options and make dispersal decisions. The datasets analyzed in the present study are available either in the manuscript (for Wilcoxon Signed-Rank tests and Pearson correlations) or through the GitHub data repository (for Bayesian models, https://github.com/lmoscov/Luikotale_bonobo_IGEs).

Results

Overview of behavior during incursions and IGEs

During the study period, the WBp bonobos were observed for 546.2 h, during which they spent over half of the observation time across the Bompusa stream in the core ranging area of the EBp community (275.6 vs. 270.6 h in their own ranging area; Fig. 1). During incursions, there was little evidence that WBp bonobos engaged in furtive patrolling behavior or concealed their presence. Rather, members of focal parties exhibited frequent long-range vocalizations ($N=62$ total, 0.29 per incursion hour) and also buttress drummed on three occasions. Regardless of whether the long-range calls were directed at in-group or out-group members, it is likely that any bonobos within 700 m would have heard the calls (Schamberg et al., 2016).

During incursions, members of the WBp community were involved in 19 independent IGEs, for a total of 60 observation hours (or 22% of total observation time while in the EBp core ranging area; Table S1). The duration of encounters ranged from 0.33 to 7.67 h and lasted $\text{mean} \pm \text{SD} = 3.3 \pm 2.2$ h. Two pregnant females remained apart from the rest of the community during the study period and were never observed during incursions or IGEs. The two lowest ranking males were present during incursions but were either not observed at all, or only observed once during IGEs. All other community members were observed in a median of 15.5 IGEs (range 2–19). During IGEs, WBp adults were involved in 39 independent aggressive incidents, of which 64% ($N=25/39$ events) involved out-group members. Out-group aggression included 10 large-scale coalitionary aggressive events, which occurred during 47% of encounters (9/19 IGEs). One IGE involved two independent coalitionary aggressive events, separated by 1.5 h of tolerant inter-community association. Out-group coalitionary aggression involved the majority of WBp adults present, targeted both males and females from the EBp community, and persisted for several minutes. Following three coalitionary intercommunity aggressions, female members of the EBp community who had been involved in the aggression were observed with wounds (Table S1). During one incident, several WBp females targeted an EBp female, May, and hit and bit her repeatedly while she tried to protect her young infant. After that encounter, May had cuts on her swelling, although her infant appeared uninjured. Following two other coalitionary aggressions, EBp female Pem was observed with wounds, including in one case a deep wound on her sexual swelling (Fig. S1). We presumed that these wounds were incurred during the aggression, although we did not directly witness this. No WBp community members were observed wounded following aggressive events.

The majority of out-group coalitionary aggression (70%, 7/10 events) occurred in feeding trees, primarily when members of one or both communities were feeding on *Dialium* sp. ($N=6$ events). However, there were also numerous occasions when members of both communities co-fed in *Dialium* trees without any aggressive interactions (Table S1), so the specific triggers of large-scale aggression remain unclear. In addition to the coalitionary out-group aggression, there were 15 dyadic out-group aggressive interactions involving a WBp individual with either a same-sex ($N=6$

events) or opposite-sex (N=9 events) out-group target. Dyadic out-group aggression also occurred in a range of contexts, including immediately following intercommunity fusions and while feeding, resting, or traveling.

During IGEs, WBP subjects were involved in 21 copulations, of which 71% (N=15/21 copulations) occurred with EBP community members. There were 50 same-sex sexual interactions, of which 56% (N=28/50 interactions) occurred with EBP individuals. Female same-sex sexual interactions (GG-rubbing and other genital contact) accounted for all of the same-sex sexual interactions with out-group members, and all but one of the same-sex sexual interactions among in-group members during IGEs. Affiliative social interactions included out-group grooming, which occurred during seven IGEs over 103 observation minutes (3% of IGE observation time) and out-group food-sharing, which occurred during two IGEs (Table S1).

Testing the ecological needs hypothesis

Comparison of fruit availability (ECO 1): The density and basal area of trees of confirmed bonobo food species were similar between habitats on the west and west of the Bompusa stream (312 trees/ha, with a basal area of 30.78 m²/ha in the west vs. 300 trees/ha, with a basal area of 35.93 m²/ha in the east; Tables S2 and S3). However, during the survey period FAI scores were higher on plots in the east (predicted mean FAI score on plots in the east=0.47, 95% CI=0.26–0.68) compared with plots in the west (predicted mean FAI score on plots in the west=0.24, 95% CI=0.10–0.40, $p_{\text{East}>\text{West}}=0.95$; Table 3).

Comparison of fruit consumption (ECO 2): The WBP bonobos also differed in their dietary selection based on their location. When in the EBP ranging area, bonobos spent a greater proportion of their daily feeding time on fruits (predicted probability of feeding on fruit when in the east: mean=0.43, 95% CI=0.38–0.49), than when in their own ranging area (predicted probability of feeding on fruit when in the west: mean=0.30, 95% CI=0.26–0.36, $p_{\text{East}>\text{West}}=1.00$; Table 4). Neither sex nor dominance rank influenced the proportion of fruit consumed (Table 4).

Comparison of activity patterns during baseline and incursions (ECO 3): WBP individuals spent less time feeding (predicted probability of feeding during incursions: mean=0.39, 95% CI=0.35–0.43, $p_{\text{Baseline}>\text{Incursion}}=1.00$) and more time resting (predicted probability of resting during incursions: mean=0.32, 95% CI=0.29–0.35, $p_{\text{Baseline}<\text{Incursion}}=1.00$) during incursions in the East compared with when in their own ranging area (predicted probability of feeding during baseline:

Table 3 Model estimates of the fruit availability index (FAI) at LuiKotale in April 2017 in the Bompusa East bonobo community core ranging area compared with the Bompusa West bonobo community core ranging area (reference category)

Term	Est ± est. error	95% CI (lower, upper)
Intercept	-1.16 ± 0.54	-2.19, -0.06
Habitat (East)	1.04 ± 0.62	-0.22, 2.22

Table 4 Model estimates of proportion of fruit in feeding scans of Bompusa West bonobos at LuiKotale from March–June 2017, when they were in the Bompusa East community core ranging area, in comparison with when in their own core ranging area

Term	Est \pm est. error	95% CI (lower, upper)
Intercept	-0.83 ± 0.12	$-1.07, -0.59$
Habitat (East) [†]	0.57 ± 0.10	$0.37, 0.77$
Sex (female) [‡]	-0.02 ± 0.08	$-0.18, 0.14$
Rank	0.09 ± 0.11	$-0.13, 0.31$

^{†,‡} Estimates refer to comparison with the reference categories:

[†] Bompusa West core ranging area.

[‡] Male.

mean = 0.51, 95% CI = 0.47–0.55; predicted probability of resting during baseline: mean = 0.22, 95% CI = 0.20–0.25; Fig. 2; Table S4). However, WBp bonobos also spent more time moving during incursions (predicted probability of moving during incursions = 0.22, 95% CI = 0.19–0.25) compared with when in their core ranging area (predicted probability of moving during baseline = 0.17, 95% CI = 0.14–0.20; $P_{\text{Baseline} < \text{Incursion}} = 1.00$; Fig. 2; Table S4).

Evaluating the intercommunity dominance and tolerance hypotheses

Responses to encounters with members of different communities (ICD/ICT 1): During IGEs, WBp bonobos were involved in more aggressive events with out-group individuals (median = 3, range = 0–10) than with in-group individuals (median = 0.5, range = 0–6, Wilcoxon, $T^+ = 136$, $N = 16$ (3 ties), $P < 0.0001$). If aggression occurred randomly following IGEs, we would expect WBp individuals to be more frequent targets, given that there were typically more WBp than EBp individuals present at each IGE. Out-group aggression often involved large-scale coalitions (10/25 events, 40% events) and sometimes involved physical contact (7/25 events, 28%), resulting in three observed injuries to EBp individuals. In comparison, in-group aggression during IGEs was less intense, with 92.8% of events ($N = 13/14$) consisting of dyadic noncontact aggression, such as displays or chases.

In contradiction to ICT 1, WBp bonobos were less likely to maintain close proximity to members of joining parties when the parties consisted of EBp individuals (predicted probability of tolerant post-fusion association with out-group member: mean = 0.05, 95% CI = 0.00–0.23) compared with fusions with other WBp individuals (predicted probability of tolerant post-fusion association with in-group member: mean = 0.47, 95% CI = 0.00–0.95, odd's ratio [OR] for probability of tolerant post-fusion association with out-group vs. in-group members = 0.12, 95% CI = 0.00–0.40, $P_{\text{OR} < 1} = 0.98$; Table 5).

Immediate outcomes of inter-group aggressive conflicts (ICD/ICT 2), and impacts of conflicts on intergroup associations (ICD/ICT 3): Of the eight cases of coalitionary aggression where data on party composition were complete for both

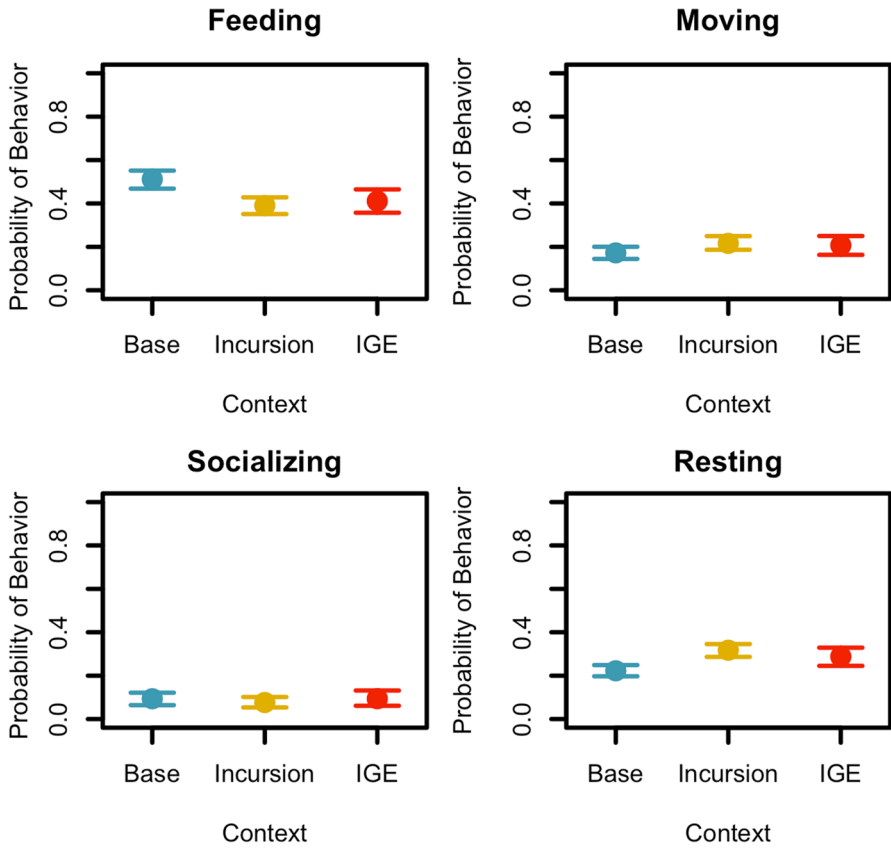


Fig. 2 Activity patterns of Bompusa West (WBp) bonobos at LuiKotale from March- June 2017 in three contexts: 1) Baseline (Base): In the WBp core ranging area, 2) Incursion: In the Bompusa East (EBp) core ranging area, but without intergroup encounters (IGEs), and 3) IGE: In the EBp core ranging area during IGEs. The y-axis is the predicted probability of an activity scan showing a given behavior, points are mean probabilities and error bars represent the 95% credible intervals. For model results refer to Table S4

Table 5 Model estimates of the proportion of scans between March-June 2017 that Bompusa West bonobos at LuiKotale spent in close proximity to members of joining parties following fusions with in-group vs. out-group members

Term	Est ± est. error	95% CI (lower, upper)
Intercept	-0.23 ± 1.94	-4.30, 3.47
Fusion type (out-group) [†]	-3.70 ± 1.73	-7.23, -0.35
Sex (female) [‡]	0.17 ± 0.72	-1.23, 1.63
Obs. time (> 1 h) [§]	1.22 ± 1.57	-1.68, 4.54
No. in focal party	0.89 ± 0.72	-0.55, 2.38
No. in joining party	0.49 ± 0.77	-1.05, 2.00

^{†,‡,§} Estimates refer to comparison with the reference categories:

[†] In-group fusion.

[‡] Male member of focal party.

[§] Post-fusion observation lasts less than an hour.

communities, in seven cases the WBP community had a numerical advantage (mean = 1.4:1), and in the remaining case the two communities had equal numbers of mature party members present (Table 6). Immediate outcomes of intercommunity coalitionary aggression were generally consistent with imbalances in fighting power (ICD 2), in that the WBP community had the numerical advantage and also clearly dominated the EBP community in 75% (6/8) of the coalitionary aggressive events where full data on community composition were available, causing them to flee the encounter area. In the remaining two events the WBP community also numerically out-numbered the EBP community, but there was no clear winner and members of both communities remained in the same area immediately after the encounter (Table 6). Regardless of short-term outcomes, following 70% of all intercommunity coalitionary conflicts ($N=7/10$ events), some members of both communities reestablished contact and continued to associate together (Table 6).

Dyadic interactions accounted for 60% (15/25) of intergroup aggression. While the dominance relationships between the individuals involved were not always known, in three instances a low-ranking WBP male (Em or Ze) aggressed against and displaced a relatively high-ranking EBP female (May or Kim). Although our analyses only include aggression among mature individuals, on several occasions we also observed one or more WBP juveniles physically attack a mature EBP female (May and an unidentified female), causing the target to flee from the area (Table S1). These observations suggest that outcomes of dyadic intergroup aggression were not decided by differences in dominance relations between specific individuals involved.

Comparison of activity patterns during incursions and IGEs (ICD/ICT 4): Party sizes increased from mean \pm SD = 9.01 ± 3.85 WBP individuals during incursions to combined party sizes of mean \pm SD = 21.76 ± 3.79 WBP and EBP individuals during IGEs. The WBP bonobos spent slightly more time feeding (probability of feeding during IGEs: mean = 0.41, 95% CI = 0.36–0.46) and less time resting (probability of resting during IGEs: mean = 0.29, 95% CI = 0.25–0.33) during IGEs compared to incursions (probability of feeding during incursions: mean = 0.39, 95% CI = 0.35–0.43, feeding $P_{\text{IGE} > \text{INCURSION}} = 0.79$; probability of resting during incursions: mean = 0.32, 95% CI = 0.29–0.35, resting $P_{\text{IGE} < \text{INCURSION}} = 0.90$; Fig. 2; Table S4). However, proportion of time spent moving did not differ between IGEs (probability of moving during IGEs: mean = 0.21, 95% CI = 0.16–0.25) and incursions (probability of moving during incursions: mean = 0.22, 95% CI = 0.19–0.25, $P_{\text{IGE} > \text{INCURSION}} = 0.34$).

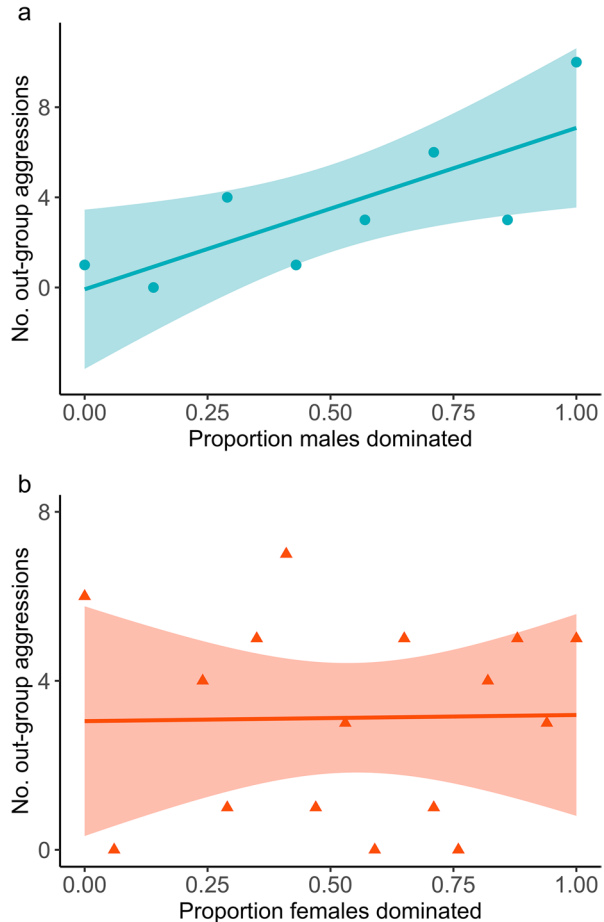
Influence of sex and rank on individual responses to IGEs

Of the WBP individuals present during incursions, 88% of males ($N=7/8$) and 81% of females ($N=13/16$) participated in out-group aggression. For males, rank was positively correlated with involvement in out-group aggression (Pearson, $r=0.77$, CI = 0.15–0.96, $t=2.96$, $df=6$, $P=0.02$; Fig. 3a), whereas for females there was no relationship between rank and involvement in out-group aggression (Pearson, $r=0.02$, CI = -0.48–0.51, $t=0.07$, $df=14$, $P=0.94$; Fig. 3b).

Table 6 Details of bonobo intercommunity coalitionary aggressive events at LuiKotale from March-June 2017. The number of mature individuals from both communities who were present immediately before the aggression are indicated

Date	WBp Males	WBp Females	WBp Total	EBp Males	EBp Females	EBp Total	Ratio of WBp Total / EBp Total	Immediate outcome of aggression	Post-aggression impact on intergroup association
20-Mar-17	5	13	18	5	8	13	1.38	West wins	IGE ends
28-Mar-17	3	10	13	2	6	8	1.63	West wins	IGE continues
28-Mar-17	4	9	13	3	3	6	2.17	No winner	IGE continues
2-Apr-17	4	12	16	5	10	15	1.07	No winner	IGE continues
4-Apr-17	6	12	18	no data	no data	no data	no data	West wins	IGE ends
5-Apr-17	5	10	15	no data	no data	no data	no data	West wins	IGE continues
7-Apr-17	4	10	14	5	9	14	1	West wins	IGE continues
7-Apr-17	5	11	16	5	10	15	1.07	West wins	IGE continues
8-Apr-17	5	12	17	5	7	12	1.42	West wins	IGE ends
18-Apr-17	4	10	14	5	4	9	1.55	West wins	IGE continues

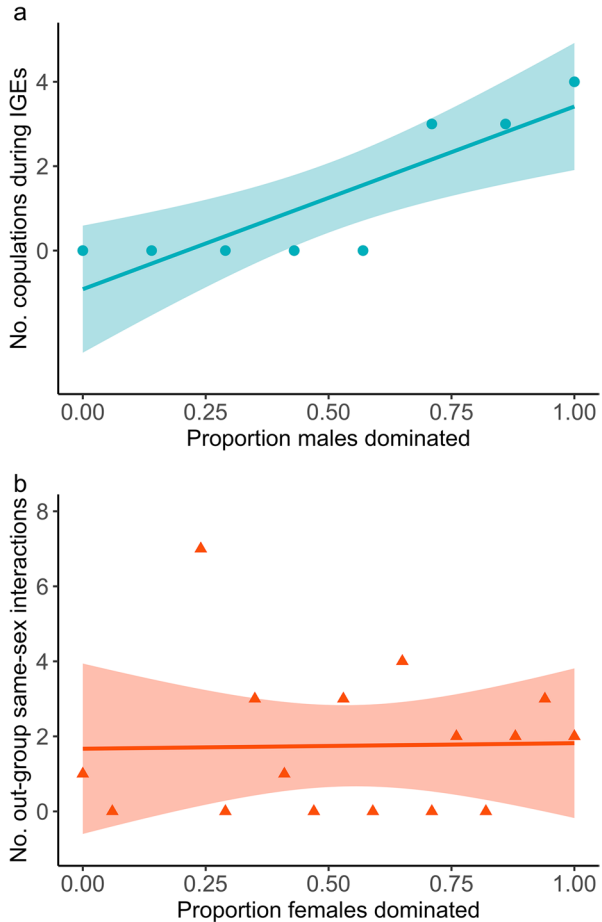
Fig. 3 Relationship between same-sex dominance rank and involvement in out-group aggression for Bompusa West bonobo males (**a**, indicated with circles) and females (**b**, indicated with triangles), at LuiKotale from March–June 2017. Plots indicate regression lines and 95% confidence intervals



Male dominance rank also predicted out-group copulation success during IGEs (Pearson, $r=0.77$, $CI=0.15-0.96$, $t=2.99$, $df=6$, $P=0.02$; Fig. 4a). Although all WBp males were present during some incursions, several lower-ranking males avoided IGEs, and the three top-ranking males were responsible for all of the out-group as well as in-group copulations during IGEs. However, there was no direct relationship between male aggression and copulation success (Pearson, $r=0.46$, $CI=-0.36-0.88$, $t=1.29$, $df=6$, $P=0.25$), because several low-ranking males were involved in out-group aggression (Fig. 3a) but were never observed copulating during IGEs. There also was little evidence that the three top-ranking WBp males used aggressive tactics to obtain copulations during IGEs. There was no aggression observed in the 15-min periods preceding the four out-group copulations that WBp males were involved in, and aggression occurred only once in the 15-min periods before the 7 in-group copulations that WBp males were involved in.

Of the WBp females who were present during incursions, 31% ($N=5/16$) were observed copulating with out-group males. Of these females, four were cycling

Fig. 4 Relationship between same-sex dominance rank of Bompusa West bonobos at LuiKotale and participation during inter-group encounters (IGEs) in (a) copulations with in-group or out-group partners for males, indicated with circles and (b) same-sex sexual interactions with out-group partners for females, indicated with triangles. Plots indicate regression lines and 95% confidence intervals. Data are from March–June 2017



and they were responsible for all but one of the WBp female out-group copulations (10/11 copulations; Table S5). In contrast to males, rank did not influence access to out-group copulation partners for females (Pearson, $r = -0.05$, $CI = -0.54-0.45$, $t = -0.21$, $df = 14$, $P = 0.83$). Of females present during incursions, 63% ($N = 10/16$ females) had sexual interactions with out-group females, and access to out-group partners for same-sex sexual interactions was also not related to female dominance rank (Pearson, $r = 0.02$, $CI = -0.48-0.51$, $t = 0.09$, $df = 14$, $P = 0.93$; Fig. 4b).

During the 3-month study period, four females transferred from the WBp to the EBp community (Table 2). Three cases involved first time transfer events of natal juvenile females between 7–8 years of age, who left the WBp community within three days of each other and associated with members of the EBp community for short periods of time, from days to weeks, in some cases moving back and forth multiple times between the two communities. All three of these females returned to the WBp community in the short-term but permanently transferred from the WBp community in the subsequent years (B. Fruth, unpublished data). In the fourth case,

a mature low-ranking female (Ev) who had emigrated from the EBp community to the WBp community shortly before the study returned to the EBp community. In contrast to the relatively fluid movement of WBp females between the two communities during this brief study period, in the entire year before this study, there were no confirmed short- or long-term transfers of WBp females from the WBp community, and only two transfers of out-group females to the WBp community. On one occasion, an unknown female transferred into the WBp community during an IGE with an unidentified community and then disappeared after 1 month. The other case involved the first time transfer described above of the female Ev from the EBp to the WBp community, which occurred outside of an IGE.

Discussion

Responses to IGEs by nonhuman primate species are highly variable across groups and among individuals, due to socioecological factors and individual attributes that influence the cost–benefit tradeoffs of adopting more competitive or tolerant strategies (Majolo et al., 2020; Pisor & Surbeck, 2019). Among bonobos as well, research from an increasing number of field sites and communities indicates the potential for high levels of out-group aggression and cooperation, sometimes even within the same encounter (Hohmann & Fruth, 2002; Tokuyama et al., 2019). Overall, our results suggest that incursions by the WBp bonobo community into the EBp core ranging area during the study period were driven by temporal variation in local food availability, consistent with ecological need. Responses to IGEs primarily supported inter-community dominance (ICD 1, ICD 2, and partial support for ICD 4). The WBp community clearly dominated the EBp community during most instances of coalitionary intergroup aggression, displacing them from preferred areas and causing several injuries. The lack of increased movement by WBp individuals during IGEs in comparison with incursions also is consistent with competitive exclusion of out-group individuals from feeding areas. However, there also was some support for intercommunity tolerance (ICT 3 and partial support for ICT 4). Members of the different communities often reformed associations following out-group coalitionary aggression, and prolonged associations facilitated out-group social interactions that benefitted females and high-ranking males. During IGEs, WBp bonobos traveled in larger party sizes and spent more time feeding and less time resting compared with incursions, all of which is consistent with increased scramble competition during associations with out-group members.

Although the two habitats did not differ in the density or basal area of confirmed bonobo food species, phenological and behavioral data indicate that during the study period, WBp bonobos had greater access to fruit foods while in the EBp ranging area. Such micro-habitat variation in fruit availability is consistent with previous phenological surveys at LuiKotale (Hohmann et al., 2006). The WBp bonobos also spent less time feeding and more time resting during incursions than when in their core ranging area, both of which are consistent with consumption of higher quality foods. The combined evidence thus indicates an ecological explanation for the shift in ranging during the study period. This study occurred over a short period, and further data are needed to determine whether periods of increased IGE frequency

at LuiKotale are related to ecological need more generally. Analyses over longer periods at the Wamba and Kokolopori bonobo field sites indicate that IGEs increase during times of habitat-wide high food availability (Lucchesi et al., 2020; Sakamaki et al., 2018). However, neither study directly compared food availability or food intake of bonobo communities while in their more exclusive core ranging areas vs. in the areas of frequent IGEs, so it is possible that microhabitat differences in food availability at these sites may have influenced ranging patterns and increased the likelihood of encounters.

Although we were not able to observe all social interactions during IGEs, our method of recording 15-min instantaneous scan samples from all visible group members should be representative of WBP bonobo responses to out-group individuals during one period of intensive IGEs. During IGEs, WBP bonobos biased their aggression towards out-group individuals and exhibited a greater intensity of aggression, including several occurrences of large-scale coalitionary aggression. Consistent with their absolute differences in community size, WBP parties almost always out-numbered EBP parties during IGEs, and showed evidence of inter-group dominance in displacing EBP parties from resources. The fact that WBP parties did not always win in intergroup conflicts, despite their numerical advantage, is not entirely inconsistent with intergroup dominance, which also predicts that independently of their size, groups defending their core ranging area may be more motivated to fight and more likely to win in IGEs (reviewed in Majolo et al., 2020). However, the aggressive responses observed here did differ in several ways from patterns typically associated with intergroup dominance in chimpanzees. Aggression never escalated to the level of lethal injuries that are sometimes observed during chimpanzee IGEs (reviewed in Wilson et al., 2014), although imbalances in power among these two bonobo communities during conflicts (max = 2:1) did not reach the stark contrasts reported during some lethal raids among chimpanzees (median ratio for attackers relative to victims = 8:1; Wilson et al., 2014). On one occasion we found a single EBP female in association with a WBP party, but soon afterwards they fused with an EBP party that was nearby. Thus, it remains unclear whether WBP bonobos would respond more aggressively in out-group interactions under more extreme imbalances in fighting power and when encountering lone individuals.

While evidence from the majority of chimpanzee study sites (reviewed in Wilson et al., 2014) and from bonobos at Wamba (Tokuyama et al., 2019) and Kokolopori (Cheng et al., 2021), suggests that males are more frequently involved in out-group aggression than females, at LuiKotale the imbalances in fighting power between the WBP and EBP communities were primarily due to the greater relative number of mature females in the WBP community. Moreover, we found that WBP females of all dominance ranks were involved in out-group aggression, suggesting that the costs of increased aggression during IGEs were more evenly shared among females. In contrast, rank positively predicted involvement in out-group aggression for males. The three highest-ranking males also monopolized mating success during IGEs, although male aggression did not directly predict male mating success, and there was little evidence that out-group mating was associated with coercion, as can occur during IGEs in chimpanzees (Boesch et al., 2008). More research is needed

to determine how community demographics and individual characteristics influence the frequency and severity of intergroup aggression in bonobos.

There also was some support for inter-community tolerance. Despite evidence that responses to IGEs were more aggressive than tolerant, more often than not following large-scale coalitionary conflicts some members of the winning and losing sides rejoined each other and continued to associate together, which is rarely reported in other primate species (e.g., spider monkeys: Aureli et al., 2006; chimpanzees: Crofoot & Wrangham, 2010; capuchins: Crofoot, 2013; Scarry, 2013). Decisions to remain in association following out-group aggression may be influenced by individuals who stand to benefit more through prolonged IGEs. These individuals include nulliparous females, based on the fluid short-term transfers (or visits) of three juvenile females, and the secondary transfer of one mature, nulliparous female (Ev), coinciding with this period of increased IGEs. At Wamba, there also is evidence that IGEs facilitate short-term visits between females from different communities (Sakamaki et al., 2015). The ability to flexibly transfer between communities multiple times within the context of tolerant IGEs may be an important part of the process by which young female bonobos make permanent dispersal decisions (reviewed in Sakamaki et al., 2015) and may reduce the numerous risks associated with female dispersal for primates more generally (Kahlenberg et al., 2008; Lee & Strier, 2015).

Our results also suggest that prolonged IGEs can provide social benefits for high-ranking males, who monopolized in-group and out-group copulations during IGEs. High-ranking males at LuiKotale and Wamba are able to effectively monopolize paternity within their own communities (Ishizuka et al., 2018; Surbeck et al., 2017), and our data suggest that they may also be more attractive to out-group females, although there is as yet little evidence for intercommunity paternity in bonobos. The majority of WBP females had socio-sexual interactions with out-group females, who represent potential out-group cooperation partners for food sharing (this study; Fruth & Hohmann, 2018) and for out-group coalitionary support against males (Tokuyama et al., 2019). Given the high social status of females within their own groups, the potential contribution of female intercommunity alliances to maintaining inter-group relations deserves more attention (Furuichi, 2011). One form of inter-group cooperation that is commonly observed in humans is reciprocal resource buffering, in which groups tolerate out-group presence in their ranging area during times of local abundance, and in turn are able to access out-group resources during times of local shortfall (reviewed in: Jaeggi et al., 2016; Robinson & Barker, 2017). Given that we analyzed only a brief period of one-sided encounters, we could not directly test for this form of inter-community cooperation at LuiKotale. However, the evidence that this frequent period of incursions did provide access to better food for WBP bonobos, that most IGEs were characterized by prolonged associations and affiliative interactions, and that tolerant incursions have been observed in the reverse direction at this same study site (Fruth & Hohmann, 2018), is suggestive of reciprocal resource buffering at LuiKotale and highlights an important area for further research using long-term data.

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Declarations

Conflict of interest statement The authors declare that they have no conflicts of interest.

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