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Original Article

Gregariousness, foraging effort, and affiliative interactions in lactating bonobos and chimpanzees

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Fission–fusion dynamics have evolved in a broad range of animal taxa and are thought to allow individuals to mitigate feeding competition. While this is the principal benefit of fission–fusion, few studies have evaluated its costs. We compared gregariousness, foraging budgets, and social budgets between lactating bonobos and chimpanzees from wild populations to evaluate potential costs. Both species exhibit fission–fusion dynamics, but chimpanzees, particularly in East African populations, appear to experience higher feeding competition than bonobos. We expected lactating chimpanzees to be less gregarious than lactating bonobos; reduced gregariousness should allow lactating chimpanzees to mitigate the costs of higher feeding competition without requiring more foraging effort. However, we expected the reduced gregariousness of lactating chimpanzees to limit their time available for affiliative interactions. Using long-term data from LuiKotale bonobos and Gombe chimpanzees, we found that lactating chimpanzees were indeed less gregarious than lactating bonobos, while feeding and travel time did not differ between species. Contrary to our predictions, lactating females did not differ in social interaction time, and lactating chimpanzees spent proportionately more time interacting with individuals other than their immature offspring. Our results indicate that lactating chimpanzees can maintain social budgets comparable to lactating bonobos despite reduced gregariousness and without incurring additional foraging costs. We discuss potential explanations for why lactating bonobos are more gregarious.

Key words: **bonobos, chimpanzees, feeding competition, fission–fusion, predation risk, sociality**

INTRODUCTION

A major goal in the study of behavioral ecology is to understand the evolution of group living under different ecological conditions (Wilson 1975; Maynard Smith and Szathmary 1997). Extensive research demonstrates that one of the primary benefits of group living is enhanced predator detection, dilution, and/or defense capabilities, while one of the major costs of group living is increased competition for food resources (reviewed in Ward and Webster 2016). Costs associated with feeding competition are particularly salient to mammalian females, given that food generally limits female reproductive success more so than males' (Trivers 1972).

Due to intragroup feeding competition, foraging effort is a function of group size: individuals living in permanently cohesive social groups experience reduced feeding efficiency as the number of intragroup competitors increases (Beauchamp 2012; Markham et al. 2015). Therefore, females in many social species cope with the high energetic requirements of lactation principally by allocating more time to foraging effort (e.g., *Lasiurus cinerus*: Barclay 1989; *Peromyscus maniculatus*: Hammond and Kristan 2000; *Odocoileus virginianus*: Therrien et al. 2008; *Myotis lucifugus*: Dzal and Brigham 2013; *Enhydra lutris nereis*: Thometz et al. 2016). However, any increase in time dedicated to foraging effort must come at the expense of time allocated to other activities (Dunbar et al. 2009), as is the case in numerous vertebrate taxa (e.g., *Octodon degus*: Ebensperger and Hurtado 2005; *Oreamnos americanus*: Hamel

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and Côté 2008; *Rhinopithecus bieti*: Xiang et al. 2010; *Morus capensis*: Rishworth et al. 2014). One activity that may be sacrificed to provide more time for foraging is affiliative social interactions; however, such interactions play an important role in maintaining social bonds in many group-living animals. Indeed, a growing body of research highlights the positive relationship between social bond strength and fitness across taxa (e.g., *Papio cynocephalus*: Silk et al. 2003; *Equus ferus caballus*: Cameron et al. 2009; *Tursiops aduncus*: Stanton and Mann 2012; *Crotophaga major*: Riehl and Strong 2018). Thus, sacrificing time for social interactions may carry costs in some taxa.

Fission–fusion social systems present additional means through which lactating females may mitigate feeding competition. Fission–fusion societies are characterized by fluid subgrouping patterns (Aureli et al. 2008) and have been described for diverse taxa (Couzin 2006), such as guppy shoals (*Poecilia reticulate*; Kelley et al. 2011), sand tiger sharks (*Carcharias taurus*; Haulsee et al. 2016), common ravens (*Corvus corax*; Loretto et al. 2017), African lions (*Panthera leo*; Mbizah et al. 2019), and Cape buffalo (*Syncerus caffer caffer*; Wielgus et al. 2020). High fission–fusion dynamics are hypothesized to allow individuals to adjust subgroup size and composition in response to fluctuations in food availability and their own energetic requirements. Thus, females can mitigate the energetic costs of lactation by altering their grouping patterns to maintain energy balance without substantial increases in foraging effort, while also grouping when possible to maximize predator defense and social opportunities. However, this raises the question of whether fission–fusion dynamics impact the extent to which lactating females suffer from increased predation and/or reduced social interactions. By ranging alone or in smaller subgroups, lactating females may not need to increase foraging effort, but they may be more vulnerable to predators and/or their social activity may be constrained as a result of spending less time in the presence of group members.

The genus *Pan* provides a comparative framework through which to focus on the social costs of fission–fusion dynamics while discounting potential effects of predation risk. The two great ape species that comprise *Pan*, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), share a recent phylogenetic history (Prüfer et al. 2012) and several core morphological and behavioral traits. In particular, both species are characterized by a relatively large body size when compared to most other primate species, as well as a largely arboreal lifestyle (Fleagle 2013); these traits are hypothesized to reduce vulnerability to their most likely predator, African leopards (*Panthera pardus pardus*; Isbell 1994; Janson and Goldsmith 1995; Zuberbühler and Jenny 2002). Indeed, evidence for leopard predation on bonobos and chimpanzees is rare (for all inferred cases of leopard predation in *Pan*, see Boesch 1991; Furuichi 2000; Zuberbühler and Jenny 2002; D'Amour et al. 2006; Pierce 2009; Nakazawa et al. 2013), despite extensive evidence of leopard predation on monkeys (reviewed in Isbell 1994), including at study sites where leopard predation on chimpanzees has been documented and deemed rare (e.g., Nakazawa 2020).

Despite broad similarities in morphology and social organization between bonobos and chimpanzees, they appear to face different levels of feeding competition and starkly different patterns of female social behavior (reviewed in Gruber and Clay 2016). Stable isotope analyses of hair samples from multiple *Pan* research sites across tropical Africa indicate clear species differences in the stability of food resources (Oelze, Fahy, et al. 2016). Stable isotope ratios provide a reliable proxy for diet because the isotopic characteristics of food components are incorporated into consumers' tissue in a predictable manner (Kohn 1999). Bonobos exhibit less variation in stable isotope ratios over time when compared to chimpanzees, indicating that bonobo diet composition is more stable, that is, less seasonal, than that of chimpanzees (Oelze, Douglas, et al. 2016; Oelze, Fahy, et al., 2016). Additionally, individual variation in females' stable isotope ratios did not vary based on dominance rank in bonobos (Oelze, Douglas, et al. 2016), whereas several studies have demonstrated variation in diet quality based on dominance rank in chimpanzees (e.g., Murray et al. 2006). These patterns strongly suggest that feeding competition is more intense in chimpanzees than in bonobos.

Reduced feeding competition among female bonobos may facilitate what appears to be a general pattern of high female gregariousness across several long-term study sites (Wamba: Furuichi 2009; LuiKotale: Moscovice et al. 2017; Lomako: Hohmann and Fruth 2002; Waller 2011). This high gregariousness may, in turn, facilitate the high degrees of intrasexual affiliative social behavior characteristic of female bonobos (Tokuyama and Furuichi 2016; Moscovice et al. 2017, 2019). In contrast, female gregariousness varies across chimpanzee populations. Females in some East African chimpanzee populations (*P*an troglodytes *schweinfurthii*) tend to be highly solitary, frequently ranging alone with their immature offspring in order to mitigate costs associated with exceptionally high feeding competition and seasonality (Wrangham and Smuts 1980). In other East African chimpanzee populations, females can be more gregarious (Wakefield 2008). Some female West African chimpanzee populations (*Pan troglodytes verus*) appear to experience reduced seasonality when compared to East African chimpanzees (Doran et al. 2002) and are more gregarious (Lehmann and Boesch 2008, 2009). What remains unclear is whether different patterns of fission–fusion dynamics differentially constrain the extent to which females can engage in affiliative social interactions because direct comparisons of gregariousness and social budgets have not been conducted in the two *Pan* species. While a study evaluating within-population variation in dyadic association strength across *Pan* populations found clear species differences that are in line with putative species differences in gregariousness, they did not make direct comparisons between the populations (Surbeck et al. 2017).

In this study, we compared gregariousness, foraging budgets, and social budgets of lactating females in wild populations of bonobos and chimpanzees. The lactation period represents the female life-history stage when energetic demands are highest and, thus, when constraints on social interactions should be most pronounced. Here, we compared the LuiKotale bonobo population to the Gombe East African chimpanzee population. LuiKotale is characterized by low seasonality, extensive primary forest, and modest resource competition (Hohmann et al. 2012; Oelze, Douglas, et al. 2016; Oelze, Fahy, et al. 2016; Nurmi et al. 2018), while Gombe appears to be characterized by high seasonality and heterogeneity in habitat structure (Wrangham and Smuts 1980; Williams et al. 2002; Murray et al. 2006). We hypothesized that lactating chimpanzees at Gombe are less gregarious than lactating bonobos at LuiKotale due to higher feeding competition at Gombe. We further hypothesized that reduced gregariousness constrains the social interaction budgets of lactating chimpanzees; while being less gregarious may allow lactating chimpanzees to maximize foraging efficiency, they may then be limited in the extent to which they can engage in social interactions. Based on this hypothesis, we predicted that the amount of time that lactating females spend engaged in feeding and travel does not differ between species but that lactating chimpanzees spend less time in groups and less time engaged in affiliative social interactions. We first compared gregariousness by evaluating the proportion of time that lactating females spend ranging alone with their immature offspring. We then compared the amount of time that lactating females spend engaged in feeding, travel, and affiliative social interactions and how lactating females allocate their affiliative social interactions.

MATERIALS AND METHODS

Study site and subjects

Data were collected on the Bompusa West bonobo community at LuiKotale, Democratic Republic of the Congo, and on the Kasekela chimpanzee community at Gombe, Tanzania. All bonobos and chimpanzees included in our study were habituated to human observation. Maternal relatedness is known for all individuals from observations and genotyping. During the study periods, the Bompusa West community included up to 54 individuals and the Kasekela community included up to 68 individuals. We focused our analyses on lactating females whose youngest infants were less than 4.5 years of age as this is the average age by which infants in wild populations of both species are nutritionally weaned based on stable isotope analyses (~4 years based on δ^{15}N and ~5 years based on δ^{13}C in both species: Ngogo chimpanzees: Bădescu et al. 2017; LuiKotale bonobos: Oelze et al. 2020). This age range also overlaps with the average weaned age derived from data on suckling behavior in our chimpanzee study population (4.7 years: (Lonsdorf et al. 2020). We used approximate periods of lactation because precise ages of weaning are likely to vary (e.g., Borries et al. 2014) and are not known for the majority of individuals in our sample. We pooled data on lactating females into three age classes based on the age of their youngest infant (0 < 1.5, 1.5 < 3, and 3 < 4.5 years), given that lactating female energetic requirements may vary based on the stage of infant development (see Emery Thompson et al. 2012).

Predictions

We tested three predictions: 1) Lactating chimpanzees spend more time alone with their immature offspring than do lactating bonobos; 2) lactating females of the two species do not differ in feeding or travel time; and 3) lactating bonobos spend more time engaged in social interactions, particularly with individuals other than their immature offspring.

Time spent alone

At both study sites, the total number of individuals ranging in subgroups (hereafter, "parties") and their identities are recorded systematically. Party scan data on lactating females are recorded during focal follows (see next section for a description of focal follows) at regular intervals and represent all individuals observed in the party during that interval; researchers record party scans every hour at LuiKotale and every 15 min at Gombe. To make party scan data comparable between sites, we aggregated all party scans over a given hour at Gombe and used the aggregated on-the-hour party scan in our analyses. We only included lactating females for which at least 20 h of party scans were available for a given infant age class (Table 1). We took several additional steps to ensure that data from both study sites are comparable. First, we used contemporaneous data from both sites, starting in July 2011, when two coauthors (C.M.M. and E.V.L.) hired several new field staff to collect data at Gombe and conducted extensive training to ensure that data collection remained consistent despite a change in field staff. Long-term party scan data were available from LuiKotale for the same period. We thus included party scan data from July 2011 through November 2016 for both study sites. Second, because the Gombe party scan data set is larger than the LuiKotale data set due to more field researchers collecting data at Gombe, we used the sample function in base R version 4.0.2 (R Core Team 2020) to randomly subsample on-the-hour party scans from Gombe without replacement to match the LuiKotale party scan sample size based on the number of lactating females, infant sex, and infant age class. For example, if we had 10 total on-the-hour party scans from two lactating bonobos, each with one female infant in the 0 < 1.5 infant age class, we subsampled the Gombe data such that we had approximately 10 total on-the-hour party scans from two lactating chimpanzees, each with one female infant in the 0 < 1.5 infant age class.

Table 1
Party scan sample size

Infant age class	Bonobo female	Bonobo male	Chimpanzee female	Chimpanzee male
0 < 1.5	2 | 78	4 | 238	2 | 78	4 | 238
1.5 < 3	3 | 318	1 | 79	4 | 318	1 | 79
3 < 4.5	3 | 243	1 | 25	4 | 243	1 | 25

Number of lactating females | number of on-the-hour party scans.

We measured gregariousness of lactating females as the proportion of party scans in which the lactating female was alone with her immature offspring, which we defined as offspring younger than 12 years of age. This definition for immature offspring is consistent with previous research on both of our study populations (e.g., Murray et al. 2006; Surbeck et al. 2011; Stanton et al. 2014; Markham et al. 2015) and a recent study indicating that chimpanzee offspring continue to associate with their mothers until 12 years of age (Stanton et al. 2020). We do not claim that 12 years of age and older qualifies as adult; rather, individuals below this age are predominantly immature. Thus, when a focal subject is alone with her immature offspring, that is, not in a party with other community members, we considered her to be "alone" in her own focal follow. Researchers attempt to remain with the focal subject at both study sites, regardless of party size.

Feeding, travel, and social interactions

In addition to party scan data, researchers collect detailed behavioral data during focal follows of a lactating female and her immature offspring. At Gombe, a given focal follow focuses on a lactating female and her two youngest offspring simultaneously and lasts from several hours to a full day; the goal is to collect at least 6 h of focal follow data on each focal subject during each month. However, focal follow lengths vary based on various uncontrollable factors, such as losing sight of the focal subject during poor weather conditions. At LuiKotale, a given focal follow focuses on a lactating female and one of her immature offspring at a time and are generally conducted for 1 h. Focal follows can be longer if the focal subject is alone with her immature offspring because researchers generally attempt to follow lone focal females continuously until she rejoins a larger party. These differences in focal follow duration and the number of immature offspring on which data are collected are due to practical constraints associated with focal following two immature bonobos simultaneously for extended durations, given that there are generally many immature bonobos present in parties and it can be very difficult to monitor multiple bonobos at once. However, to ensure consistency in our comparative analyses, the behavioral ethogram in place at LuiKotale was developed in collaboration with Gombe researchers and designed to be comparable by utilizing the same definitions for all behaviors of interest and by employing the same point sampling interval; behavioral data on the lactating female and her immature offspring are recorded during 1-min point samples and include the identity of social partners.

Despite using the Gombe protocol as a model to design the protocol at LuiKotale, we took additional steps to ensure that data are comparable between the two study sites. Focal follow data on bonobos were collected between July 2015 and July 2018; however, chimpanzee focal follow data were only available through November 2016. We thus utilized focal follow data on chimpanzees between November 2013 and November 2016 to match the number of years during which bonobo data were collected. Second, we again subsampled the larger Gombe data set to approximately match the LuiKotale sample size, again using the sample function in base R; however, instead of subsampling 1-min point samples, we subsampled 60 consecutive point samples from a given focal female. We did this so the Gombe subsample more closely resembled the sample of predominantly 1-h focal follows from LuiKotale. Lastly, we again restricted our analyses to lactating females for which at least 20 h of party scans were available for a given infant age class (Table 2). Good observations included those 1-min point samples in which the activity of the lactating female could be determined as opposed to bad observations in which the activity could not be determined due to poor visibility.

We used focal follow data to compare foraging and social budgets by analyzing the following behaviors (following Lonsdorf et al. 2014):

1. Feeding—ingestion of solid food.
2. Travel—continuous movement from one point to another.
3. Social interactions—engaging in either of the following behaviors:
   a. Social groom—parting of another individual's hair with hands, fingers, and/or lips and removal of debris or ectoparasites and/or receiving this behavior from another individual.
   b. Social play—nonaggressive interaction between two or more individuals that include one or more of the following: tickling, wrestling, chasing, kicking, rubbing, thrusting, biting, or pullin. May incorporate an object (e.g., tugging of sticks back and forth).

Table 2
Focal follow sample size

Infant age class	Bonobo female	Bonobo male	Chimpanzee female	Chimpanzee male
0 < 1.5	4 | 125	4 | 177	4 | 120	6 | 172
1.5 < 3	3 | 119	1 | 23	2 | 140	1 | 23
3 < 4.5	3 | 99	2 | 63	3 | 97	2 | 62

Number of lactating females | total focal follow observation time.

Statistical analyses

We conducted all analyses in R version 4.0.2 (R Core Team 2020) and RStudio version 1.3.1 (RStudio Team 2020) using the glmmTMB version 1.0.2 (Brooks et al. 2018), DHARMa version 0.3.2 (Hartig 2020), car version 3.0–9 (Fox et al. 2012), and emmeans version 1.5.0 (Lenth 2018) packages. To test our three predictions (described above), we fitted generalized linear mixed models (GLMMs) to each response variable (response variables for each prediction described below) using the glmmTMB function in the glmmTMB package with a beta-binomial error structure. We initially fitted GLMMs using binomial error structures but found that all models were overdispersed. Overdispersion occurs when variance is higher than predicted by the model because the model lacks an adjustable dispersion parameter (e.g., as in binomial and Poisson models; Bolker et al. 2009; Zuur et al. 2009). Beta-binomial models include an adjustable dispersion parameter that allows the model to predict variance appropriately for binomial proportion data (Harrison 2015). We reported results of nonparametric dispersion tests for all models using the testDispersion function (case sensitive) in the DHARMa package. None of our beta-binomial models exhibited overdispersion. We evaluated model assumptions by visually assessing quantile–quantile plots and the distribution of residuals plotted against fitted values using the simulateResiduals (case sensitive) function in the DHARMa package.

For all models, we first tested the interaction between species and infant age class. To determine the significance ($\alpha = 0.05$) of interaction effects, we conducted Wald chi-squared tests using the Anova (case sensitive) function in the car package (Kenward–Roger degrees of freedom [df] approximation and type III sum of squares). If the interaction between species and infant age class was not significant, we removed it and refitted the model using species and infant age class as independent fixed-effect predictors and conducted Wald chi-squared tests, again using the Anova function in the car package (Kenward–Roger df approximation and type II sum of squares). If the interaction between species and infant age class was significant, we conducted Tukey's pairwise post hoc comparisons between species within each infant age class using the emmeans function in the emmeans package. For all models, we included lactating female identity as a random effect because the same lactating female could be represented in multiple infant age classes.

To test our first prediction that lactating chimpanzees spend more time alone than lactating bonobos, we ran one set of models called Time Alone (here and below, we refer to one set of models as the interaction effect model followed by the refitted independent effects model if necessary). We calculated our response variable by dividing the number of party scans that a given lactating female was in a party alone with her immature offspring during each infant age class by the total number of party scans collected on that lactating female during that infant age class. We expected a significant interaction effect between species and infant age class or a significant effect of species, with lactating chimpanzees spending more time alone than lactating bonobos.

To test our second prediction that lactating females do not differ in feeding or travel time, we ran two sets of models called Feeding and Travel. We calculated our response variables by dividing the number of point samples that a given lactating female was engaged in feeding or travel, respectively, during each infant age class by the total number of good observations collected on that lactating female during that infant age class. We did not expect to find a significant interaction effect between species and infant age class nor a significant effect of species.

To test our third prediction that lactating bonobos spend more time engaged in social interactions, we ran two sets of models called Social Interactions and Adjusted Social Interactions. We calculated our response variable for social interactions by dividing the number of point samples that a given lactating female was engaged in social interactions during each infant age class by the total number of good observations collected on that lactating female during that infant age class. We calculated our response variable for adjusted social interactions by dividing the number of point samples that a given lactating female was engaged in social interactions with individuals other than her immature offspring during each infant age class by the total number of social interaction point samples collected on that lactating female during that infant age class.

RESULTS

In support of our first prediction, we found that lactating chimpanzees spent more time alone with their immature offspring than did lactating bonobos (Figure 1; Table 3). The interaction between species and infant age class was not significant in the model for time alone ($X^2 = 1.510$, df = 2, $P = 0.470$; Table 4), but when we tested independent effects of species and infant age class, species had a significant effect ($X^2 = 26.321$, df = 1, $P < 0.001$), while infant age class did not have a significant effect ($X^2 = 0.414$, df = 2, $P = 0.813$). The nonparametric dispersion tests were not significant for either Time Alone model (interaction effect model: deviance ratio = 0.957, $P = 0.960$; independent effects model: deviance ratio = 1.002, $P = 0.928$).

In support of our second prediction, lactating females of the two species did not differ in feeding time (Figure 2) or travel time (Figure 3; Table 3). The interaction between species and infant age class was not significant in the model for feeding ($X^2 = 4.359$, df = 2, $P = 0.113$) or travel ($X^2 = 0.850$, df = 2, $P = 0.654$; Table 4). When we tested independent effects of species and infant age class, species was not significant in either model (feeding: $X^2 = 0.032$, df = 1, $P = 0.857$; travel: $X^2 = 1.334$, df = 1, $P = 0.248$). However, infant age class had a significant effect in both models (Feeding: $X^2 = 8.379$, df = 2, $P = 0.015$; Travel: $X^2 = 7.153$, df = 2, $P = 0.028$); lactating females with older infants fed more (Figure 2) and traveled more (Figure 3; Table 3). The nonparametric dispersion tests were not significant for either Feeding model (interaction effect model: deviance ratio = 1.066, $P = 0.496$; independent effects model: deviance ratio = 1.146, $P = 0.216$) or for either Travel model (interaction effect model: deviance ratio = 0.859, $P = 0.200$; independent effects model: deviance ratio = 0.895, $P = 0.328$).

Against our third prediction, lactating females of the two species did not differ in time engaged in social interactions with any community member (Figure 4), and lactating chimpanzees spent proportionately more of their social interaction time interacting with individuals other than their immature offspring (Figure 5; Table 3). The interaction between species and infant age class was not significant in our model for social interactions ($X^2 = 0.870$, df = 2, $P = 0.647$) or for adjusted social interactions ($X^2 = 3.702$, df = 2, $P = 0.157$; Table 4). When we tested independent effects of species and infant age class in the model for social interactions, neither species ($X^2 = 0.266$, df = 1, $P = 0.606$) nor infant age class ($X^2 = 2.745$, df = 2, $P = 0.253$) had significant effects. When we tested independent effects of species and infant age class in the model for adjusted social interactions, species had a significant effect ($X^2 = 12.998$, df = 1, $P < 0.001$) while infant age class did not have a significant effect ($X^2 = 0.082$, df = 2, $P = 0.960$). The nonparametric dispersion tests were not significant for either social interactions model (interaction effect model: deviance ratio = 1.066, $P = 0.608$; independent effects model: deviance ratio = 1.043, $P = 0.704$) or adjusted social interactions model (interaction effect model: deviance ratio = 0.988, $P = 1.000$; independent effects model: deviance ratio = 0.977, $P = 0.984$).

DISCUSSION

Many studies across animal taxa indicate that fission–fusion dynamics allow individuals to reduce feeding competition by adjusting the size and composition of the subgroups that they range in (e.g., *Tursiops aduncus*: Heithaus and Dill 2002; *Ocaella heinsohni* and *Sousa chinensis*: Parra et al. 2011; *Macropus giganteus*: Favreau et al. 2018; *Giraffa camelopardalis*: Bond et al. 2019; *Neophron percnopterus majorensis*: van Overveld et al. 2020). Given that feeding competition generally increases with increasing group size, females in fission–fusion societies can offset the high energetic costs of lactation by reducing

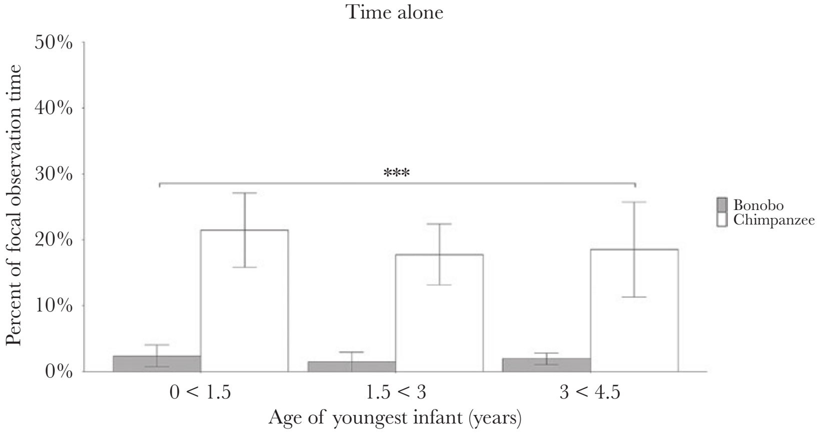

Figure 1

Mean ± standard error percentage of time that lactating females spent ranging in parties with only their immature offspring. Note: This figure and all following figures represent raw data; asterisks indicate where the independent fixed effect of species was statistically significant.

Table 3

GLMM parameter estimates for independent effects models

Model	Term	Estimate	Standard error	*z*	*P*
Time alone	Intercept	−3.804	0.509	−7.481	—
	Chimpanzee	2.470	0.481	5.130	<0.001
	Infant age class 1.5 < 3	−0.267	0.419	−0.637	0.524
	Infant age class 3 < 4.5	−0.140	0.405	−0.345	0.730
Feeding	Intercept	−0.507	0.109	−4.662	—
	Chimpanzee	−0.023	0.126	−0.180	0.857
	Infant age class 1.5 < 3	0.354	0.151	2.344	0.019
	Infant age class 3 < 4.5	0.319	0.132	2.411	0.016
Travel	Intercept	−1.606	0.069	−23.338	—
	Chimpanzee	−0.093	0.080	−1.155	0.248
	Infant age class 1.5 < 3	0.251	0.094	2.657	0.008
	Infant age class 3 < 4.5	0.105	0.085	1.242	0.214
Social interactions	Intercept	−1.755	0.115	−15.224	—
	Chimpanzee	0.067	0.130	0.516	0.606
	Infant age class 1.5 < 3	−0.157	0.163	−0.960	0.337
	Infant age class 3 < 4.5	−0.249	0.162	−1.534	0.125
Adjusted social interactions	Intercept	−3.101	0.210	−14.802	—
	Chimpanzee	0.782	0.217	3.605	<0.001
	Infant age class 1.5 < 3	−0.082	0.298	−0.276	0.782
	Infant age class 3 < 4.5	−0.031	0.229	−0.135	0.892

Table 4

GLMM parameter estimates for interaction effect models

Model	Term	Estimate	Standard error	*z*	*P*
Time alone	Intercept	−3.900	0.719	−5.425	—
	Chimpanzee × Age 1.5 < 3	0.680	1.302	0.523	0.601
	Chimpanzee × Age 3 < 4.5	−0.805	1.03	−0.779	0.436
Feeding	Intercept	−0.484	0.116	−4.013	—
	Chimpanzee × Age 1.5 < 3	0.531	0.284	1.871	0.061
	Chimpanzee × Age 3 < 4.5	−0.054	0.249	−0.215	0.829
Travel	Intercept	−1.593	0.078	−20.415	—
	Chimpanzee × Age 1.5 < 3	0.204	0.259	0.788	0.431
	Chimpanzee × Age 3 < 4.5	−0.069	0.164	−0.422	0.673
Social interactions	Intercept	−1.749	0.126	−13.840	—
	Chimpanzee × Age 1.5 < 3	−0.126	0.324	−0.390	0.696
	Chimpanzee × Age 3 < 4.5	0.206	0.292	0.705	0.481
Adjusted social interactions	Intercept	−2.910	0.211	−13.799	—
	Chimpanzee × Age 1.5 < 3	0.506	0.495	1.023	0.306
	Chimpanzee × Age 3 < 4.5	0.878	0.470	1.869	0.062

their levels of gregariousness, thereby reducing feeding competition. We, therefore, hypothesized that lactating chimpanzees at Gombe mitigate the intense feeding competition that they face by being less gregarious than lactating bonobos, who are thought to be facing less-intense feeding competition. In support of our first two predictions, lactating chimpanzees spent more time alone than lactating bonobos, while feeding and travel time did not differ between the species. These results support the hypothesis that lactating chimpanzees mitigate high feeding competition by being less gregarious, given that, in doing so, they maintained foraging budgets comparable to their more gregarious bonobo counterparts. Our results thus add evidence to the existing body of research indicating that fission–fusion dynamics are a counterstrategy to feeding competition across taxa (see above).

We also hypothesized that the social budgets of lactating chimpanzees are constrained as a result of being less gregarious. However, we did not find support for this hypothesis: against our third prediction, lactating females did not differ in total social interaction time, and lactating chimpanzees spent proportionately more of their social interaction time interacting with individuals other than their immature offspring. These results suggest that, despite being less gregarious, lactating chimpanzees spend as much time engaged in direct social interactions as do lactating bonobos. It is, therefore, unclear how lactating bonobos benefit from higher gregariousness if they do not engage in more social interactions when compared to lactating chimpanzees. One possibility is that grouping provides lactating bonobos with opportunities to enhance social relationships in ways that do not require direct interactions. In some animal taxa, spatial association with conspecifics is related to fitness and not necessarily direct social interaction. For example, in the greater ani (*Crotophaga major*), females that consistently nested together were considered to have stable social relationships, and this stability increased fitness (Riehl and Strong 2018). Similarly, in feral horses (*Equus ferus caballus*), composite social integration scores were positively related to fitness, and these scores were based on measures of spatial affinity between mares (Cameron et al. 2009). Thus, there are numerous ways in which gregarious individuals could gain social benefits without necessarily engaging in direct

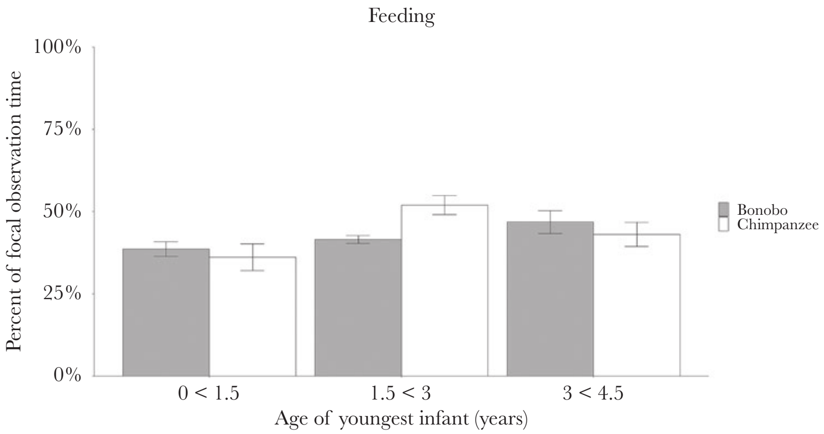

Figure 2
Mean ± standard error percentage of time that lactating females spent feeding.

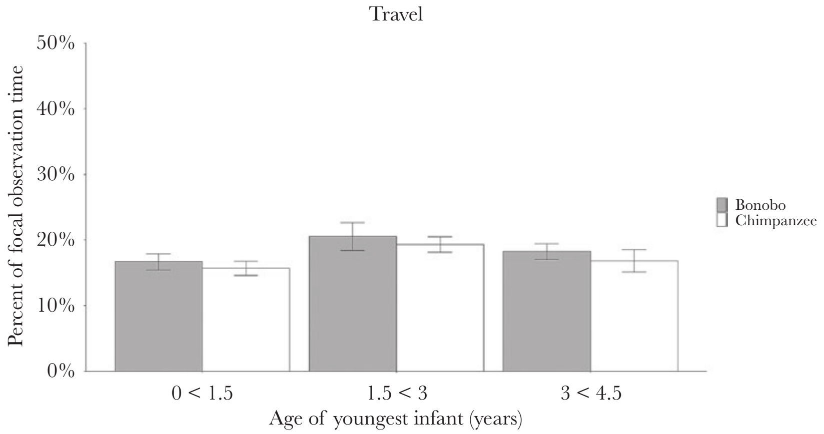

Figure 3
Mean ± standard error percentage of time that lactating females spent traveling.

social interactions. In this view, gregariousness could be favored at LuiKotale simply because being in relatively close spatial proximity to other group members confers social benefits.

On the other hand, grouping may also provide lactating bonobos with opportunities for modes of direct social interaction that we did not consider in our study. While our results indicate that lactating chimpanzees invest more time in grooming and playing with the broader social milieu, it may be that bonobos add to their social budget through other direct interactions. For example, female bonobos engage in genito-genital rubbing, a behavior that is thought to contribute to bond formation and maintenance (Furuichi 1989; Hohmann and Fruth 2000; Fruth and Hohmann 2006). Genito-genital rubbing requires little time investment as it more closely resembles a behavioral event rather than a state. Female bonobos may thus have additional social currency at their disposal that does not require substantial time investments, but it is difficult to make direct comparisons with chimpanzees because chimpanzees do not habitually engage in genito-genital rubbing (but see Anestis 2004; Zamma and Fujita 2004). Similarly, another mode of social interaction not captured by our study is female–female coalitionary behavior. Female–female coalitions against males are prevalent in bonobos (Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016; Nurmi et al. 2018) but not in chimpanzees (but see Newton-Fisher 2006), again restricting direct comparisons between the species. It may be the case that benefits accrued through modes of social interaction that we did not consider in this study are beneficial enough to favor grouping by lactating bonobos.

More gregarious bonobos could also gain benefits associated with predator defense. Evidence for variation in grouping patterns resulting from differences in predation risk is widespread across nonprimate taxa (e.g., *Suricata suricatta*: Clutton-Brock et al. 1999; *Junco hyemalis*: Lima et al. 1999; *Cervus elaphus*: Childress and Lung 2003; *Perdix perdix*: Watson et al. 2007); however, such predator–prey systems are often characterized by relatively high rates of predation. In generating our hypothesis, we assumed that grouping patterns are primarily driven by feeding competition based on the limited empirical evidence for leopard predation on bonobos and chimpanzees (see Introduction); indeed the underlying assumption of most fission–fusion systems is that predation is sufficiently low enough to allow groups to fission (but see food-safety trade-off in *Tursiops aduncus*: Heithaus and Dill 2002). However, predation pressure is not absent from LuiKotale. Leopards have not been observed at Gombe since roughly 1975 (see Pierce 2009) and are presumed to be locally extinct; at LuiKotale, bonobo hard tissue was found in leopard scat (D'Amour et al. 2006) and researchers recently observed a nonlethal confrontation between bonobos and a leopard (unpublished data, Fruth and Hohmann), suggesting that leopards are indeed a threat to bonobos. Thus, we cannot rule out that predation risk at LuiKotale can have major impacts on bonobo sociality. This would be broadly in line with the influential predator

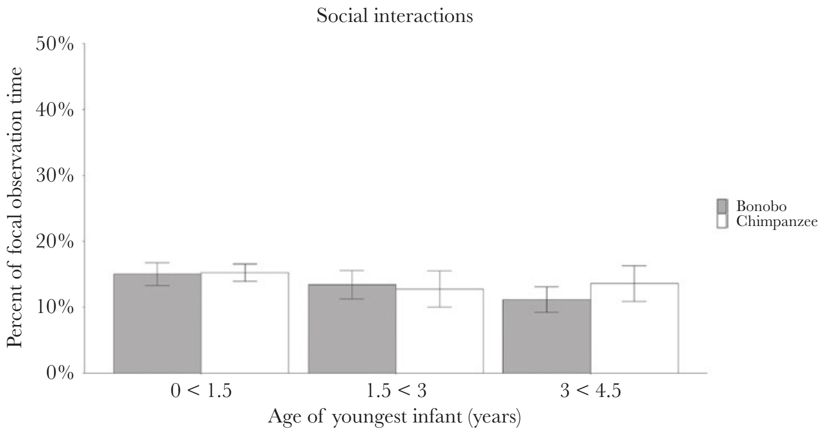

Figure 4
Mean ± standard error percentage of time that lactating females spent engaged in social interactions with any community member.

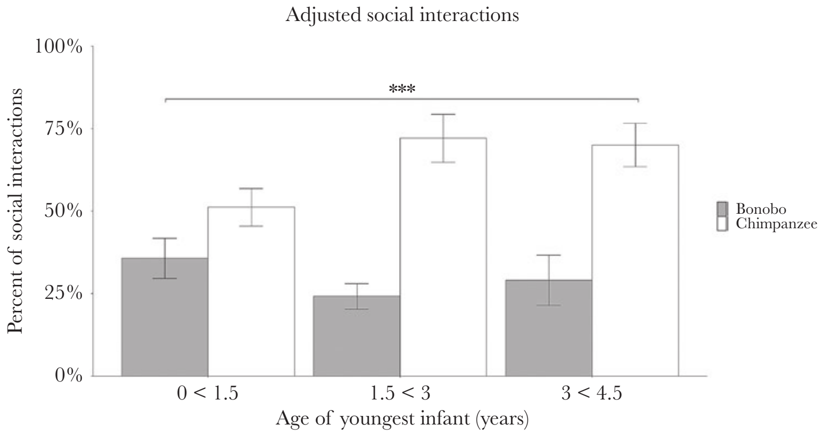

Figure 5
Mean ± standard error percentage of social interactions in which lactating females spent engaged in social interactions with individuals other than their immature offspring.

risk allocation hypothesis (Lima and Bednekoff 1999), which posits that the trade-off between foraging and vigilance is less a function of immediate presence/absence of predators and more of the temporal pattern of predation risk over time.

Irrespective of the costs and benefits of grouping, our finding that lactating chimpanzees can maintain social budgets comparable to lactating bonobos despite reduced gregariousness underscores the benefits associated with the flexibility in behavior that fission–fusion dynamics provide. Bechstein's bats (*Myotis bechsteinii*) also illustrate this sort of flexibility: Kerth et al. (2011) showed that individuals are able to maintain long-term social relationships despite high fission–fusion dynamics. Similarly, we showed in a separate study that immature females from LuiKotale and Gombe do not differ in time engaged in social play or social grooming, indicating that the reduced gregariousness of lactating females at Gombe does not constrain immature female social budgets either (Lee, Murray, et al. 2020). Results from our studies and the study by Kerth et al. (2011) suggest that individuals in fission–fusion societies need not spend extensive time together in order to maintain relationships with the broader social milieu. In those fission–fusion species for which social relationships are likely critical components of fitness, selection may have favored social skills that enable bond partners to maintain relationships even with limited association time. Future research could evaluate this further by identifying the mechanisms by which individuals develop and maintain such relationships in species that appear to exhibit even less frequent encounters with some associates, such as African forest elephants (*Loxodonta cyclotis*) (Fishlock and Lee 2013) or sperm whales (*Physeter macrocephalus*) (Whitehead et al. 1991). More specifically, such research could focus on the role of differing latencies between fusions within and between species to determine whether it is the absolute amount of time that individuals associate and/or the temporal patterning of fusions that influences bond formation and maintenance.

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DATA AVAILABILITY:

Analyses reported in this article can be reproduced using the data provided by Lee, Hohmann, et al. (2020).

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REFERENCES

Anestis SF. 2004. Female genito-genital rubbing in a group of captive chimpanzees. Int J Primatol. 25:477–488.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Fiore AD, Dunbar RIM, Henzi SP, et al. 2008. Fission-fusion dynamics. Curr Anthropol. 49:627–654.

Bădescu I, Katzenberg MA, Watts DP, Sellen DW. 2017. A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. Am J Phys Anthropol. 162:285–299.

Barclay RMR. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behav Ecol Sociobiol. 24:31–37.

Beauchamp G. 2012. Foraging speed in staging flocks of semipalmated sandpipers: evidence for scramble competition. Oecologia. 169:975–980.

Boesch C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour. 117:220–241.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol. 24:127–135.

Bond ML, Lee DE, Ozgul A, König B. 2019. Fission-fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. Oecologia. 191:335–347.

Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A. 2014. The meaning of weaning in wild Phayre's leaf monkeys: last nipple contact, survival, and independence. Am J Phys Anthropol. 154:291–301.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2018. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9:378–400.

Cameron EZ, Setsaas TH, Linklater WL. 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci USA. 106:13850–13853.

Childress MJ, Lung MA. 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? Anim Behav. 66:389–398.

Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll ADC, Kansky R, Chadwick P, Manser M, Skinner JD, Brotherton PNM. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. J Anim Ecol. 68:672–683.

Couzin ID. 2006. Behavioral ecology: social organization in fission-fusion societies. Curr Biol. 16:R169–R171.

D'Amour DE, Hohmann G, Fruth B. 2006. Evidence of leopard predation on bonobos (*Pan paniscus*). Folia Primatol. 77:212–217.

Doran DM, Jungers WL, Sugiyama Y, Fleagle JG, Heesy CP. 2002. Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In: Boesch C, Hohmann G, Marchant L, editors. Behavioural diversity in chimpanzees and bonobos. 1st ed. Cambridge (UK): Cambridge University Press. p. 14–34.

Dunbar RIM, Korstjens AH, Lehmann J. 2009. Time as an ecological constraint. Biol Rev. 84:413–429.

Dzal YA, Brigham RM. 2013. The tradeoff between torpor use and reproduction in little brown bats (*Myotis lucifugus*). J Comp Physiol B. 183:279–288.

Ebensperger LA, Hurtado MJ. 2005. Seasonal changes in the time budget of degus, *Octodon degus*. Behaviour. 142:91–112.

Emery Thompson M, Muller MN, Wrangham RW. 2012. The energetics of lactation and the return to fecundity in wild chimpanzees. Behav Ecol. 23:1234–1241.

Favreau FR, Goldizen AW, Fritz H, Pays O. 2018. Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. Anim Behav. 135:165–176.

Fishlock V, Lee PC. 2013. Forest elephants: fission-fusion and social arenas. Anim Behav. 85:357–363.

Fleagle JG. 2013. Primate adaptation and evolution. Cambridge (MA): Academic Press.

Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Firth S, Friendly M, Gorjanc G, Graves S, et al. 2012. Package 'car'. Vienna: R Foundation for Statistical Computing.

Fruth B, Hohmann G. 2006. Social grease for females? Same sex genital contacts in wild bonobos. In: Sommer V, Vasey PL, editors. Homosexual behaviour in animals: an evolutionary perspective. Cambridge: Cambridge University Press. p. 294–315.

Furuichi T. 1989. Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. Int J Primatol. 10:173–197.

Furuichi T. 2000. Possible case of predation on a chimpanzee by a leopard in the Petit Loango Reserve, Gabon. Pan Afr News. 7:21–23.

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

Gruber T, Clay Z. 2016. A comparison between bonobos and chimpanzees: a review and update. Evol Anthropol. 25:239–252.

Hamel S, Côté SD. 2008. Trade-offs in activity budget in an alpine ungulate: contrasting lactating and nonlactating females. Anim Behav. 75:217–227.

Hammond KA, Kristan DM. 2000. Responses to lactation and cold exposure by deer mice (*Peromyscus maniculatus*). Physiol Biochem Zool. 73:547–556.

Harrison XA. 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. PeerJ. 3:e1114.

Hartig F. 2020. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. The Comprehensive R Archive Network (CRAN), R Package Version 0.3. 2.0.

Haulsee DE, Fox DA, Breece MW, Brown LM, Kneebone J, Skomal GB, Oliver MJ. 2016. Social network analysis reveals potential fission-fusion behavior in a shark. Sci Rep. 6:1–9.

Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology. 83:480–491.

Hohmann G, Fowler A, Sommer V, Ortmann S. 2012. Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates. 1st ed. Cambridge (UK): Cambridge University Press. p. 123–159.

Hohmann G, Fruth B. 2000. Use and function of genital contacts among female bonobos. Anim Behav. 60:107–120.

Hohmann G, Fruth B. 2002. Dynamics in social organization of bonobos *(Pan paniscus)*. In: Boesch C, Hohmann G, Marchant L, editors. Behavioural diversity in chimpanzees and bonobos. 1st ed. Cambridge (UK): Cambridge University Press. p. 138–150.

Isbell LA. 1994. Predation on primates: ecological patterns and evolutionary consequences. Evol Anthropol. 3:61–71.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6: 326–336.

Kelley JL, Morrell LJ, Inskip C, Krause J, Croft DP. 2011. Predation risk shapes social networks in fission-fusion populations. PLoS One. 6:e24280.

Kerth G, Perony N, Schweitzer F. 2011. Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. Proc Biol Sci. 278:2761–2767.

Kohn MJ. 1999. You are what you eat. Science. 283:335–336.

Lee S, Hohmann G, Lonsdorf EV, Fruth B, Murray M. 2020. Gregariousness, foraging effort, and social interactions in lactating bonobos and chimpanzees. Behav Ecol. doi: 10.5061/dryad.d51c5b01v.

Lee SM, Murray CM, Lonsdorf EV, Fruth B, Stanton MA, Nichols J, Hohmann G. 2020. Wild bonobo and chimpanzee females exhibit broadly similar patterns of behavioral maturation but some evidence for divergence. Am J Phys Anthropol. 171:100–109.

Lehmann J, Boesch C. 2008. Sexual differences in chimpanzee sociality. Int J Primatol. 29:65–81.

Lehmann J, Boesch C. 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. Anim Behav. 77:377–387.

Lenth R. 2018. Emmeans: estimated marginal means, aka least-squares means. R Package Version 1.1. 1:3.

Lima SL, Bednekoff PA. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat. 153:649–659.

Lima SL, Zollner PA, Bednekoff PA. 1999. Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). Behav Ecol Sociobiol. 46:110–116.

Lonsdorf EV, Markham AC, Heintz MR, Anderson KE, Ciuk DJ, Goodall J, Murray CM. 2014. Sex differences in wild chimpanzee behavior emerge during infancy. PLoS One. 9:e99099.

Lonsdorf EV, Stanton MA, Pusey AE, Murray CM. 2020. Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania. Am J Phys Anthropol. 171:419–429.

Loretto MC, Schuster R, Itty C, Marchand P, Genero F, Bugnyar T. 2017. Fission-fusion dynamics over large distances in raven non-breeders. Sci Rep. 7:1–9.

Markham AC, Gesquiere LR, Alberts SC, Altmann J. 2015. Optimal group size in a highly social mammal. Proc Natl Acad Sci USA. 112:14882–14887.

Markham AC, Lonsdorf EV, Pusey AE, Murray CM. 2015. Maternal rank influences the outcome of aggressive interactions between immature chimpanzees. Anim Behav. 100:192–198.

Maynard Smith J, Szathmary E. 1997. The major transitions in evolution. Oxford: Oxford University Press.

Mbizah MM, Valeix M, Macdonald DW, Loveridge AJ. 2019. Applying the resource dispersion hypothesis to a fission–fusion society: a case study of the African lion (*Panthera leo*). Ecol Evol. 9:9111–9119.

Moscovice LR, Douglas PH, Martinez-Iñigo L, Surbeck M, Vigilant L, Hohmann G. 2017. Stable and fluctuating social preferences and implications for cooperation among female bonobos at LuiKotale, Salonga National Park, DRC. Am J Phys Anthropol. 163:158–172.

Moscovice LR, Surbeck M, Fruth B, Hohmann G, Jaeggi AV, Deschner T. 2019. The cooperative sex: sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. Horm Behav. 116:104581.

Murray CM, Eberly LE, Pusey AE. 2006. Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). Behav Ecol. 17:1020–1028.

Nakazawa N. 2020. Primates are an important food resource for leopards (*Panthera pardus*) in Mahale, Tanzania. Afr J Ecol. 58:399–408.

Nakazawa N, Hanamura S, Inoue E, Nakatsukasa M, Nakamura M. 2013. A leopard ate a chimpanzee: the first evidence from East Africa. J Hum Evol. 65:334–337.

Newton-Fisher NE. 2006. Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. Int J Primatol. 27:1589–1599.

Nurmi NO, Hohmann G, Goldstone LG, Deschner T, Schülke O. 2018. The "tolerant chimpanzee"—towards the costs and benefits of sociality in female bonobos. Behav Ecol. 29:1325–1339.

Oelze VM, Douglas PH, Stephens CR, Surbeck M, Behringer V, Richards MP, Fruth B, Hohmann G. 2016. The steady state great ape? long term isotopic records reveal the effects of season, social rank and reproductive status on bonobo feeding behavior. PLoS One. 11:e0162091.

Oelze VM, Fahy G, Hohmann G, Robbins MM, Leinert V, Lee K, Eshuis H, Seiler N, Wessling EG, Head J, et al. 2016. Comparative isotope ecology of African great apes. J Hum Evol. 101:1–16.

Oelze, VM, Hohmann G, O'Neal I, Lee SM, Fruth B. 2020. Competing siblings and invested first time mothers: weaning patterns in wild bonobos (*Pan paniscus*) revealed by stable isotope analysis. 89th Annual Meeting of the American Association of Physical Anthropologists; 2020 April 15–18; Los Angeles, CA. Am J Phys Anthropol. 171(269):205.

Parra GJ, Corkeron PJ, Arnold P. 2011. Grouping and fission-fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins. Anim Behav. 82:1423–1433.

Pierce AH. 2009. An encounter between a leopard and a group of chimpanzees at Gombe National Park. Pan Afr News. 16:22–24.

Prüfer K, Munch K, Hellmann I, Akagi K, Miller JR, Walenz B, Koren S, Sutton G, Kodira C, Winer R, et al. 2012. The bonobo genome compared with the chimpanzee and human genomes. Nature. 486:527–531.

R Core Team. 2020. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Riehl C, Strong MJ. 2018. Stable social relationships between unrelated females increase individual fitness in a cooperative bird. Proc R Soc B Biol Sci. 285:20180130.

Rishworth GM, Tremblay Y, Green DB, Connan M, Pistorius PA. 2014. Drivers of time-activity budget variability during breeding in a pelagic seabird. PLoS One. 9:e116544.

RStudio Team. 2020. RStudio: integrated development environment for R. Boston (MA): RStudio Team.

Silk JB, Alberts SC, Altmann J. 2003. Social bonds of female baboons enhance infant survival. Science. 302:1231–1234.

Stanton MA, Lonsdorf EV, Murray CM, Pusey AE. 2020. Consequences of maternal loss before and after weaning in male and female wild chimpanzees. Behav Ecol Sociobiol. 74:1–11.

Stanton MA, Lonsdorf EV, Pusey AE, Goodall J, Murray CM. 2014. Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*): increased investment by first-time mothers. Curr Anthropol. 55:483–489.

Stanton MA, Mann J. 2012. Early social networks predict survival in wild bottlenose dolphins. PLoS One. 7:e47508.

Surbeck M, Girard-Buttoz C, Boesch C, Crockford C, Fruth B, Hohmann G, Langergraber KE, Zuberbühler K, Wittig RM, Mundry R. 2017. Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. R Soc Open Sci. 4:161081.

Surbeck M, Hohmann G. 2013. Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). Behav Ecol Sociobiol. 67:1767–1780.

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.

Therrien JF, Côté SD, Festa-Bianchet M, Ouellet JP. 2008. Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction. Anim Behav. 75:235–243.

Thometz NM, Staedler MM, Tomoleoni JA, Bodkin JL, Bentall GB, Tinker MT. 2016. Trade-offs between energy maximization and parental care in a central place forager, the sea otter. Behav Ecol. 27:1552–1566.

Tokuyama N, Furuichi T. 2016. Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. Anim Behav. 119:27–35.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. 1st ed. New York: Aldine de Gruyter. p. 136–179.

van Overveld T, Gangoso L, García-Alfonso M, Bouten W, de la Riva M, Donázar JA. 2020. Seasonal grouping dynamics in a territorial vulture: ecological drivers and social consequences. Behav Ecol Sociobiol. 74:28.

Wakefield ML. 2008. Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. Int J Primatol. 29:907–929.

Waller MT. 2011. The ranging behavior of bonobos in the Lomako Forest. Eugene (OR): University of Oregon.

Ward A, Webster M. 2016. Sociality: the behaviour of group-living animals. Cham (Switzerland): Springer International Publishing.

Watson M, Aebischer NJ, Cresswell W. 2007. Vigilance and fitness in grey partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. J Anim Ecol. 76:211–221.

Whitehead H, Waters S, Lyrholm T. 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. Behav Ecol Sociobiol. 29:385–389.

Wielgus E, Cornélis D, de Garine-Wichatitsky M, Cain B, Fritz H, Miguel E, Valls-Fox H, Caron A, Chamaillé-Jammes S. 2020. Are fission-fusion dynamics consistent among populations? A large-scale study with Cape buffalo. Ecol Evol. 10:9240–9256.

Williams JM, Liu H-Y, Pusey AE. 2002. Costs and benefits of grouping for female chimpanzees at Gombe. In: Boesch C, Hohmann G, Marchant L, editors. Behavioural diversity in chimpanzees and bonobos. 1st ed. Cambridge (UK): Cambridge University Press. p. 192–203.

Wilson EO. 1975. Sociobiology: the new synthesis. Cambridge (MA): Harvard University Press.

Wrangham RW, Smuts BB. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. J Reprod Fertil. 28:13–31.

Xiang Z, Huo S, Xiao W. 2010. Activity budget of *Rhinopithecus bieti* at Tibet: effects of day length, temperature and food availability. Curr Zool. 56:650–659.

Zamma K, Fujita S. 2004. Genito-genital rubbing among the chimpanzees of Mahale and Bossou. Pan Afr News. 11:5–8.

Zuberbühler K, Jenny D. 2002. Leopard predation and primate evolution. J Hum Evol. 43:873–886.

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Berlin (Germany): Springer Science & Business Media.