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How to measure chimpanzee party size? A methodological comparison

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Abstract

Chimpanzees (*Pan troglodytes*) live in fission–fusion societies where community members form temporary parties that frequently change in size and composition. Chimpanzee party size and composition have been widely studied to identify proximate causes of grouping patterns, and party size estimates are used to assess population sizes and densities. Numerous socio-ecological factors influence chimpanzee party size, but findings differ across studies. Various methods to measure party size exist, including direct observations, motion-triggered camera (MTC) observations, and nest counts. However, comparative analyses of these methods are lacking. Here, we assess relative differences in four commonly used party size methods and we examine socio-ecological factors influencing party size of unhabituated chimpanzees (*P. t. verus*) at Seringbara, Nimba, Guinea. We also assess which method(s) best reflect the influence of socio-ecological factors on party size. Using data collected over 69 months, we show that night nest counts resulted in relatively larger party size estimates than the other methods, and day nest counts resulted in relatively smaller party size estimates. Direct and MTC observations did not differ in relative estimates of party size and composition. Both fruit abundance and presence of estrous females positively influenced party size, but this effect was only evident when measuring party size with MTCs. Methods thus differ in relative party size estimates and their ability to assess the impact of socio-ecological factors. We conclude that MTC observations best represent party size and the effect of socio-ecological factors at Nimba. MTCs show promising potential for studying grouping patterns in unhabituated chimpanzees.

Keywords Chimpanzees · Party size · Fruit availability · Estrous females · Nest counts · Camera traps

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Introduction

Animal group living has been studied extensively in terms of costs and benefits, and group size is often interpreted as an adaptive trait that responds to social and ecological factors (Chapman et al. 1995; Lehmann and Boesch 2004). Chimpanzees (*Pan troglodytes*) live in flexible fission–fusion societies, in which members of a stable community form temporary subgroups, or parties, that frequently change in size and composition (Itoh and Nishida 2007; Matsumoto-Oda et al. 1998; Newton-Fisher et al. 2000). Chimpanzee party size and composition have been widely studied to identify the proximate causes of chimpanzee grouping patterns (Anderson et al. 2002; Basabose 2004; Doran 1997). Whereas early studies focused on identifying a single factor responsible for grouping patterns, later studies have demonstrated that a complex interplay of factors determines party size (Doran 1997; Hashimoto et al. 2001; Mitani et al. 2002). The socio-ecological factors influencing chimpanzee party

size include predation pressure (Boesch 1991; Lehmann and Boesch 2004), food supply (Chapman et al. 1995; Newton-Fisher et al. 2000), demographic factors (Lehmann and Boesch 2004; Mitani 2006), and presence of estrous females (Anderson et al. 2002; Wakefield 2008). Studies of chimpanzee party size have also been used to estimate community sizes, population densities and/or distributions, especially for unhabituated chimpanzees (Després-Einspenner et al. 2017; Furuichi et al. 2001a; Ndiaye et al. 2018).

Fruit availability, both in terms of abundance (i.e. amount) and distribution (i.e. spatial arrangement), was found to be an important ecological factor influencing chimpanzee party size across studies. Following the prediction that party size increases with higher fruit abundance and larger (i.e. clumped) food sources due to decreased costs of co-feeding, positive correlations have been found between party size and fruit abundance (Taï, Ivory Coast: Anderson et al. 2002; Doran 1997; Kibale, Uganda: Chapman et al. 1995; Mitani et al. 2002; Kalinzu, Uganda: Furuichi et al. 2001b; Mahale, Tanzania: Itoh and Nishida 2007; Matsumoto-Oda et al. 1998), and between party size and fruit distribution (Kahuzi-Biega, DRC: Basabose 2004; Kibale: Chapman et al. 1995). Conversely, other studies found that party size was not influenced by fruit abundance (Kalinzu: Hashimoto et al. 2001; Budongo, Uganda: Newton-Fisher et al. 2000; Kahuzi-Biega: Basabose 2004), or fruit distribution (Kalinzu: Hashimoto et al. 2001; Taï: Anderson et al. 2002; Budongo: Newton-Fisher et al. 2000).

The presence of estrous females was found to be an important social factor influencing chimpanzee party size (Anderson et al. 2002; Wakefield 2008). For the purpose of copulation, sexually receptive females are predicted to join parties and attract males, leading to larger parties (Anderson et al. 2002; Wallis 2002). Following this prediction, positive correlations between the presence of estrous females and party size have been observed at a number of sites (Taï: Anderson et al. 2002; Kibale: Mitani et al. 2002; Wakefield 2008; Mahale: Matsumoto-Oda et al. 1998; Kalinzu: Hashimoto et al. 2001; Budongo: Wallis 2002; Gombe, Tanzania: Wallis 2002; Gashaka-Gumti, Nigeria: Sommer et al. 2004).

Inconsistencies in the influence of socio-ecological factors on chimpanzee party size may stem from temporal and/or spatial variability in chimpanzee grouping patterns across sites and studies, but may also be a consequence of differences in field methodologies to measure fruit abundance (e.g. Chapman et al. 1995; Doran 1997; Hashimoto et al. 2001; Itoh and Nishida 2007), fruit distribution (e.g. Anderson et al. 2002; Basabose 2004; Newton-Fisher et al. 2000), estrous females (e.g. Anderson et al. 2002; Sommer et al. 2004), and/or party size (see below). As the causes of variation between studies are unknown, comparisons of the socio-ecological factors influencing chimpanzee party size are rendered problematic. Yet, based on the majority of studies outlined above, fruit availability and presence of estrous females can be expected to positively influence chimpanzee party size.

Across studies, methods of measuring chimpanzee party size differ. Four methods are commonly used: direct observations, motion-triggered camera observations, day nest counts and night nest counts (Basabose 2004; Brownlow et al. 2001; McCarthy et al. 2018). The properties of each of these methods differ, which likely affects their ability to correctly represent chimpanzee party sizes (Basabose 2004; Brownlow et al. 2001; Després-Einspenner et al. 2017). To date, these different methods have not been assessed all together at the same study site. Hence, comparative analyses to assess the relative differences in party size estimates across these methods are long overdue. This is especially important when studying unhabituated chimpanzee communities, where actual party sizes are unknown.

Measuring chimpanzee party size during direct observations is the most commonly used method (Chapman et al. 1995; Matsumoto-Oda et al. 1998; Newton-Fisher et al. 2000), and involves researchers collecting data on the number of chimpanzees present (Anderson et al. 2002; Basabose 2004). If chimpanzees are unhabituated, direct observations can be challenging as chimpanzees can be difficult to find due to their large home range and fission–fusion dynamics (Bertolani and Boesch 2008). As a consequence of behavioral and methodological factors, large parties may be found more easily and tolerate humans better than small parties; yet individuals, especially females, may flee upon encountering humans and peripheral individuals may be missed, which may affect relative party size estimates (Table 1, H1-H4; Basabose 2004; Bertolani and Boesch 2008; Sommer et al. 2004).

Motion-triggered camera (MTC) observations provide an indirect measure of party size that circumvents these difficulties when dealing with unhabituated chimpanzees (Boyer-Ontl and Pruetz 2014; Després-Einspenner et al. 2017; McCarthy et al. 2018). With minimal human interference and environmental disturbance, camera traps can provide detailed data on chimpanzee behavior in the absence of human observers (Boyer-Ontl and Pruetz 2014; McCarthy et al. 2018). However, MTCs do have limitations. Methodological difficulties, for example, include camera placement and the restricted film frame of the camera (Després-Einspenner et al. 2017; McCarthy et al. 2018). With regards to behavior, chimpanzees may actively avoid MTCs (Després-Einspenner et al. 2017; McCarthy et al. 2018). These limitations may allow some individuals to pass unnoticed and may lead to relatively lower party size estimates as compared to the other methods (Table 1, H5 and H6).

A last indirect method of measuring party size is using nest counts (Brownlow et al. 2001; Furuichi et al. 2001b; Ogawa et al. 2007). Nests built together in time and space

Table 1 Hypotheses and predictions with regards to the relative differences in party size estimates that are likely observed between the four methods, as well as their causal factors, i.e. behavior or methodology

Hypotheses	Predictions per party size method				Causal factor
	Direct	MTC	Day	Night	
Direct observations					
H1: chimpanzees show higher tolerance to human observers in larger parties	+	−	−	−	Behavior
H2: larger parties of chimpanzees are more easily located (e.g. vocalizations, traces)	+	−	−	−	Method
H3: chimpanzees flee when encountering human observers	−	+	+	+	Behavior
H4: individuals may be missed by humans when observing unhabituated chimpanzees	−	+	+	+	Method
MTC observations					
H5: chimpanzees actively avoid motion-triggered cameras	+	−	+	+	Behavior
H6: chimpanzees pass out of view of the film frame of the camera	+	−	+	+	Method
Day nest counts					
H7: not all chimpanzees build a nest during the day as a place to rest	+	+	−	+	Behavior
H8: chimpanzee day nests may be missed by humans when locating nest groups	+	+	−	+	Method
H9: chimpanzees build more than one nest during the day as a place to rest	−	−	+	−	Behavior
H10: larger daytime nest groups are more easily located	−	−	+	−	Method
Night nest counts					
H11: chimpanzees aggregate at night and sleep in larger parties	−	−	−	+	Behavior
H12: larger nighttime nest groups are more easily located	−	−	−	+	Method
H13: chimpanzee night nest may be missed by observers when locating nest groups	+	+	+	−	Method

For each method and under each specific hypothesis, a '+' indicates relatively larger party size estimates and a '−' indicates relatively smaller party size estimates as compared to the party size estimates of the other methods

H hypothesis, *direct* direct observations, *MTC* motion-triggered camera observations, *day* day nest counts, *night* night nest counts

are referred to as nest groups (or parties), and nest counts are often used as an indicator of party size (Brownlow et al. 2001; Furuichi et al. 2001b; Ogawa et al. 2007). A distinction should be made between day and night nest counts, as day and night nests differ in function and construction (Brownlow et al. 2001; Koops et al. 2012a). Chimpanzees build simple day nests as a place to rest during the day, yet construct complex nests each night to sleep in (Brownlow et al. 2001; Koops et al. 2012a). Day and night nest counts may result in relatively lower party size estimates as compared to the other methods, as (1) not all chimpanzees may build a nest at daytime (Table 1, H7: Brownlow et al. 2001; Goodall 1962); and (2) some nests may be missed by human observers when searching for nest groups (Table 1, H8 and H13: van Leeuwen *personal experience*). Alternatively, day and night nest counts may result in relatively higher party size estimates as compared to the other methods, as (1) some chimpanzees may build more than one nest during the day (Table 1, H9: Plumptre and Reynolds 1997); (2) chimpanzees may aggregate at night (Table 1, H11: Anderson et al. 2002; Ogawa et al. 2007); and (3) larger nest groups may be more easily located by human observers (Table 1, H10 and H12: van Leeuwen *personal experience*).

This study aims to explore party size methods and grouping patterns for the unhabituated chimpanzees at the Seringbara study site in the Nimba Mountains (Guinea).

Specifically, we investigate (1) relative differences in estimating chimpanzee party size between the four methods, (2) which socio-ecological factors influence chimpanzee party size at Nimba, and (3) which party size method(s) best reflect the influence of these factors. Relative differences between party size methods are expected according to the hypotheses and predictions outlined in Table 1. We focus here on relative differences in party size estimates, since actual party sizes are unknown for the unhabituated chimpanzees. Moreover, we are thus unable to test the causal factors, i.e. methodology or behavior, of the relative differences in party size estimates between methods. Fruit abundance, fruit distribution, and presence of estrous females are all predicted to have a positive influence on party size. As relative party size estimates are expected to differ between the four methods, the methods are also expected to differ in their ability to reflect the influence of these socio-ecological factors.

Methods

Study site and species

We studied chimpanzees (*P. t. verus*) at the Seringbara study site (N 07.37°; W 08.28°) in the Nimba Mountains,

Guinea, West Africa. The Seringbara study area covers approximately 25 km^2, and is situated ~6 km from Bossou, where a chimpanzee community has been studied since 1976 (Matsuzawa et al. 2011). The Seringbara study site is characterized by great topographical diversity with steep hills and deep valleys ranging in altitude from 600 to 1752 m above sea level. Vegetation includes primary tropical forest interspersed with secondary forest, riverine forest, terrestrial herbaceous vegetation (THV) dominated forest, and savanna grassland (Koops et al. 2012a). The climate is characterized by a 9-month rainy season between February and November, and 3-month dry season (Koops 2011). The Nimba Mountains have been surveyed for chimpanzees intermittently since 1992 (Humle and Matsuzawa 2001; Matsuzawa and Yamakoshi 1996; Shimada 2000), and a near-constant research presence at the Seringbara study site has been maintained since 2003 (Koops et al. 2007, 2012a, b, 2013). The study area is inhabited by at least two chimpanzee communities (Tongbongbon and Gahtoy communities), based on repeated direct and MTC observations of known individuals (Koops *personal observation*), as well as genetic evidence (Koops et al. 2012b). The chimpanzees remain largely unhabituated to the presence of human observers (i.e. only some individuals tolerate human presence), due to the difficulties of habituating chimpanzees in such extremely mountainous terrain. As such, the exact demographic compositions of the study communities are unknown.

Data collection

Data collection took place over 69 months of study between July 2003 and April 2014 (Jul 2003–May 2004, Apr–Aug 2006, Dec 2006, Nov 2007–Dec 2008, Mar 2011–Apr 2014). Data were collected by KK (2003–2014) and KL (2011) with the help of local field guides and an international team of research assistants.

Party size methods

We used four party size methods. For direct and MTC observations, party size was measured as "the [total] number of individuals present [during a single encounter] that feed and travel independently", i.e. excluding infants and juveniles (Anderson et al. 2002, p. 92). For day and night nest counts, party size was measured as the total number of nests of the same age present in a nest group, i.e. < 30 m from the nearest nest (Furuichi et al. 2001a; Koops et al. 2012a).

Direct observations (Sep 2003–Apr 2014; data collected for 48 months in total) were defined as all visual chimpanzee encounters. Chimpanzees were encountered following traces and/or vocalizations. Parties were scored as female(s) only, female(s) and offspring, male(s) only, and mixed sex (following Koops et al. 2019). When measured on the same day, parties were defined as separate parties when no overlap between individuals was observed, and when subsequent party observations around the same location were more than 1 h apart. This 1 h cut-off point was selected based on the frequency distribution between subsequent party observations from MTC data [Electronic Supplementary Material (ESM), Online Resource 1], and hence parties are statistically independent. Due to the incomplete habituation of the chimpanzees, parties of unknown type, i.e. parties where too few individuals could be reliably identified so no assessment of party composition could be made, as well as individuals of unknown age/ sex class were excluded from analyses.

Motion-triggered cameras (Bushnell Trophy Cam XLT 8MP Trail Cameras, PixController DVREye™, and TrailMaster TM700v Passive IR Trail Monitors with a Sony DCR-HC9: Jan 2008–Apr 2014; data collected for 42 months in total) were set up at 39 randomly selected locations of known chimpanzee activity (e.g. trails, feeding sites) within the home range. We therefore used a targeted camera placement approach (Boyer-Ontl and Pruetz 2014; Després-Einspenner et al. 2017; McCarthy et al. 2018), which is expected to increase detection probability and is recommended for party size data collection (Després-Einspenner et al. 2017). All MTCs recorded videos of one minute in length for data collection, with one second re-trigger time between subsequent videos. We included only traveling parties for analyses (N = 399, out of 587 parties in total) in order to minimize the confounding influence of camera placement, i.e. chimpanzee party size may vary systematically depending on the activity (Anderson et al. 2002; Boesch 1996). Parties observed on the same day at the same location were considered to be the same party when there was overlap between individuals or when subsequent parties were filmed within 1 h of each other. Due to incomplete habituation of the chimpanzees, parties of unknown type and individuals of unknown age/sex class were excluded from analyses.

For day nest counts (Aug 2003–Mar 2014; data collected for 49 months in total) and night nest counts (Aug 2003–Mar 2014; data collected for 62 months in total), all nests that were less than 1 week old were included. Nest age was assessed by the state of leaves and branches (sensu Koops et al. 2012a). For each nest group, nest status was scored as either (1) day nests: nests that were simple in construction and were judged structurally too weak to hold a chimpanzee's weight overnight; (2) night nests: nests that were elaborately constructed and often associated with feces or urine below the nests; or (3) nests of unknown status (sensu Koops et al. 2012a). Day nests and night nests were analyzed separately (Brownlow et al. 2001; Koops et al. 2012a), and based on nest age and distance between nests, nests groups were statistically independent.

Nest groups of unknown status were excluded from the analyses.

Party composition and estrous females

For parties observed during direct encounters and filmed with MTCs, data were recorded on party composition and presence of estrous females. Data were recorded on the sex class, age class (i.e. adult: > 11 years, adolescent: 8–11 years, juvenile: 4–7 years, infant: 0–4 years; Sugiyama 1999), and sexual status (i.e. adult and adolescent females: estrous or no estrous) of all individuals present. As results were similar, no distinction was made between full and semi-anogenital swellings, and all swollen females were analyzed as 'estrous females'. Parties with estrous females were scored as '1', and parties without estrous females were scored as '0'. Information on the age- and sex class of the individuals in a party was used to calculate the adult sex ratio. Adult sex ratio was calculated using the formula:

$$\text{sex ratio} = \frac{(\#\text{adult males})}{(\#\text{adult males}) + (\#\text{adult females})}$$

in which the sex ratio denotes the proportion of adult males in a given party. This calculation differs from the standard sex ratio measure to include unisexual, i.e. female(s) only or male(s) only, parties.

Rainfall

Rainfall data (Aug 2003–Apr 2014; data collected for 65 months in total) were recorded daily at 17.30 h with a manual rain gauge at the base camp (Madei camp), which is located at an altitude of 670 m. Daily rainfall measures were used to calculate monthly amounts of precipitation.

Fruit availability

To monitor the temporal and spatial availability of ripe fruit (Jul 2003–Mar 2014; data collected for 56 months in total), twenty-four 500 m transects were set up on 12 hills/valleys throughout the study site. Transects were located according to a stratified random design. Confirmed chimpanzee feeding tree and vine species with a DBH $\geq$ 10 cm within 5 m of the transect line were monitored for the presence of ripe fruit on a monthly basis (i.e. first half of each month). Ripe fruit was scored on a 0–4 scale, with: (0) ripe fruit absent; (1) 1–25% of canopy containing ripe fruit; (2) 26–50% of canopy containing ripe fruit; (3) 51–75% of canopy containing ripe fruit; and (4) 76–100% of canopy containing ripe fruit.

As a measure of fruit abundance, ripe fruit scores were used to calculate monthly Fruit Availability Indices (FAI) using the following formula (sensu Hockings et al. 2010; Takemoto 2004):

$$\text{FAI} = \frac{\sum \left(P_i \times F_i \right)}{\sum \left(P_i \times 4 \right)} \times 100$$

where FAI is the fruit availability index (%), P_i is the basal area of the tree (cm^2) and F_i is the ripe fruit availability score of the tree or vine. Months with a FAI score of > 1 were considered as high fruit abundance months, and months with a FAI score of < 1 were considered as low fruit abundance months (Koops 2011).

As a measure of ripe fruit distribution, Coefficients of Dispersion (CD) were calculated using the following formula (sensu Basabose 2004; Chapman et al. 1995):

$$\text{CD} = \frac{\sigma^2}{\mu}$$

in which μ is the mean and σ^2 is the variance of the mean of the cumulative DBHs of trees and vines providing ripe fruit in a given month. CD values equal 1 when fruit distribution is random, < 1 when fruit distribution is uniform, and > 1 when fruit distribution is clumped. CD could not be calculated for months with FAI = 0.

Data analysis

Data were tested for normality using Kolmogorov–Smirnov tests (Field 2009). All analyses were performed two-tailed, and the significance level alpha (α) was set at 0.05. Statistical tests were performed using IBM SPSS Statistics (version 22). Data from the Gahtoy and Tongbongbon communities were combined for analyses, as results were similar for the two communities.

Individual party size measures obtained for each method per month were used to calculate average 'monthly' party sizes. To compare monthly party sizes across the four methods on a month-by-month basis, we used a Friedman's analysis of variance (ANOVA) test. Post hoc Wilcoxon signed-rank tests were used to assess individual differences between methods (Field 2009). To control for multiple comparisons, a Bonferroni procedure was used (i.e. $\alpha = 0.05/6 = 0.008$). Sex ratios of parties recorded during direct and MTC observations were compared with Mann–Whitney U tests.

To assess the influence of estrous females on party size (i.e. for parties measured during direct encounters and with MTC observations), we compared the size of parties with and without estrous females with Mann–Whitney U tests. To assess the influence of estrous females on sex ratios,

we compared sex ratios of parties with and without estrous females with Mann–Whitney *U* tests.

Monthly FAI (fruit abundance) and CD (fruit distribution) values were correlated using Spearman's correlation coefficient (Field 2009). To assess the effect of fruit availability on party size, we used linear regression (Field 2009) for all four methods. In case of a significant correlation between FAI and CD, monthly party sizes were related to monthly FAI and CD values separately, as well as combined using a multiple linear regression model (fruit availability). A Bonferroni correction was used to control for multiple comparisons (i.e. $\alpha = 0.05/4 = 0.0125$). As residuals in the linear regression models were not normally distributed, we used Spearman's correlation coefficients for all methods to check for significant rank correlations between monthly party size, FAI and CD (Field 2009). Monthly party sizes during high and low fruit abundance months were compared using Mann–Whitney *U* tests; monthly party sizes for all party size methods were analyzed separately, and a Bonferroni correction was used to control for multiple comparisons (i.e. $\alpha = 0.05/4 = 0.0125$).

Table 2 Mean monthly party size estimates as measured with the four methods: 'Direct' stands for direct observations, 'MTC' stands for motion-triggered camera observations, 'Day' stands for day nest counts and 'Night' stands for night nest counts. Also other descriptive statistics are included: 'N_{months}' stands for sample size in number of months for which data were collected for each method, 'SD' stands for standard deviation of the mean, 'median' stands for median party size estimates, and 'range' stands for the range of monthly party size estimates across months for all methods

Method	Monthly party size estimates (69 months of study)				
	N_{months}	Mean	SD	Median	Range
Direct	48	3.29	1.57	3.00	1.00–8.25
MTC	42	3.23	1.58	2.94	1.00–8.50
Day	49	2.26	1.54	2.00	1.00–9.00
Night	62	5.01	4.24	4.04	1.00–27.00

Results

Party size methods compared

Month-by-month party size estimates varied significantly across methods (Fig. 1 and Table 2; Friedman's ANOVA: $\chi^2 = 23.91$, $df = 3$, $p < 0.001$). Post hoc Wilcoxon signed-rank tests showed that monthly party sizes measured with night nest counts were significantly larger than those measured with direct observations ($T_- = 13$, $Z = -3.23$,
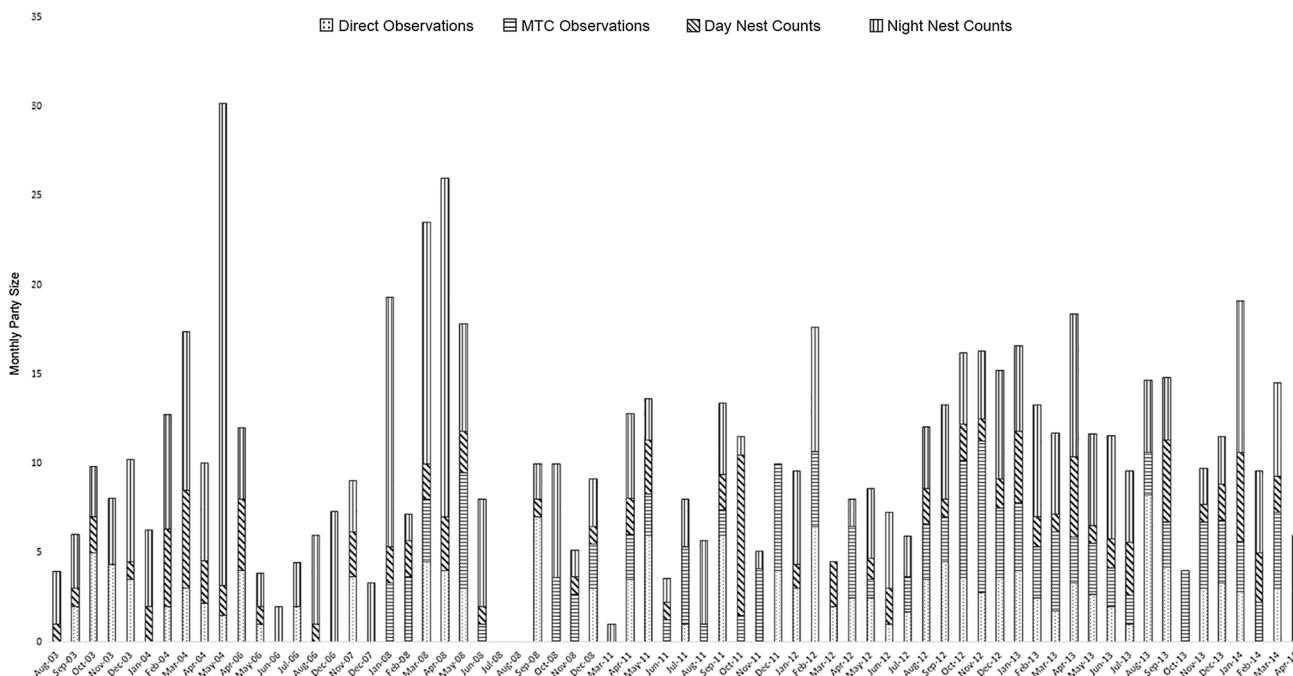

Fig. 1 Monthly party sizes measured with direct observations, MTC observations, day nest counts, and night nest counts over 69 months. The monthly party sizes of the four methods are presented in a stacked way that shows all values
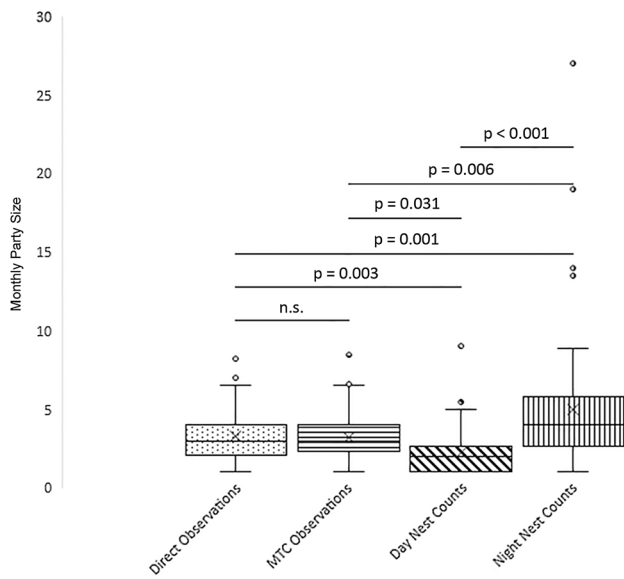
Fig. 2 Mean monthly party sizes for direct observations, MTC observations, day nest counts, and night nest counts over 69 months. Significant differences between methods are indicated with *p* values. *n.s.* not significant

Table 3 Mean sex ratio of parties measured with direct observations ('Direct') and motion-triggered camera observations ('MTC')

Method	Sex ratio				
	$N_{parties}$	Mean	SD	Median	Range
Direct	118	0.50	0.31	0.50	0.00–1.00
MTC	354	0.46	0.42	0.50	0.00–1.00

The table also includes details on the total number of parties per method for which sex ratio data could be collected ('$N_{parties}$'), as well as the standard deviation ('SD'), median ('median') and range ('range') of sex ratios observed for each method

$p = 0.001$, Fig. 2), MTCs ($T_- = 11$, $Z = -2.70$, $p = 0.006$, Fig. 2) and day nest counts ($T_- = 4$, $Z = -5.29$, $p < 0.001$, Fig. 2). Monthly party sizes measured with day nest counts were significantly smaller than those measured with direct observations ($T_+ = 10$, $Z = -2.94$, $p = 0.003$, Fig. 2), and tended to be smaller than monthly party sizes based on MTCs ($T_+ = 10$, $Z = -2.15$, $p = 0.031$, Fig. 2). Monthly party sizes measured with direct observations and MTCs were not significantly different ($T_- = 13$, $Z = -0.07$, $p = 0.947$, Fig. 2).

The sex ratio of parties measured through direct observations and MTC observations did not differ between methods (Table 3; Mann–Whitney *U* test: $U = 19549.50$, $Z = -1.07$, $p = 0.284$).

Party size, party composition and estrous females

The presence of estrous females had a significant effect on party size measured with MTC observations: Parties with estrous females had significantly more individuals than parties without estrous females (Table 4; Mann–Whitney *U* test: $U = 3599.50$, $Z = -6.29$, $p < 0.001$). No significant difference was observed when party sizes were measured with direct observations (Table 4; Mann–Whitney *U* test: $U = 573.50$, $Z = -0.95$, $p = 0.348$).

For MTC observations, sex ratios of parties with estrous females were significantly higher than sex ratios of parties without estrous females (Table 5; Mann–Whitney *U* test: $U = 4771.50$, $Z = -3.91$, $p < 0.001$). No significant differences in sex ratios between parties with and without estrous females were observed for direct observations (Table 5; Mann–Whitney *U* test: $U = 434.50$, $Z = -1.15$, $p = 0.256$).

Party size and fruit availability

Measures of FAI, CD and rainfall varied over the 69 months of study (Fig. 3), and month-by-month comparisons of FAI and CD showed a significant positive correlation ($N_{months} = 54$, $r_s = 0.529$, $p < 0.001$). No significant linear relationships were observed across the four methods between party size and (1) fruit abundance (FAI), (2) fruit

Table 4 Mean party size estimates for parties with and without estrous females as measured by direct observations ('Direct') and motion-triggered camera observations ('MTC')

Method	Party size estimates (69 months of study)					
		$N_{parties}$	Mean	SD	Median	Range
Direct	Parties with estrous females	16	4.13	2.75	3.00	2.00–13.00
	Parties without estrous females	84	3.45	2.03	3.00	1.00–11.00
MTC	Parties with estrous females	78	6.15	4.81	4.50	1.00–19.00
	Parties without estrous females	178	2.93	3.01	2.00	1.00–19.00

Data are also included on the total number of parties per method with and without estrous females for which party size estimates could be calculated, as well as the standard deviation ('SD'), median ('median') and range ('range') of party size estimates

Table 5 Mean sex ratio of parties with and without estrous females as measured with direct observations ('Direct') and motion-triggered camera observations ('MTC')

Method	Sex ratio	$N_{parties}$	Mean	SD	Median	Range
Direct	Parties with estrous females	13	0.48	0.18	0.50	0.00–0.67
	Parties without estrous females	83	0.39	0.24	0.50	0.00–0.75
MTC	Parties with estrous females	76	0.35	0.26	0.43	0.00–0.83
	Parties without estrous females	176	0.21	0.29	0.00	0.00–1.00

The table also includes data on the total number of parties with and without estrous females per method for which sex ratios could be calculated, as well as the standard deviation ('SD'), median ('median') and range ('range') of sex ratios across parties
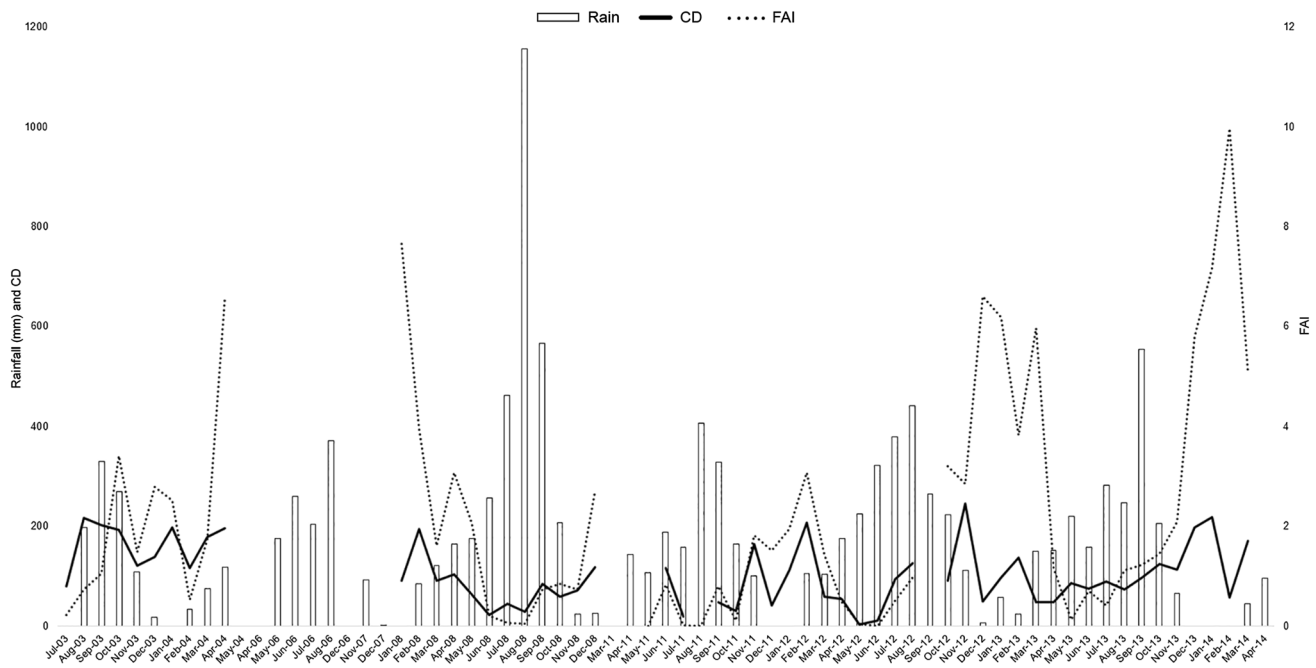
Fig. 3 Fruit availability index (FAI), coefficient of dispersion (CD) and rainfall over 69 months

distribution (CD), and (3) fruit availability (FAI and CD combined; ESM, Online Resource 2). Correlations of monthly party size, FAI and CD resulted in one significant correlation [ESM, Online Resource 3]. Monthly party size measured with MTCs showed a significant positive correlation with FAI (Spearman's rank correlation: $N_{months} = 39$, $r_s = 0.502$, $p = 0.001$).

Monthly party size estimates measured with MTCs were significantly larger during high as compared with low fruit abundance months (Fig. 4 and Table 6; Mann–Whitney U test: $U = 62.50$, $Z = -3.47$, $p < 0.001$). No significant differences in party size estimates between high and low fruit abundance months were found with direct observations (Fig. 4 and Table 6; Mann–Whitney U test: $U = 109.50$, $Z = -1.91$, $p = 0.056$), day nest counts (Fig. 4 and Table 6; Mann–Whitney U test: $U = 160.50$, $Z = -1.12$, $p = 0.268$),

and night nest counts (Fig. 4 and Table 6; Mann–Whitney U test: $U = 190.00$, $Z = -2.18$, $p = 0.029$).

Discussion

This study compared four commonly used methods to estimate chimpanzee party size, and examined the socio-ecological factors influencing party size in unhabituated chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea. The four methods differed in their party size estimates, with night nest counts resulting in relatively larger estimates and day nest counts resulting in relatively smaller estimates as compared to the other methods. Direct encounters and MTC observations did not differ in their relative estimates of party size and composition. Parties with estrous females were relatively larger and had more adult males
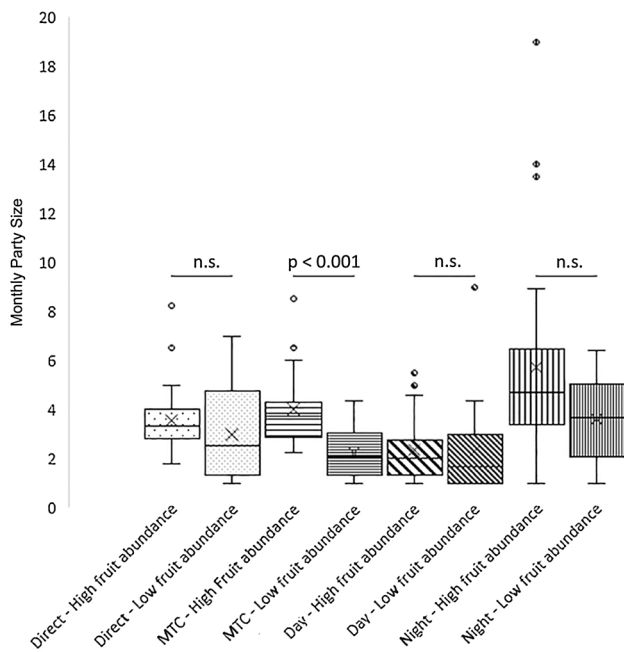
Fig. 4 Mean monthly party sizes over 69 months for direct observations ('Direct'), MTC observations ('MTC'), day nest counts ('Day'), and night nest counts ('Night') in high versus low fruit abundance months. Significant differences are indicated with *p* values. *n.s.* not significant

present. This effect was evident when party size and composition were measured with MTCs, but not through direct observations. Fruit abundance also had a significant effect on party size, with relatively larger parties occurring when fruit was abundant. Again, this finding was only apparent when measuring party size using MTCs and not through direct observations or nest counts. Party size was not influenced by fruit distribution.

The finding that night nest counts resulted in relatively larger party size estimates than the other methods supports the hypothesis that chimpanzees aggregate at night and/or that larger nighttime nest groups may be more easily located (Table 1, H11 and H12). We cannot currently distinguish between these methodological and behavioral causal factors of chimpanzee party size estimates. Nonetheless, the relatively larger party size estimates found with night nest counts indicate that this method may not be the most suitable method in detecting diurnal party size variation. However, as actual party sizes remain unknown for the unhabituated Seringbara chimpanzee community, the conclusion that night nest counts may lead to overestimations of chimpanzee party size remains preliminary and needs to be further explored. Day nest counts resulted in relatively smaller party size estimates than direct observations, and tended to be relatively smaller than MTC observations, which supports the hypothesis that not all chimpanzees build a nest during the day and/ or that some chimpanzee day nests may be missed by human observers when locating daytime nest groups (Table 1, H7 and H8). Although it is currently impossible to separate these hypotheses, the latter hypothesis seems unlikely due to the experience of the field assistants and researchers in tracing nest groups. The finding that day nest counts result in relatively smaller party size estimates indicates that this may not be the most appropriate method for estimating chimpanzee party sizes. Additionally, the smaller nest group sizes resulting from day nests counts as not all individuals build daytime nests may affect estimates of chimpanzee population sizes, densities and distributions, for which nest counts are often used (e.g. Furuichi et al. 2001a). Again, however, this conclusion towards potential underestimations of chimpanzee party sizes from day nest counts is preliminary as actual chimpanzee party sizes remain unknown for our study. No support was found in our study for the following hypotheses that: (1) direct observations result in relatively larger

Table 6 Mean monthly party size estimates during high (FAI > 1) and low (FAI < 1) fruit abundance months as measured with the four methods: 'Direct' stands for direct observations, 'MTC' stands for motion-triggered camera observations, 'Day' stands for day nest counts and 'Night' stands for night nest counts

Method	Monthly party size estimates (69 months of study)				
		N_{months}	Mean	SD	Median	Range
Direct	High fruit abundance months	27	3.56	1.38	3.33	1.75–8.25
	Low fruit abundance months	13	2.99	2.05	2.50	1.00–7.00
MTC	High fruit abundance months	23	3.99	1.56	3.73	2.25–8.50
	Low fruit abundance months	16	2.24	1.09	2.07	1.00–4.33
Day	High fruit abundance months	27	2.35	1.29	2.00	1.00–5.50
	Low fruit abundance months	15	2.28	2.10	1.67	1.00–9.00
Night	High fruit abundance months	30	5.73	3.91	4.69	1.00–19.00
	Low fruit abundance months	20	3.58	1.75	3.68	1.00–6.40

Also other descriptive statistics are included: N_{months} sample size as measured in the total number of high/low fruit abundance months for which data were collected for each method, *SD* standard deviation of the mean, *median* median party size estimates during high/low fruit abundance months, *range* range of monthly party size estimates across methods

party size estimates as a consequence of increased tolerance to humans in larger parties or because larger parties may be more easily located (Table 1, H1 and H2); (2) direct observations result in relatively smaller party size estimates due to chimpanzees fleeing or human observers failing to detect all individuals (Table 1, H3 and H4); (3) MTC observations lead to relatively smaller party size estimates because chimpanzees pass outside of the film frame of the camera either due to active avoidance or the restricted frame (Table 1, H5 and H6); (4) day nest counts result in relatively larger party size estimates as a consequence of chimpanzees building more than one nest during the day or human observers more easily locating larger daytime nest groups (Table 1, H9 and H10); and (5) night nest counts result in relatively smaller party size estimates as some nests may be missed by human observers when locating nighttime nest groups (Table 1, H13).

Direct and MTC observations did not differ in their relative estimates of party size and composition. Boyer-Ontl and Pruetz (2014) also found that camera trap observations of unhabituated chimpanzees in Senegal generally corroborated observational data from habituated chimpanzees at Fongoli (Senegal), but no specific data on party size or composition were presented. Similarly, McCarthy et al. (2018) studied the accuracy of camera trap observations in comparison to observational data for a habituated chimpanzee community at Taï and found that direct and MTC observations resulted in similar demographic compositions. However, they also showed that MTCs underestimated party size as compared with observational data (McCarthy et al. 2018). This finding differs from ours, possibly due to a difference in habituation status between the two sites. With actual party sizes known for the habituated Taï chimpanzees (McCarthy et al. 2018), this suggests that both direct and MTC observations of unhabituated chimpanzees may underestimate party size. Future research at Nimba will assess party size estimates as habituation levels increase. In sum, our findings show that different methods to measure party size result in different relative party size estimates for chimpanzees. These results are important to take into consideration when comparing chimpanzee party size measures across studies, and when using these methods to estimate community sizes, population densities and distributions.

In line with other studies, we found that fruit abundance had a positive effect on party size at Nimba, which supports the prediction that more individuals are able to join a party when fruit is abundant, and costs of co-feeding are low. This effect was, however, only observed when measuring party size with MTCs. Additionally, we found no influence of fruit distribution on party size. At Kahuzi-Biega, chimpanzee party size was positively influenced by the distribution of fruit from preferred tree species (Basabose 2004), whereas our study focused on all identified

chimpanzee food tree species. Investigating the effect of fruit distribution of preferred tree species only at Nimba is recommended for future studies. Our study adds to a growing body of evidence that the presence of estrous females has a positive influence on party size. Sex ratios were higher in parties with estrous females, indicating that more males were present (Matsumoto-Oda 1999). Again, the effect of estrous females on party size and composition was only evident when parties were measured using MTCs. Additional factors may further influence party size at Nimba, such as predation pressure, demography, time of day, location in home range, behavior, and presence of non-fruit food items (e.g. Anderson et al. 2002; Boesch 1991; Lehmann and Boesch 2004; Wrangham et al. 1996). Future research is needed to address the effects of these factors on party size. In sum, differences in the factors influencing party size may stem from temporal and spatial variability in chimpanzee grouping patterns, but our findings highlight that the use of different party size methods may also affect research outcomes.

This study highlights the potential for the use of MTCs to investigate chimpanzee grouping patterns. Our findings show that at Nimba, MTC observations did not result in relatively larger or smaller party size estimates as compared with the other methods when measuring party size in unhabituated chimpanzees. Additionally, MTCs were the only method to reflect the influence of fruit abundance and estrous females on party size and composition. These findings suggest that the MTC method is suitable for capturing the patterns and proximate causes of chimpanzee grouping patterns. In their study of habituated chimpanzees at Taï, McCarthy et al. (2018) also highlighted the usefulness of camera traps in investigating chimpanzee grouping patterns and demographic variations. Even though their camera trap observations showed smaller party size estimates than observational data, their results showed similar seasonal fluctuations and demographic compositions as direct observations (McCarthy et al. 2018). Recent behavioral studies of unhabituated chimpanzee communities also showed potential for MTC observations (Boesch et al. 2016; Kühl et al. 2016; Tagg et al. 2018). MTCs have, furthermore, proven useful for investigating presence and densities of other species (Rovero and Marshall 2009; Rowcliffe et al. 2008; Widness and Aronsen 2017). MTCs enable the collection of relatively accurate, fine-scaled data non-invasively with minimal human interference and ecological disturbance (McCarthy et al. 2018; Rowcliffe et al. 2008), and thus provide an important conservation tool. As with all methods, camera traps have limitations. For example, species' shyness to MTCs, heterogeneity in camera detection probability, and restricted filming angles may affect data collection (Després-Einspenner et al. 2017; McCarthy et al. 2018). Furthermore, technological issues

and weather conditions may pose challenges (Boyer-Ontl and Pruetz 2014; van Leeuwen *personal observation*). Although caution is warranted, MTCs provide an efficient and promising method.

In conclusion, this study showed that the four commonly used methods to assess chimpanzee party size differed in their relative party size estimates. Party size at Nimba was influenced by fruit abundance and estrous females, but the effect of these factors was only reflected by the MTC method. Our findings should be taken into account when selecting a 'best' method of party size for a particular study focus. At Nimba, our results showed that MTC observations best reflected chimpanzee party size and its influencing socio-ecological factors. MTC observations thus show promising potential in the study of unhabituated chimpanzees.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This research was non-invasive, complied with the laws of Guinea, and was approved by the Direction General de la Recherche Scientifique et l'Innovation Technologique (DGERSIT). Moreover, this research adhered to the guidelines as set down by the Division of Biological Anthropology, University of Cambridge, the host institute of the lead researcher (K. Koops) during the study.

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