








## RESEARCH ARTICLE

## Flexible grouping patterns in a western and eastern chimpanzee community

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## Funding information

Newnham College, University of Cambridge; Royal Zoological Society of Scotland; Homerton College, University of Cambridge; Gates Cambridge Trust; Ministry of Education, Culture, Sports, Science and Technology, Grant/Award Numbers: #12002009, #16002001, #20002001, #24000001, #16H06; Stichting Lucie Burgers; Schweizerischer Nationalfonds zur Förderung

## Abstract

Primate social organizations, or grouping patterns, vary significantly across species. Behavioral strategies that allow for flexibility in grouping patterns offer a means to reduce the costs of group living. Chimpanzees (*Pan troglodytes*) have a fission-fusion social system in which temporary subgroups ("parties") change in composition because of local socio-ecological conditions. Notably, western chimpanzees (*P. t. verus*) are described as showing a higher degree of bisexual bonding and association than eastern chimpanzees, and eastern female chimpanzees (*P. t. schweinfurthii*) are thought to be more solitary than western female chimpanzees. However, reported comparisons in sociality currently depend on a small number of study groups, particularly in western chimpanzees, and variation in methods. The inclusion of additional communities and direct comparison using the same methods are essential to assess whether reported subspecies differences in sociality hold in this behaviorally heterogeneous species. We explored whether sociality differs between

**Abbreviations:** FAI, Fruit availability index.

Twitter (95 characters)

Flexibility in grouping patterns of eastern and western chimpanzees.

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der Wissenschaftlichen Forschung,  
Grant/Award Number: PCEFP3\_186967

two communities of chimpanzees using the same motion-triggered camera technology and definitions of social measures. We compare party size and composition (party type, sex ratio) between the western Gahtoy community in the Nimba Mountains (Guinea) and the eastern Waibira community in the Budongo Forest (Uganda). Once potential competition for resources such as food and mating opportunities were controlled for, subspecies did not substantially influence the number of individuals in a party. We found a higher sex-ratio, indicating more males in a party, in Waibira; this pattern was driven by a greater likelihood in Gahtoy to be in all-female parties. This finding is the opposite of what was expected for eastern chimpanzees, where female-only parties are predicted to be more common. Our results highlight the flexibility in chimpanzee sociality, and caution against subspecies level generalizations.

#### KEYWORDS

camera trapping, chimpanzee, party composition, party size, sociality

## 1 | INTRODUCTION

Primate grouping patterns, or social organizations, describe the number and sex of independent individuals that compose a social unit (Strier, 2021). Grouping patterns vary significantly across the primate order: from solitary species to those living in complex multi-level groups (Kappeler & van Schaik, 2002). Life in a social group with other individuals involves an inherent trade-off between associated benefits, such as protection from predation, and incurred costs, such as increased competition for food (Alexander, 1974; Janson & Goldsmith, 1995; van Schaik, 1989). Individual fitness in male primates is closely linked to the number of successful fertilizations, and their sociality is typically shaped by the fertility and distribution of available mates (Dunbar, 1988; Roberts & Cords, 2013; Snyder-Mackler et al., 2012). Sociality in female primates, for whom fertility is heavily dependent upon nutrition to address the costs of pregnancy and lactation, is strongly shaped by access to resources and associated feeding competition (Beicovrtch, 1987; Cheney et al., 2004; Gittleman & Thompson, 1988; Harris et al., 2010).

To reduce the costs of group-living, some primate species have evolved behavioral strategies that allow flexibility in group structure to respond to local and short-term changes in socio-ecological conditions. For example, a fission-fusion social system allows for flexibility in grouping patterns: the main social group or unit, regularly subdivides into smaller sub-groups of variable size and membership, termed “parties” (Amici et al., 2008; Kummer, 1971). Chimpanzees are a classic fission-fusion species (Nishida, 1968; although c.f. Badihi et al., 2022). In chimpanzee society, the main social unit group or ‘community’ is a large group in which all individuals are acquainted, engage in positive interactions, and coordinate to defend a common home range, but are rarely—if ever—all found in a single party (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Sugiyama, 1973). The duration for which a party remains together varies greatly, and

members may join from or leave for other parties throughout the day (Boesch & Boesch-Achermann, 2000).

Multiple socio-ecological factors influence chimpanzee party size and composition (Giuliano et al., 2022; Samuni et al., 2020; van Leeuwen et al., 2020). Both the abundance and spatial distribution of food patches affect the number of individuals in a party (Basabose, 2004; Boesch, 1991, 1996; Chapman et al., 1995; Giuliano et al., 2022; Matsumoto-Oda et al., 1998; Mitani et al., 2002; van Leeuwen et al., 2020). Similarly, the presence of estrus females at a reproductive peak has been found to affect party size and composition, typically by increasing the number of males (Anderson et al., 2002; Boesch, 1996; Giuliano et al., 2022; Hashimoto et al., 2001; Hockings et al., 2012; Matsumoto-Oda et al., 1998; Mitani et al., 2002; Sakura, 1994; Samuni et al., 2020; Sommer et al., 2004; Tutin et al., 1983; van Leeuwen et al., 2020; Wakefield, 2008; Wallis, 2002). In contrast, females with young offspring who are still lactating, are more likely to spend time alone or in small parties (Lowe et al., 2020; Wrangham & Smuts, 1980). Predation pressure also appears to drive increases in party size (Boesch, 1991; Lehmann & Boesch, 2004), which may be linked to reported increases in chimpanzee gregariousness in more open habitats (Giuliano et al., 2022; Itani & Suzuki, 1967).

Despite widespread flexibility in chimpanzee grouping patterns, systematic differences in social characteristics have been linked to subspecies membership. Genetic evidence suggests that the ancestors of the western subspecies of chimpanzee (*P. t. verus*) and the Nigeria-Cameroon chimpanzees (*P. t. ellioti*) split from the ancestors of eastern (*P. t. schweinfurthii*) and central chimpanzees (*P. t. troglodytes*) approximately 500,000 years ago (Prado-Martinez et al., 2013). While both eastern and western chimpanzees are primarily male-bonded (Boesch, 2009; Wrangham, 1975), western chimpanzees are described as showing a higher degree of bisexual bonding, with males and females associating more frequently than

reported in eastern chimpanzee populations (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2005). Compared to western females, eastern female chimpanzees are typically more solitary and occupy more spatially restricted “core areas” (Wrangham & Smuts, 1980; Wrangham et al., 1992) that form subsections of the community's overall territory (Williams et al., 2002). In contrast, western females appear more gregarious and regularly range across at least 85% of the community's collective territory (Lehmann & Boesch, 2005). Perhaps as a result, eastern chimpanzee females immigrating into a new community must compete for membership and access to high-quality foraging areas (Kahlenberg et al., 2008), whereas western females do not (Boesch & Boesch-Achermann, 2000).

Importantly, the reported differences in sociality between eastern and western chimpanzees are largely based on data from only one study site with three communities of western chimpanzees (i.e., Taï, Côte d'Ivoire). Taï chimpanzee communities are extremely cohesive and fall toward the smaller end of the spectrum of chimpanzee community size (Taï: 7–43 individuals; chimpanzees: range 7–144, median = 42 individuals; Wilson et al., 2014). As a result, the currently described variation in subspecies sociality may reflect those present in Taï chimpanzees, as opposed to being representative of western chimpanzees more generally (*sensu* STRANGE framework, Webster & Rutz, 2020). The inclusion of additional western and eastern chimpanzee communities is essential to assess whether reported differences in sociality hold across populations.

Moreover, research on measures of chimpanzee sociality such as party size and composition has suffered from significant variability in methodology, in part due to long-running differences in the operational definition of a chimpanzee “party” (reviewed in: Giuliano et al., 2022). To date, there remains a lack of research comparing chimpanzee communities from the western and eastern subspecies with comparable methodology. Camera traps provide a standardized way to measure party size and composition. Several studies have compared chimpanzee party size estimates from camera traps with direct observations *within* a given study site (Issa, Tanzania: Vink et al., 2020; Taï, Ivory Coast: McCarthy et al., 2018; Seringbara, Nimba Mountains, Guinea: van Leeuwen et al., 2020). Party size estimates from camera traps were generally smaller than those from direct observations (McCarthy et al., 2018; Vink et al., 2020; but see van Leeuwen et al., 2020) but showed similar patterns of seasonal variation (McCarthy et al., 2018). Moreover, studies comparing party composition between camera traps and direct observations found similar demographic compositions across the two methods (McCarthy et al., 2018; van Leeuwen et al., 2020). Hence, a targeted comparison of party size and composition using standardized camera trap methodology *across* study sites of western and eastern chimpanzees offers a promising way forward.

Camera trap placement is an important consideration when using motion-triggered cameras to study species abundance, richness, activity (e.g., Hofmeester et al., 2021; Tanwar et al., 2021), as well as when investigating specific behaviors (e.g., Boesch et al., 2017; Koops

et al., 2019). When comparing sociality measures across chimpanzee study sites, the location of camera traps may influence estimates of grouping patterns. For example, chimpanzees in Cantanhez National Park (Guinea-Bissau) were found to balance human-induced risks with food availability in their use of space, which likely also affected their social grouping patterns (Bersacola et al., 2021). The location in the home range in terms of the associated risk from neighboring conspecifics may also influence chimpanzee party composition. For example, in Kanyawara (Uganda) more adult male chimpanzees were found to be present in parties visiting the periphery compared to the core of the home range (Wilson et al., 2007). Moreover, the placement of camera traps at specific resources may influence party composition. For example, chimpanzee males at Bakoun, Guinea, were found to algae fish almost twice as often as females (Boesch et al., 2017). Hence, it is key to compare grouping patterns in similar locations and at comparable resources across study sites.

We explored whether sociality differs between two communities of western and eastern chimpanzees using the same motion-triggered camera technology and the same definition of social measures. We compared party size and composition (i.e., party type, sex ratio) between the western Gahtoy community in the Nimba Mountains (Guinea) and the eastern Waibira community in the Budongo Forest (Uganda). Gahtoy and Waibira provide an ideal comparison in terms of similarity in habitat type (mainly primary rainforest), predation pressure (low), habituation level (semi-habituated at the time of data collection), community size (relatively large), and some prior exposure to camera traps (Nimba: ~1–3 years; Waibira: ~0–4 years). We investigated whether differences in sociality in terms of party size and composition exist between these communities of western and eastern chimpanzees, beyond the predicted effects of food availability (i.e., ripe fruit) and reproductive opportunities (i.e., estrous females). At Gahtoy, we measured chimpanzee party size and composition at stream beds where Gahtoy chimpanzees fish for crabs. At Waibira, we measured chimpanzee party size and composition at a comparable aquatic resource, a seasonal water hole (Péter et al., 2022). In both cases, the (aquatic) resources are of high value but are not primary food sources (Koops et al., 2019; Péter et al., 2022). We tested two hypotheses and associated predictions: (1) western chimpanzees are described as more bisexually bonded than eastern chimpanzees, and thus will show more frequent bisexual association; and (2) eastern chimpanzee females are described as less gregarious than western chimpanzees, and thus will be more frequently found alone or in female-only parties. To test whether context has a significant effect on within-site party size and composition estimates, we examined differences in party size and composition *within* the Gahtoy community across two different contexts (i.e., resource, travel). In Gahtoy, we measured chimpanzee party size and composition both at crab-fishing sites and at control sites on chimpanzee trails (Koops et al., 2019). With this we aimed to assess to what extent our estimates were consistent across locations, and thus to see whether our findings were generalizable beyond the aquatic resource context and may reflect more general community/sub-species level patterns of association.

## 2 | METHODS

### 2.1 | Study sites and subjects

Western chimpanzees were studied at the Seringbara study site, located within the Mount Nimba Strict Nature Reserve in the Nimba Mountains of Guinea, West Africa. The study site spans an area of circa 30 km<sup>2</sup> and the chimpanzees have been the subjects of research since 2003 (Koops, 2011). Due to the challenging terrain the chimpanzees remain largely unhabituated to the presence of researchers. The study site has great topographic diversity with altitudes ranging from 600 m in the deepest valley to over 1750 m at the highest peak (Koops, 2011). The climate is characterized by an extended rainy season (min. monthly rainfall: 2.2 mm; max. monthly rainfall: 555.0 mm), lasting 9 months from March to November, followed by a 3-month dry season (Koops et al., 2013, 2015; Koops, 2011). Vegetation comprises primary tropical forest, with areas of savannah grassland, terrestrial herbaceous vegetation, and riverine forest (Koops et al., 2012a). Two chimpanzee communities reside in the Seringbara research area: the Gahtoy and Tongbongbon communities (Koops et al., 2012b; Koops et al., 2023). Here, we focus on the Gahtoy community with an estimated total of 47 independent (i.e., adolescents, adults) chimpanzees (Koops et al., 2023). Based on published information on community sizes (i.e., with and

without independent individuals) across long-term chimpanzee study sites, we calculated an estimated total community size of ~75 individuals for Gahtoy (see Table 1).

Eastern chimpanzees were studied at the Budongo Conservation Field Station, located within the Budongo Central Forest Reserve in Uganda. The forest reserve spans 435 km<sup>2</sup>. There are ~600 chimpanzees living in the reserve, split across multiple communities, some of which have been studied since the 1960s (Reynolds, 2005). The forest has minimal topographic variation, sloping gently down towards the northeast, with an average altitude above sea level of 1100 m (Reynolds, 2005). The climate is characterized by a bimodal rainfall distribution, with rainy seasons between March and May, and then again between August and November (min. monthly rainfall: 0 mm; max. monthly rainfall: 425.0 mm). The major dry season falls between December and February, with a second minor dry season in June and July (Fawcett, 2000). The forest primarily comprises secondary tropical semi-deciduous rainforest, with strips of riverine forest extending into surrounding cropland (Reynolds, 2005). The Budongo Conservation Field Station has operated since 1990, first habituating the Sonso chimpanzee community and then, in 2011, the Waibira community (Samuni et al., 2014). The chimpanzees are habituated, but some peripheral females and their families remain rarely encountered. At the end of the study period the Waibira

**TABLE 1** Chimpanzee community sizes at eastern and western chimpanzee study sites: without dependents (i.e., excluding infants, juveniles), with dependents (adapted from Giuliano et al., 2022), and the calculated ratio of community size with/without dependents.

Subspecies	Study site	Community size (w/o dependents)	Community size (with dependents)	With/without dependents
<i>P. t. schweinfurthii</i>	Sonso, Budongo	31	43	1.4
<i>P. t. schweinfurthii</i>	Sonso, Budongo	36	71	2.0
<i>P. t. schweinfurthii</i>	Waibira, Budongo	64	114	1.8
<i>P. t. schweinfurthii</i>	Gombe	28	43	1.5
<i>P. t. schweinfurthii</i>	Issa	18	26	1.4
<i>P. t. schweinfurthii</i>	Kahuzi-Biega	14	22	1.6
<i>P. t. schweinfurthii</i>	Kanyawara, Kibale	30	55	1.8
<i>P. t. schweinfurthii</i>	Ngogo, Kibale	101	145	1.4
<i>P. t. schweinfurthii</i>	Ngogo, Kibale	95	140	1.5
<i>P. t. schweinfurthii</i>	Mahale	45	85	1.9
<i>P. t. schweinfurthii</i>	Mahale	31	44	1.4
<i>P. t. verus</i>	Fongoli	17	35	2.1
<i>P. t. verus</i>	Bossou	13	20	1.5
<i>P. t. verus</i>	Bossou	9	14	1.6
<i>P. t. verus</i>	Bossou	10	13	1.3
<i>P. t. verus</i>	Taï North	36	70	1.9
<i>P. t. verus</i>	Taï North	17	31	1.8
<i>P. t. verus</i>	Taï South	25	39	1.6
<i>P. t. verus</i>	Gahtoy, Nimba	47	75*	1.6 (mean)

Note: \*Estimated community size (this study) based on the mean ratio of 1.6 (with/without dependents).

community contained ~114 individuals of which 64 were independent individuals (see Table 1).

## 2.2 | Data collection

At Nimba, data were collected continuously over 26 months, from March 2012–April 2014. Data collection was carried out by KK, together with HDC, MF, GM, and a team of research assistants and staff. At Waibira, data were collected over 10 months, between January 2013 and January 2017. Motion-triggered cameras were deployed from December to March each year. The periods of data collection were: January 2013–March 2013; December 2013–January 2014; January 2015–March 2015; February 2016–March 2016; January 2017. Data collection was carried out by CH, together with WA, KV, DE, HP, and a team of research assistants and staff.

To maximize environmental parity, the motion-triggered camera data for both sites were collected at areas of high-resource importance and thus regularly visited by chimpanzees. At Nimba, we selected sites used by the Gahtoy chimpanzees for crab-fishing in stream beds (Koops et al., 2019). At Waibira, chimpanzees do not feed on crabs, and the most comparable resource location was the site of a central water hole (Péter et al., 2022). This water hole is the only available source of surface water in the late dry season outside of peripheral areas that are shared with neighboring communities, and which represent high-risk zones. At Gahtoy, eight cameras (Bushnell Trophy Cam XLT 8MP Trail Camera) were located at four crab fishing sites (Koops et al., 2019). Each crab fishing site was thus covered by two cameras. We also placed cameras (Bushnell Trophy Cam XLT 8MP Trail Camera) at eight ‘control sites’ throughout the home range of the Gahtoy chimpanzees using one camera per site. Control sites were placed on chimpanzee trails with active use (e.g., knuckle prints) and without any feeding trees, or other food sources, recorded nearby (Koops et al., 2019). Cameras were placed on mature trees (height 42–117 cm from the ground; and several meters back from crab fishing sites/trails). Videos were recorded 24 h a day (daytime: 60-second videos, 1-second re-trigger; nighttime: 15-second videos, 1-second re-trigger). At Waibira, a single camera (Bushnell NoGlow Trophy Cam) kept in the same location at the main drinking point was used each year during the main dry season, and no additional control sites were monitored at Waibira. The camera was placed on a mature tree and facing down the slope to target a preferred place for drinking (height ~25 cm from the ground; and several meters back from the water's edge). Videos were recorded 24 h a day (daytime: 60-second videos, 1-second re-trigger; nighttime: 15-second videos, 1-second re-trigger).

### 2.2.1 | Party size and composition

Where multiple parties were captured on camera in the same day, they were defined as separate when sequential observations occurred more than 1 h apart and had no overlap in observed individuals. Parties in

which individuals could not be reliably identified or sexed were excluded from the data set. Party composition was recorded as the number of individuals in each age group (adults >11 years; adolescents 8–11 years; juveniles 4–8 years; infants 0–4 years (Sugiyama, 1999). Party size was defined as “the number of individuals present that feed and travel independently” (Anderson et al., 2002). Using this definition, we excluded immature (or dependent) individuals (estimated or known age <8 years old, i.e., infants and juveniles). Party type was classed based on the sex of independent individuals present as: female-only, male-only, or mixed sex.

Sex ratios were calculated for each party using the following formula: sex ratio = (# independent males)/((# independent males) + (# independent females)) giving the proportion of independent males in the party (*sensu* van Leeuwen et al., 2020). We include both adults and adolescents in our calculation of sex ratio, since both can have offspring. Moreover, our measure is different from the usual sex ratio calculation (i.e., # adult males/# adult females) to allow for inclusion of female-only and male-only parties.

### 2.2.2 | Estrous females

The sexual status of females was recorded for adults and adolescents through observation of ano-genital swellings. These sexual swellings were classified as either: (0) absent–no swelling, with maximal wrinkling; (1) partial tumescence–relative increase or decrease in size and loss or appearance of wrinkles versus stages 0 or 2; or (2) full tumescence–full size swelling, with no wrinkling and turgid appearance (Furuichi, 1987). In the analyses, partial and full swellings were combined, with parties classified as either with estrus (1) or without estrus (0).

### 2.2.3 | Fruit availability

At Nimba, data on the availability of ripe fruit were collected for 25 of the 26 study months (i.e., March 2012–March 2014). No data were available from April 2014 due to an Ebola outbreak. Using a stratified random design, twenty-four 500 m transects were placed throughout the study site. Trees of fruit bearing species with a diameter at breast height (DBH)  $\geq 100$  mm within 5 m of the transect line, known to be chimpanzee food sources, were monitored monthly for ripe fruit. The abundance of ripe fruit was scored from 0 to 4 as follows: (0) no ripe fruit; (1) 1%–25% of tree canopy bearing ripe fruit; (2) 26%–50% bearing ripe fruit; (3) 51%–75% bearing ripe fruit; and (4) 76%–100% of tree canopy bearing ripe fruit (Koops et al., 2013, 2015, 2019). These scores for ripe fruit presence were applied to the following formula to provide monthly Fruit Availability Indices, or FAI (*sensu* Hockings et al., 2010; Takemoto, 2004):  $FAI = 100 * (\sum (p * f) / \sum (p * 4))$ , in which FAI is the fruit availability index percentage,  $p$  is the basal area of the tree in  $cm^2$  and  $f$  is the abundance of ripe fruit.

At Waibira, feeding phenology data were extracted from the long-term data for the months in which video data were analyzed.

For each of 18 fruit-bearing tree species, known to be chimpanzee food sources, two to 30 trees were monitored monthly for ripe fruit (total number of trees = 382). The abundance of ripe fruit was scored as present (1) or absent (0). These scores for ripe fruit presence were applied to the same formula to provide monthly Fruit Availability Indices, or FAI, as above. Data were not available for January 2017, the average January value across all other years in the data set was substituted here. While there is a variation in the absolute FAI score across the two sites (both in the number of trees, and in the scoring of fruit availability), FAI were used to control for month-to-month variation in food availability *within* sites and thus the absolute values were not directly compared.

## 2.3 | Data analysis

We coded a matched sample of parties ( $N = 177$ ) for both communities (Gahtoy, Waibira) at the respective aquatic resources (crab-fish sites, water hole). At Gahtoy, we also recorded videos at control sites ( $N = 155$ ). Party composition (independent individuals) was coded as mixed sex (0), female only (1), or male only (2).

To estimate the effects of subspecies and party location on party size (the number of independent individuals in a party) we used a Linear Mixed Model (LMM; Baayen, 2008). To control for their potential effects, we included group (Waibira-aquatic; Gahtoy-aquatic; Gahtoy-control) and the presence of females in estrus (yes = 1, no = 0) as fixed effects. We included food availability (FAI), date, and sex ratio as random effects. We log-transformed party size, and z-transformed Sex Ratio and FAI to a mean of 0 and a standard deviation of 1 to achieve a more easily interpretable model (Schielzeth, 2010) and ease model convergence.

$$\text{Party size model} = \text{Imer}(\log. \text{PartySize} \sim \text{Group} * \text{Oestrus} + (1|\text{date}) + (1|z. \text{SexR}) + (1|z. \text{FAI})).$$

We included the interaction between group and estrus, to control for the possibility that the presence of estrus females differently affects party size in either subspecies, or across the aquatic and control contexts. As a general test of the effects of group on party size we conducted a full-null model comparison (Forstmeier & Schielzeth, 2011) in which the null model included all fixed and random effects except for group. As we found no overall effect, we simplified the model removing the interaction effect.

$$\text{Party size model} = \text{Imer}(\log. \text{PartySize} \sim \text{Group} + \text{Oestrus} + (1|\text{date}) + (1|z. \text{SexR}) + (1|z. \text{FAI})).$$

We then re-ran the full-null comparison with this simplified model.

We conducted a second similar model to explore the effect of these factors on party sex ratio. In this model we included party size as a random factor.

$$\text{Sex Ratio model} = \text{Imer}(z. \text{SexRatio} \sim \text{Group} + \text{Oestrus} + (1|\text{date}) + (1|\log. \text{PartySize}) + (1|z. \text{FAI})).$$

Here, again, the null model used for full-null model comparison included the same model structure with the exclusion of the factor group.

We compared party types (i.e., female-only, male-only, or mixed sex) across the three groups (i.e., Waibira-aquatic; Gahtoy-aquatic; Gahtoy-control) using Chi Square tests with Bonferroni corrected post-hoc comparisons.

All analyses were performed in R version 4.2.3 (2023-03-15; Shortstop Beagle). We fitted the model using the function `lmer` (version 1.1-32; Bates et al., 2015). We determined Variance Inflation Factors using the function `vif` of the package `car` (version 3.1-1; Fox & Weisberg, 2011). We assessed model stability using a function generously provided by Roger Mundry.

## 3 | RESULTS

### 3.1 | Party size

Party size ranged from 1 to 38 individuals, with a median = 2 (Gahtoy-control: range 1-18, median = 2; Gahtoy-aquatic: range 1-16, median = 2; Waibira-aquatic: range 1-38, median = 3, Figure 1).

We found no variation in party size across the three types of groups (full-null model comparison:  $X^2 = 1.755$ ,  $df = 2$ ,  $p = 0.416$ , see Table 2).

### 3.2 | Sex ratios

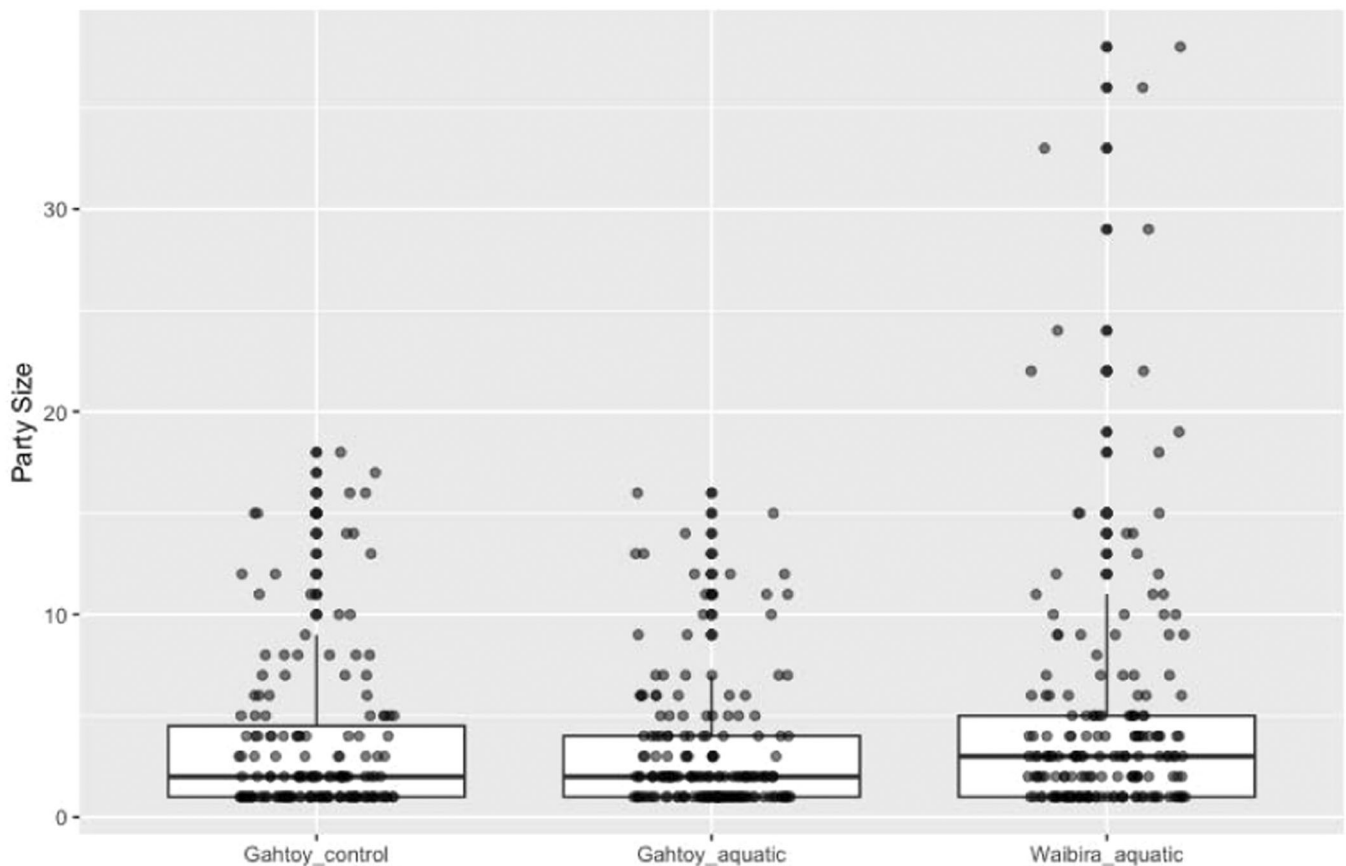
Party sex ratios ranged from 0 (female-only) to 1 (male-only), with a median = 0.5 (Gahtoy-control median = 0.25, Gahtoy-aquatic median = 0.4, Waibira-aquatic median = 0.6, Figure 2).

We found a clear effect of group (Waibira-aquatic, Gahtoy-aquatic, Gahtoy-control) on sex ratio (full-null model comparison:  $X^2 = 13.22$ ,  $df = 2$ ,  $p = 0.0013$ , see Table 3). More specifically we found no difference in sex ratio between the Gahtoy-aquatic and Gahtoy-control groups, but we found a higher sex ratio (indicating a greater proportion of males in the party) in the Waibira-aquatic group.

### 3.3 | Party types

When comparing female-only, male-only, and mixed sex parties (see Table 3), we found a significant difference between the distribution of party types between the three types of group ( $X^2 = 36.45$ ,  $df = 4$ ,  $p < 0.0001$ , Figure 3).





**FIGURE 1** Number of individuals in a party at the Gahtoy control location, and the Gahtoy and Waibira aquatic resource locations. Boxes represent the InterQuartile Range (IQR), with whiskers indicating the range of the data up to 1.5× the IQR.

**TABLE 2** Parameter estimates for party size model: number of individuals in a party across the three locations, controlling for presence of estrus females, sex ratio, food availability, and date.

Parameter	Estimate	SE	z value	p
Intercept	1.86	0.11	(1)	(1)
Gahtoy-aquatic	-0.03	0.06	-0.544	0.588
Waibira-aquatic	0.06	0.07	0.862	0.393
Estrus	0.38	0.05	(2)	(2)

Note: The reference category was Gahtoy-control. <sup>(1)</sup> Not indicated because of limited interpretive value. <sup>(2)</sup> Not indicated because it was included as a control factor.

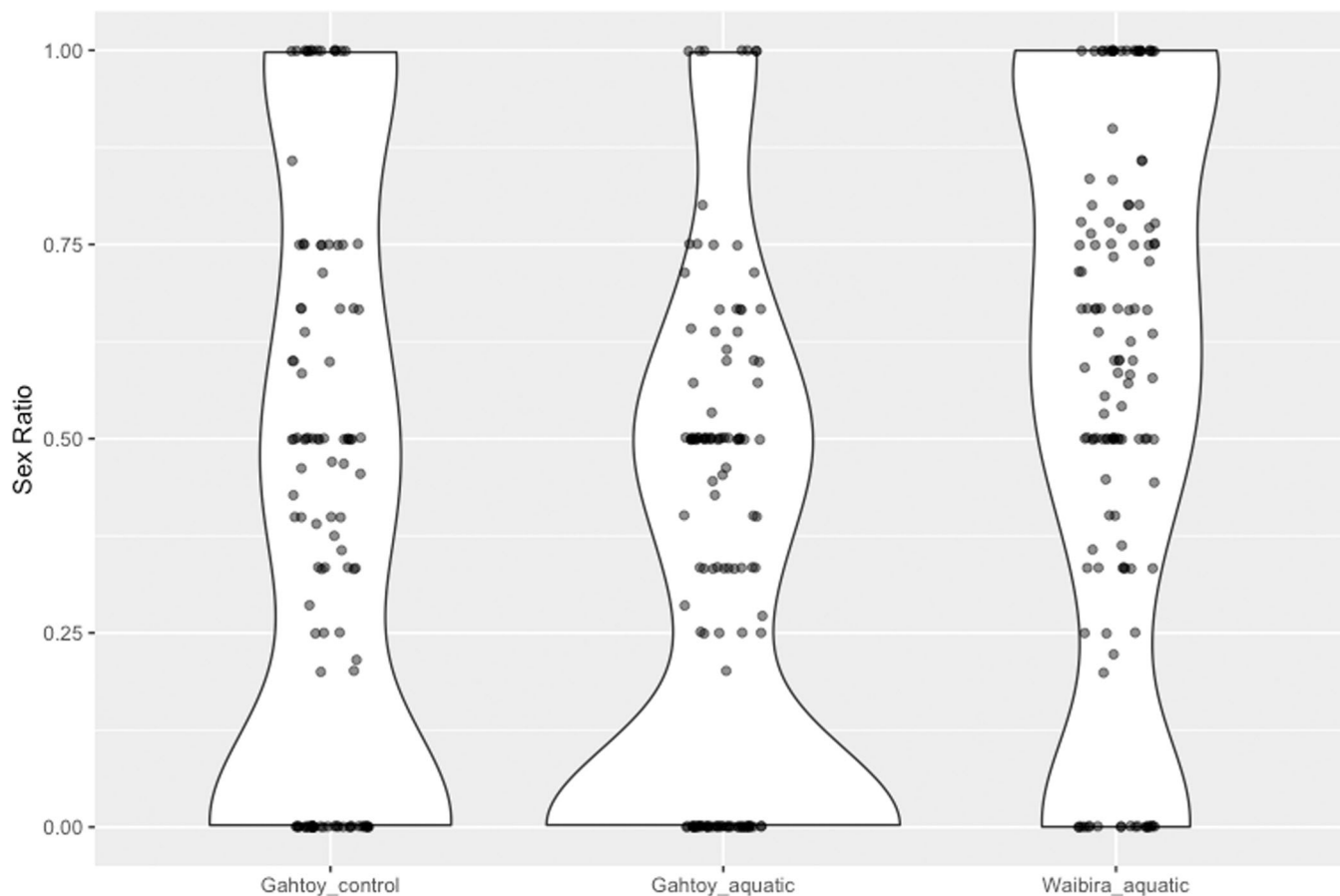
We found no difference across the groups in the relative frequency of mixed-sex parties ( $X^2 = 0.008$ ,  $df = 2$ ,  $p = 1.000$ ). Female-only parties were more common in both the Gahtoy-control and Gahtoy-aquatic locations than in Waibira-aquatic (Bonferroni-corrected pairwise tests, Waibira-aquatic and Gahtoy-aquatic  $p < 0.001$ ; Waibira-aquatic and Gahtoy-control  $p = 0.0064$ ; Gahtoy-aquatic and Gahtoy-control  $p = 0.2154$ ). Male-only parties were more common in Waibira-aquatic and Gahtoy-control locations, than in the Gahtoy-aquatic (Bonferroni-corrected pairwise tests;

Waibira-aquatic and Gahtoy-aquatic  $p < 0.001$ ; Waibira-aquatic and Gahtoy-control  $p = 0.5469$ ; Gahtoy-aquatic and Gahtoy-control  $p = 0.0085$ ).

#### 4 | DISCUSSION

We compared measures of sociality (party size, sex ratio, party type) between a community of western chimpanzees (Gahtoy, Nimba Mountains, Guinea) and a community of eastern chimpanzees (Waibira, Budongo Forest, Uganda) using comparable camera trap methodology, as well as the same definitions and measures of sociality. Moreover, we controlled for the predicted effects of the presence of estrous females and fluctuations in food availability. The two study communities differed in size (Gahtoy:  $N = \sim 75$  individuals, Waibira:  $N = \sim 114$  individuals), but both are considered relatively large communities for the species (chimpanzee median = 42 individuals; Wilson et al., 2014). We measured chimpanzee party size and composition at two similar aquatic resource locations (i.e., Gahtoy: crab-fishing sites, Waibira: water hole), as well as at control sites (traveling trails) for the Gahtoy community.

We found no difference in terms of party size between the two study communities, despite the difference in total community size.



**FIGURE 2** Sex ratio per party at the Gahtoy-control location, and the Gahtoy and Waibira aquatic resource locations. Higher values indicate more males per party (1 = all male, 0 = all female).

**TABLE 3** Parameter estimates for sex ratio model: Sex ratio of a party across the three locations, controlling for presence of estrus females, party size, food availability, and date.

Parameter	Estimate	SE	z value	p
Intercept	0.432	0.14	(1)	(1)
Gahtoy_aquatic	-0.277	0.15	-1.910	0.062
Waibira_aquatic	0.360	0.16	2.201	0.032
Estrus	-0.341	0.10	(2)	(2)

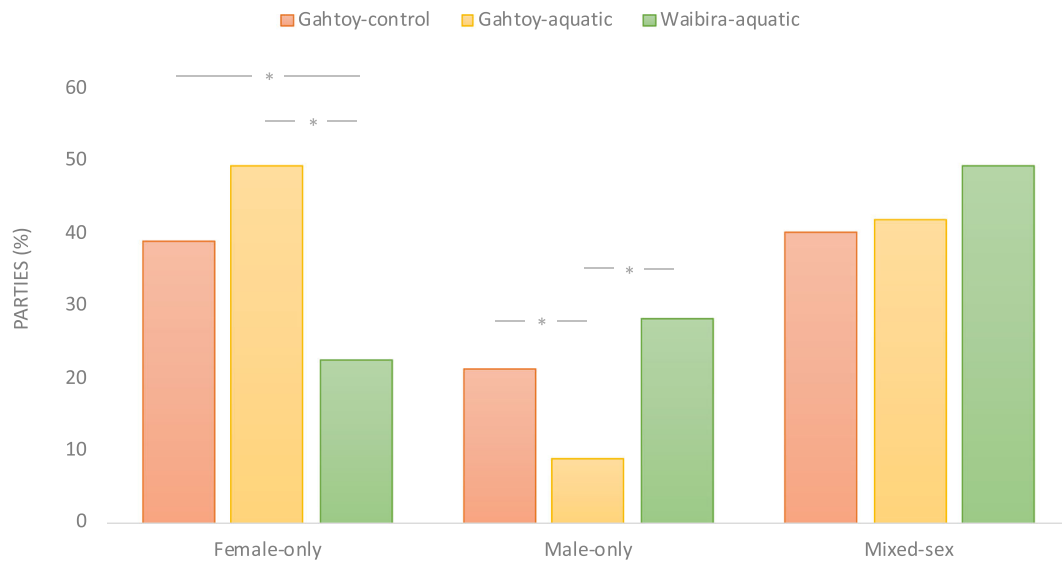
Note: The reference category was Gahtoy-control. We report p-values for the individual levels of group from the multcomp function. <sup>(1)</sup> Not indicated because of limited interpretive value. <sup>(2)</sup> Not indicated because it was included as a control factor.

We also found no difference in party size between the aquatic and control sites within the Gahtoy community. These findings validate our subsequent comparison of party composition between the Gahtoy and Waibira communities, as we can exclude the possibility that there was a differential likelihood of finding mixed-sex parties due to differences in party size between the communities. Furthermore, the fact that party size did not differ between the two communities supports the idea that chimpanzees manage competition through fission-fusion dynamics in a similar way across

differently sized groups in both subspecies. While we do not explore their effect here, in other comparisons of differently-sized communities (Badihi et al., 2022), pressures such as competition for food and mates, and territorial defense act to shape immediate party size independently from the total number of individuals in a community.

Second, the two chimpanzee communities did differ in terms of party composition. We found a stronger female-bias in the sex ratio of Gahtoy parties - across both control and aquatic resource locations - and a stronger male-bias in Waibira. Strikingly, we found relatively few all-female parties in Waibira compared to both Gahtoy locations. This finding is the opposite of what would be predicted for eastern chimpanzees, where the literature suggests that eastern females spend more time either alone or in all-female parties (Wrangham & Smuts, 1980; Wrangham et al., 1992). The presence of female-skewed and female-only parties in the Gahtoy-aquatic location could have been driven by access to a highly valuable food resource, which may be of particular importance to mothers with dependent offspring (Koops et al., 2019). Previous research indeed showed that parties of females and offspring fished for crabs more than predicted and for longer durations than males (Koops et al., 2019). However, we found a similar pattern of results in the Gahtoy-control locations, where cameras were placed along traveling routes, which suggests that the observed difference in sociality from the Waibira chimpanzees is stable across contexts.





**FIGURE 3** Proportion of parties belonging to different party types at the Gahtoy-control location, and the Gahtoy and Waibira aquatic resource locations.

Moreover, the proportion of mixed-sex parties did not differ between the western and eastern chimpanzee communities. Previous studies have reported higher levels of bisexual bonding and association in western chimpanzees (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2005). The higher frequency of all-male parties in Waibira may be linked to the unusually large number of independent males in this community, which results in cliques of satellite males (Badihi et al., 2022). The greater presence of all-male parties in Gahtoy-control locations may be the result of picking up either solitary males or male parties patrolling, although, again, this pattern of association is the opposite of what would be predicted for western chimpanzees if they are more bisexually bonded, and highlights that the behavioral context or location of data collection can importantly shape the sex-ratio. Importantly, the (unexpected) differences in party types between the two study sites is not an effect of a data collection bias towards certain individuals, because the water hole is a key resource that all chimpanzees visit regularly in the dry seasons at Waibira (Péter et al., 2022) and our use of camera-trapping methodology also excludes the possibility that human presence may have deterred certain individuals (females) from visiting sites more than others (males).

While our methods were similar across sites there were limitations to our approach. Control data were not available for the Waibira community to assess to what extent the patterns of party size and sex ratio were generalizable to other behavioral contexts in this community. Future studies employing camera trap methods should take camera trap location under explicit consideration due to potential effects of any unaccounted differences. Similarly, while we controlled for some seasonally variable features such as food availability and the presence of females in estrus (Boesch & Boesch-Achermann, 2000; Matsumoto-Oda et al., 1998; Wallis, 1995), the chimpanzees' exploitation of the aquatic resources

differed by season in the two communities (year-round in Gahtoy, dry-season only in Waibira), and there may be further untested effects of season on their behavior. Furthermore, there may be untested effects on party size of differential levels of habituation to researchers, as well as potential differences in predation risk at the two sites. While Waibira chimpanzees were more habituated to human observers than Gahtoy chimpanzees, predation risk was similarly low at both sites (i.e., no indirect or direct evidence of leopards at either study site during or before the study period). Finally, while we measured patterns of bisexual association, association is not a direct measure of bonding. There are many reasons to travel in the same party as other individuals, for example a shared need for particular resources, such as food. In some cases, it may be important to maintain spatial proximity, or association, with individuals with whom one is explicitly not closely bonded, for example competitor males. Bonding, or at least more prosocial association, is better assessed through measures that capture the quality of social interactions and, where available, endocrinological measures (e.g., Crockford et al., 2013; Mitani, 2009; Samuni et al., 2018).

Our study highlights the benefits of using camera traps when studying wild, and often elusive, great apes. Camera traps allow for standardized comparisons between sites and provide detailed observations without disturbing the chimpanzees by having human observers present. However, camera-trap data collection can also be vulnerable to variation in methods and comparability across data-sets (e.g., in camera placement and settings) remains crucial for accurate comparisons (Caravaggi et al., 2020). It has been argued that chimpanzees may avoid locations in which camera traps have been established; in which case some individuals may not be captured as a party passes (Caravaggi et al., 2020; McCarthy et al., 2018). However, a recent comparison of chimpanzee party size and composition in

Nimba found no difference in relative estimates provided by direct observations and camera traps (van Leeuwen et al., 2020). The use of camera traps, rather than direct observations, also has several additional benefits, including reduced potential for transmission of anthroponotic diseases to the apes (Epstein & Price, 2009), less unintended behavioral change (McDougall, 2012), and potentially a reduced vulnerability to poaching in some communities (Robbins & Boesch, 2019) depending on the nature of local threats.

## 5 | CONCLUSION

Our findings call attention to the flexibility of both eastern and western chimpanzee sociality. We caution against sweeping assumptions on subspecies differences, particularly when these are based on a limited number of data-points in a species known for its substantial behavioral flexibility. Our results show that chimpanzee sociality is highly flexible and that *where* and *how* you measure party size, party composition, and party type may shape conclusions on a community's social patterns. Here, we showed that, in some cases, eastern females appear to be more sociable and associate bisexually more frequently than western ones. Similarly, eastern chimpanzees in Issa, Tanzania, were reported to be as cohesive as western chimpanzees (Giuliano et al., 2022), attenuating earlier findings suggesting that high cohesion is specific to the western subspecies (Boesch, 1996). As findings from more chimpanzee study sites across Africa add new pieces to the puzzle of chimpanzee sociality, it is becoming clear that there is no one-size-fits-all description of eastern versus western chimpanzee social grouping patterns.

### AUTHOR CONTRIBUTIONS

**Kathelijne Koops:** Conceptualization (lead); Data curation (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Visualization (lead); Writing—original draft (lead); Writing—review & editing (lead). **Walter Akankwasa:** Investigation (equal). **Henry Didier Camara:** Investigation (equal); Methodology (supporting); Project administration (supporting). **Maegan Fitzgerald:** Investigation (equal); Project administration (supporting); Writing—review & editing (supporting). **Alex Keir:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Writing—original draft (supporting). **Gnan Mamy:** Investigation (equal); Methodology (supporting); Project administration (supporting). **Tetsuro Matsuzawa:** Funding acquisition (supporting); Resources (supporting); Writing—review & editing (supporting). **Hella Péter:** Data curation (supporting); Investigation (equal). **Kizza Vicent:** Investigation (equal). **Klaus Zuberbühler:** Funding acquisition (supporting); Resources (supporting). **Catherine Hobaiter:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Supervision (supporting); Visualization (lead); Writing—original draft (lead); Writing—review & editing (lead).

### ACKNOWLEDGMENTS

We thank the Direction General de la Recherche Scientifique et l'innovation Technologique (DGERSIT) and the Institut de Recherche Environnementale de Bossou (IREB) in Guinea for research authorization in Nimba. We thank research assistants, K. Doré, F. Doré, F. Zogbila, N. Doré, D. Zogbila, Y. Zogbila, C. Samy, N. Gbouomy, K. van Leeuwen, M. O'Reilly, P. Le Sommer, J. Caraway, W. Edwards, D. Montanari, N. James, I. Vélez del Burgo Guinea, D. Hassler, M. McCann, and S. Canington, for their help in the field. Research was supported by grants from the Gates Cambridge Trust (Cambridge, UK), the Lucie Burgers Foundation for Comparative Behaviour Research (Netherlands), Homerton College and Newnham College (Cambridge, UK), SNSF Eccellenza Professorial Fellowship (no. PCEFP3\_186967) to K. Koops, by funding from the European Union's 8th Framework Program, Horizon 2020, under grant agreement no 802719 to C. Hobaiter, and MEXT (#12002009, #16002001, #20002001, #24000001, #16H06283) grants to T. Matsuzawa. We thank the staff of the Budongo Conservation Field Station, and the Uganda Wildlife Authority and the Uganda National Council of Science and Technology for permission to work in Uganda. The Budongo Conservation Field Station is supported by the Royal Zoological Society of Scotland. We thank the editor and two reviewers for their constructive feedback that helped to improve the manuscript. Open access funding provided by Universitat Zurich.

### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available upon reasonable request from the corresponding authors. All code for the analyses is available in our Github repository: <https://github.com/Wild-Minds/EWChimpSociality>

### ETHICS STATEMENT

Data collection in the Republic of Guinea was approved by the Direction General de la Recherche Scientifique et l'Innovation Technologique (DGERSIT) and adhered to the guidelines as set down by the Division of Biological Anthropology, Department of Archaeology & Anthropology at the University of Cambridge (UK). Data collection in Uganda was approved by the Uganda Wildlife Authority and the Ugandan National Council for Science and Technology as well as by the University of St. Andrews Animal Welfare and Ethics Committee. Researchers followed the Code of Best Practices for Field Primatology established by the International Primatological Society.

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**How to cite this article:** Koops, K., Akankwasa, W., Camara, H. D., Fitzgerald, M., Keir, A., Mamy, G., Matsuzawa, T., Péter, H., Vicent, K., Zuberbühler, K., & Hobaiter, C. (2024). Flexible grouping patterns in a western and eastern chimpanzee community. *American Journal of Primatology*, e23593. <https://doi.org/10.1002/ajp.23593>