




Camera traps unveil demography, social structure, and home range of six unhabituated Western chimpanzee groups in the Moyon Bafing National Park, Guinea

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Abstract

Precise estimates of population dynamics and social grouping patterns are required for effective conservation of wild animal populations. It is difficult to obtain such information on non-human great apes as they have slow reproductive rates. To gain a better understanding of demography in these populations, previous research has typically involved habituation, a process that requires years. Here, we collected data continuously over year-long periods to monitor an unhabituated population of critically endangered Western chimpanzees (*Pan troglodytes verus*) in the Moyon Bafing National Park, Guinea. We used two arrays of 100 camera traps that were placed opportunistically in two distinct 100 km² sites, named Bakoun and Koukoutamba. We identified 227 individuals in Bakoun and 207 in Koukoutamba through their unique facial features. Our camera trap data make clear that these individuals belong to six and seven closed groups, respectively. Six of those groups were near-completely sampled with an average minimum size of 46.8 individuals (range: 37–58), and a mean adult sex ratio of 1.32 (range: 0.93–2.10). We described the demographic composition of these groups and use Bayesian social network analysis to understand population structure. The network analyses suggested that the social bonds within the two populations were structured by sex homophily, with male chimpanzees being more or equally likely to be observed together than other adult associations. Through estimation of minimum convex polygons, we described the minimum home range for those groups. Compared to other chimpanzee groups living in a similar environment (mosaic savanna-forest), the Moyon Bafing region seems to host a high-density of chimpanzees with small home ranges for their group size. Our research highlights the potential of camera traps for studying the demographic composition of chimpanzee populations with high resolution and

Abbreviations: HPDI, highest posterior density interval; MBNP, Moyon Bafing National Park; MCP, Minimum Convex Polygon; WCF, Wild Chimpanzee Foundation.

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obtaining crucial information on several groups in a time-efficient and cost-effective way.

KEYWORDS

camera traps, chimpanzees, conservation, demography, monitoring

1 | INTRODUCTION

Precise data on population dynamics are necessary for assessing the effectiveness of conservation projects for wild animal populations (Conroy et al., 2012; Nichols & Williams, 2006). For elusive species with slow reproductive rates, the challenge of detecting population trends based on traditional methods of density estimation can be difficult to overcome (e.g., sperm whales, Carroll et al., 2014; mountain gorillas, Granjon et al., 2020). In this study, we test the potential of camera traps to efficiently collect detailed data on social grouping, home range and demography of several groups (i.e., chimpanzee community) of wild unhabituated chimpanzees in the Moyon Bafing National Park (MBNP), Guinea.

Monitoring is the process of measuring state variables at different points in time to estimate the state of a system and its change over time (Yoccoz et al., 2001). Less monitoring effort has focused on the demography of wild populations compared to abundance estimates (Jones, 2011), even though population dynamics is intertwined with demographic processes (Lawler, 2011). Detailed demographic information requires individual identification, which is difficult for many elusive species and typically constrains the scale of demographic studies. Demographic data are especially valuable for social species, as reproductive events occur within social groups. If external factors (e.g., poaching or habitat degradation) disturb such groups and reduce their size, their reproductive output may decline (Dunham et al., 2008; Sugiyama, 1994). Hence, it is important for conservation projects to discern whether an animal population has stable group composition and whether it displays a demographic profile that is reflective of a healthy reproducing population.

Here, we focus on the conservation and monitoring of a population of Western chimpanzees (*Pan troglodytes verus*), whose numbers across their range have declined by 80% over a 24-year period (Kühl et al., 2017). Forest destruction related to agricultural or mining activities (Palminteri et al., 2018), poaching (Campbell et al., 2008), and diseases transmitted because of increased human-wildlife contact (Köndgen et al., 2008) are largely responsible for that decline. To monitor chimpanzee populations, three commonly used methods allow for the identification of individuals. First, individual chimpanzees can be habituated to human presence, generating the most precise data on chimpanzee groups (Emery Thompson et al., 2020; Wittig & Boesch, 2019). To habituate a wild group of chimpanzees, human observers must initiate contact with them repeatedly until they realize that the human observers are not dangerous (Crockford et al., 2019). However, habituation is a slow

process, taking at least 5 years. Therefore, only one or two groups are typically habituated, potentially limiting the generalizability of findings produced by this method (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1968). Moreover, the habituation process can be costly. Increased human-chimpanzee proximity facilitates pathogen transmission from humans, despite precautions taken by researchers (Grützmacher et al., 2018), and can lead to increased mortality (Crockford et al., 2019; Goodall, 1983; Köndgen et al., 2008). An alternative approach is to identify unique individuals via the extraction of DNA from fecal samples (Arandjelovic et al., 2011; Chancellor et al., 2012). To ensure the best sampling of a target population, a restricted area is searched during several months—sometimes years—to obtain enough samples to precisely estimate population density (Arandjelovic & Vigilant, 2018; Koops et al., 2023). However, the age of individuals cannot be extracted from genetic data and this approach is therefore unable to provide information about the demographic structure of a population, other than sex and kinship structure. Another non-invasive method is camera trapping, which has increased in popularity over the past decades in the field of ecology (Wearn & Glover-Kapfer, 2017). Camera traps have typically been used in studies on chimpanzees for behavior (Bessa et al., 2022; Boesch et al., 2017, 2020; Estienne et al., 2017; Kühl et al., 2019), or estimation of population density (Cappelle et al., 2019; Després-Einspenner et al., 2017). However, few existing studies have employed camera trap methods to identify individuals and characterize social grouping in unknown chimpanzee populations (but see Head et al., 2013; McCarthy et al., 2019).

In the present paper, we use camera traps to identify individual chimpanzees in two 100 km² sites. Three initial questions motivated this study:

1. Can we identify social groups within a multigroup site with camera traps and obtain precise estimates of group composition with camera trap data?
2. Can we uncover some of the features of a population's social networks drawn from camera trap data?
3. Can we estimate the home range of the chimpanzee groups with camera trap?

Given the habitat types in the MBNP, and the absence of agricultural activities other than cattle grazing within the study areas, we expected a lower population density, smaller groups and larger home ranges compared to chimpanzees inhabiting dense forest, reflecting the lower density of food resources (Pruetz, 2018). We

further expected that groups in the study area would have sex ratios similar to those observed in other groups living in dry environments, i.e. greater than or close to one (e.g., mean ratio of 1.68 for Fongoli in Senegal, Wilson et al., 2014).

2 | METHODS

2.1 | Study site

The landscape in the MBNP, located in the Fouta Djallon region in Guinea (10.97°N to 11.46°N and 11.67°W to 10°97W) is mountainous and comprises a variety of habitats that range from grassy savanna on the plateaus to gallery forest along the rivers, with woodland and bushy savannas scattered in-between. The dry season lasts from October to April and the rainy season from May to October. We designed two study sites of 10 × 10 km, called Bakoun (11.65°N to 11.74°N and 11.23°W to 11.14°W) and Koukoutamba (11.18°N to 11.27°N and 11.46°W to 11°37W), this latter overlapping the Bafing River (Figure 1). A total of 12.4% of Bakoun study area and 26.5% of Koukoutamba is gallery forest. One and two

villages are within a 3 km buffer around the grids in Bakoun and Koukoutamba, respectively. Some areas near rivers were secondary forest from previous cultivated land. However, we did not find any active fields within the study area during the sampling periods. Capture rates of humans in the cameras were low, 0.07% for Bakoun and 1.75% for Koukoutamba.

2.2 | Data collection

We placed one passive infrared triggered camera in each of the 100 1 km² cells in each study site (Figure 1). We installed the cameras opportunistically to maximize the capture rate of chimpanzees (close to trails, water sources, or feeding trees). If cameras did not capture chimpanzees for several months, we changed their locations inside their 1 km² cells to try to increase the capture rate. Cameras were all Bushnell Trophy CAM, but different models. We set the cameras at around 60 cm height and programmed the cameras to record 60-s-long videos, with the minimum time interval between successive triggers (0.6 s or 1 s depending on the camera model). We set the sensor level parameter of the camera to high, and the infrared to

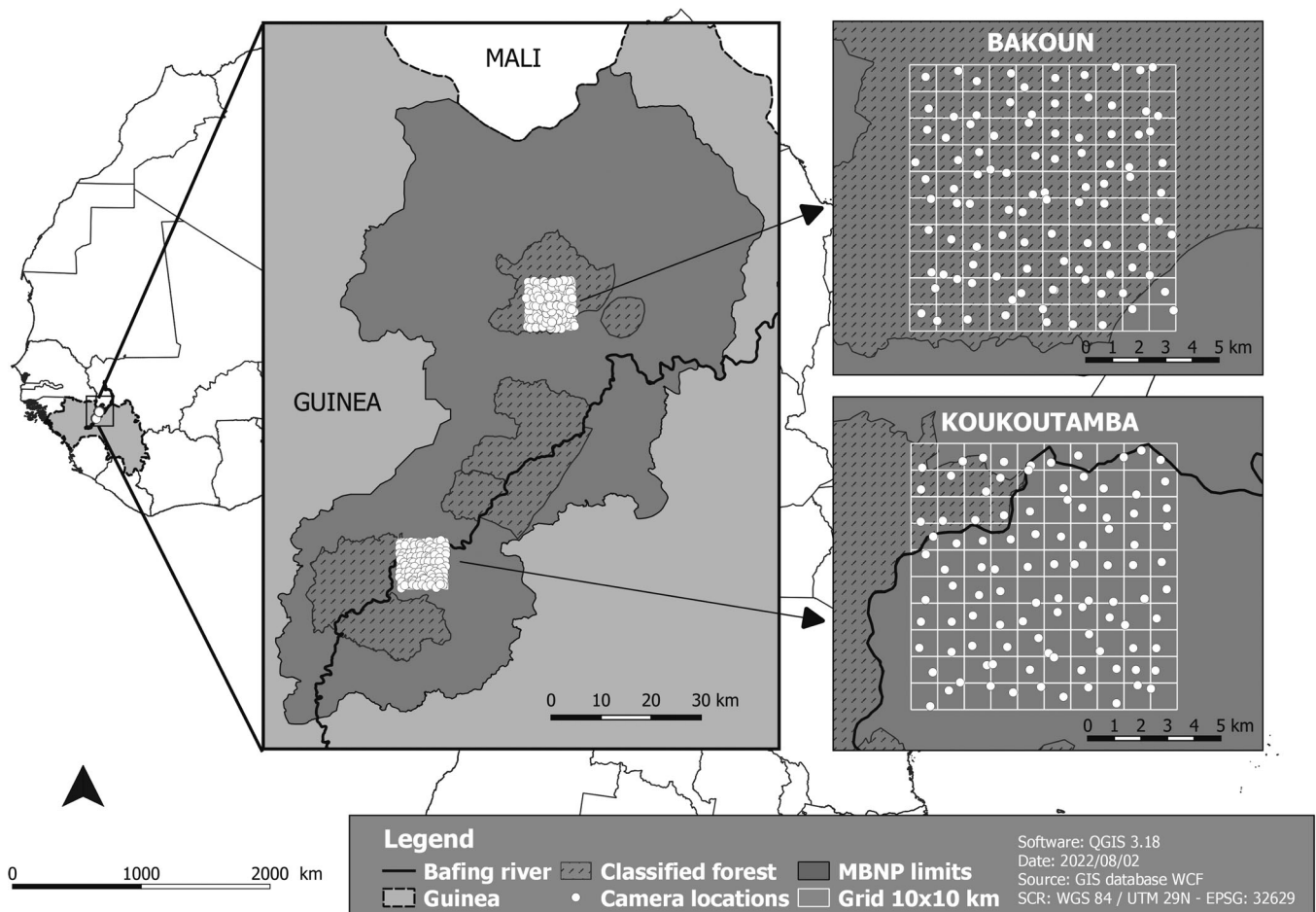


FIGURE 1 Location of the Moyen Bafing National Park (MBNP) and the two 100 km² study sites, Bakoun and Koukoutamba, with the detail of the grid cells and the opportunistic location of the camera traps in each of them (white dots).

medium. We used rechargeable batteries and visited the cameras every 4–8 weeks to change the SD card and the batteries. We first set one hundred cameras in the Bakoun site, then supplemented a few locations (maximum 16 of them at a time) with a second camera that faced the first in highly used trails to capture the faces of chimpanzees, regardless of their direction of travel. The Bakoun study took place between February 24th 2018 and January 19th 2019. We applied the same method for the second site, Koukoutamba, where 103 cameras were placed in a 100 km² area (three locations had double cameras) between March 4th 2019 to March 20th 2020. The cameras captured 2045 videos of chimpanzees in Bakoun and 2046 videos in Koukoutamba.

2.3 | Data analysis

2.3.1 | Workflow for individual identification

We sexed and assigned an age class (infant, juvenile, adolescent, adult) to all individual chimpanzees in the videos, according to their size and genital development following categories first proposed by Dr. Jane Goodall (1968). We followed the common practice of filtering low quality videos and we only tried to match recognizable individuals—i.e., if we could see the face with adequate video quality, or spot unique bodily characteristics to prevent misidentification. For the videos from Bakoun, four analysts that worked for the Wild Chimpanzee Foundation (WCF), including BD, compared independently each pair of recognizable adult males and females. Each WCF analyst coded independently each pair of individuals as being the same, different, or whether they were unsure, meaning they thought they might be the same. Then, the analysts reviewed as a group each pair considered as either unsure or the same by at least one analyst, debating their choices. After discussion, each analyst gave their final thoughts on the match. A match was validated if at least two analysts thought the pair was the same with no-one denying it. Once all adults were thus identified, we identified adolescents and juveniles using the same procedure. We followed the same workflow for the data collected in Koukoutamba, with three WCF analysts doing all the pairwise comparisons, while a fourth analyst and BD joined for the collective final decision.

2.3.2 | Interobserver reliability

The four original WCF analysts had not previously worked with chimpanzees. Training consisted of self-administered practice and collective discussion. Accordingly, we performed an interobserver reliability test 1 year after starting the identification.

Agreement between WCF analysts

A total of 16 pairs of adult males and 16 pairs of adult females were selected by BD, and the WCF analysts were asked to assess independently whether each pair of videos represented the same

individual. Chimpanzee pairs were selected to ensure a standardized video quality and similar body size. For male chimpanzees, we balanced the sample of pairs, such that 50% of the 16 presented pairs were the same individual. For female chimpanzees, 38% of the 16 pairs presented to raters were the same individuals. We calculated Cohen's Kappa (κ) coefficient (Cohen, 1960) to assess inter-rater reliability. If κ is positive, the agreement between the observers is higher than would be expected by chance. We assessed the magnitude of agreement using the scale created by Landis and Koch (1977). We found that the ratings by the observers showed substantial agreement, with κ for the four observers being 0.94, 0.88 (almost perfect agreement), 0.75 and 0.69 (substantial agreement, Tables S1–S4).

Agreement between WCF analysts and citizen scientists

To confirm independently the identification of individuals, we compared ratings (Table S5) made by WCF analysts with those made by citizen scientists—who have experience with chimpanzee identification—using the [Chimpanzee.org](https://chimpanzee.org) platform (McCarthy et al., 2021). We provided citizen scientists with 50 chimpanzee videos, from which 74 individuals were recognizable. A match between two chimpanzees was confirmed for the citizen scientists if all individuals involved in the match (at least three persons) agreed. Of the 2732 pairwise comparisons, the WCF team and the citizen scientists agreed on 30 pairs of individuals being the same and 2682 pairs being different. This led to an agreement of 99.3% between the two teams and a κ of 0.75, reflecting a substantial agreement.

2.3.3 | Group composition and social networks

Even though chimpanzee parties are relatively unstable, party members are usually members of the same social group (Boesch & Boesch-Achermann, 2000; Goodall, 1986). Hence to assign group membership, we specified a weighted adjacency matrix based on observed associations, stating how many times we saw two individuals together in the same video event, to build social networks. We define a video event as a succession of videos at the same location with their starting time separated by less than 15 min (Head et al., 2013; McCarthy et al., 2018). We plotted the social network graphs using the *igraph* (Csardi & Nepusz, 2006) and *ggraph* (Pedersen, 2022) packages in R (version 1.2.6 and version 2.0.5). We considered individuals that were observed in the same social network to be in the same group. We also computed descriptive social networks measures. Network density is the number of observed associations divided by the number of possible associations, multiplied by the number of events. It expresses how connected the groups are. Transitivity (ranging from 0 to 1) measures the tendency of individuals to cluster together and was computed using the function *transitivity* from the R package *igraph* as the ratio of the count of triangles and connected triples in the graph. If transitivity is high, if A was associated with B and C, then B and C were also likely associated with each other. Degree is calculated for each individual

and describes the number of unique individuals to which it was connected.

We applied Bayesian social network analysis to estimate whether the demographic features of the population structured these social networks. More specifically, we applied a combined social relations and stochastic block model using the *STRAND* R package (Redhead, McElreath et al., 2023; Ross et al., 2023, version 0.2.0). We specified a model for binomial data and adjusted for the number of times an individual was observed in the data within the model. We included a combined variable for age class and sex, with adult males and adult females being specified as blocks within the stochastic blockmodel. Accordingly, we were able to estimate whether the probability of observing associations was higher between adults of the same or different sexes (see Redhead, McElreath et al., 2023; Ross et al., 2023, for detailed technical outlines). To aid in interpretation of the results, we computed the contrast coefficient Δ and highest posterior density intervals (HPDI) from the posterior distribution of the age/sex parameters included in our stochastic blockmodel (reflecting how such models have been interpreted in previous research, e.g., Gettler et al., 2023, Redhead, Ragione et al., 2023). Δ represents the estimated change in the probability of observing associations between individuals of a given age/sex category (e.g., between female adults and male adults) in comparison to the probability of observed association between adult males (i.e., the reference group). We chose adult male-male associations as the reference group because chimpanzees follow a philopatric male system, hence we could expect higher bonds between them compared to individuals of the dispersing sex (Lehmann et al., 2007). Our modeling approach allowed us to estimate and condition on whether some individuals had more associations than others, and whether certain associations between two individuals were more likely observed together—irrespective of their demographic features (Table S6).

2.3.4 | Home range size and spatial segregation of the groups

Home range size is typically estimated through direct observation of chimpanzees. In the present study, we were limited by the camera trapping method, and used the point location of the camera as the observations of individuals. As the cameras were placed only within the 10×10 km grid, we cannot make any conclusions about potential use of the home range outside of the camera grid, and therefore we may underestimate home range size.

The Minimum Convex Polygon (MCP) method allowed us to calculate the smallest polygon that encompassed all locations where individuals from a given group were detected (with internal angles lower than 180° ; Hayne, 1949). Different isopleths can be considered, censoring part of the extreme data to a defined percentage to draw the smallest polygon (Worton, 1995). To avoid bias induced by the difference in the amount of time each camera filmed, we used the capture rate at each camera to feed the MCP for each chimpanzee group. We defined the capture rate by camera as

the number of video events with at least one member of the group present, divided by the number of days each camera filmed. We computed the capture rate for each camera and group and standardized it with the lowest value of capture rate. We consequently obtained a standardized capture rate of one for the camera that had the lowest capture rate and of higher values for cameras with higher capture rates. To calculate the MCP, we used a data frame comprising each location repeated x times, where x represented the standardized capture rate at that location. As the isopleths are a percentage of values, the amount of repetition in the data set is not important but the proportion is. We used the package *adehabitatHR* in R (Calenge, 2006, version 0.4.19) to compute the MCP for different intensities of use by the chimpanzees (100%, 95%, or 75% of the observations). Furthermore, we used the ratio of the 75% MCP divided by the 100% MCP to measure how much space use was concentrated in the central part of the estimated home range.

3 | RESULTS

3.1 | Identifying groups within a multigroup site with camera traps

Within the 10×10 km grid, we identified 227 individuals in Bakoun and 207 in Koukoutamba. We mapped the associations between each pair of identified individuals. Four groups of spatially separated points were evident in Bakoun (Figure 2). The few individuals in light blue and orange in the Northeast and Southwest of the grid seem to belong to two additional groups that range mainly outside of the limits of the Bakoun grid. In Koukoutamba, we identified five main groups and at least one potential additional group (triangles West from Koukoutamba 4). For the entire data collection period, no individuals belonging to one group were seen with individuals belonging to a different group.

3.2 | Capture effort and success

To assess to what extent we were able to capture most of the individuals in the different groups, we plotted a cumulative curve of the number of individuals identified over the study period (Figure 3). We expect the curve to reach an asymptote when we are close to have identified all individuals. Ideally, the slope of the curve starts close to one, before reaching a plateau, as there are fewer new individuals to identify. The cumulative curves for the four groups ranging in the centre of the Bakoun study area and two groups in Koukoutamba follow that expected shape with a change in slope after roughly 100 days of data collection. Therefore, we are confident that we identified most individuals belonging to those six groups and we detail their composition in Table 1. Mean group size was 46.8 individuals, with a mean adult sex ratio of 1.32 and a mean ratio of infant by number of adult females of 0.85. The other three groups

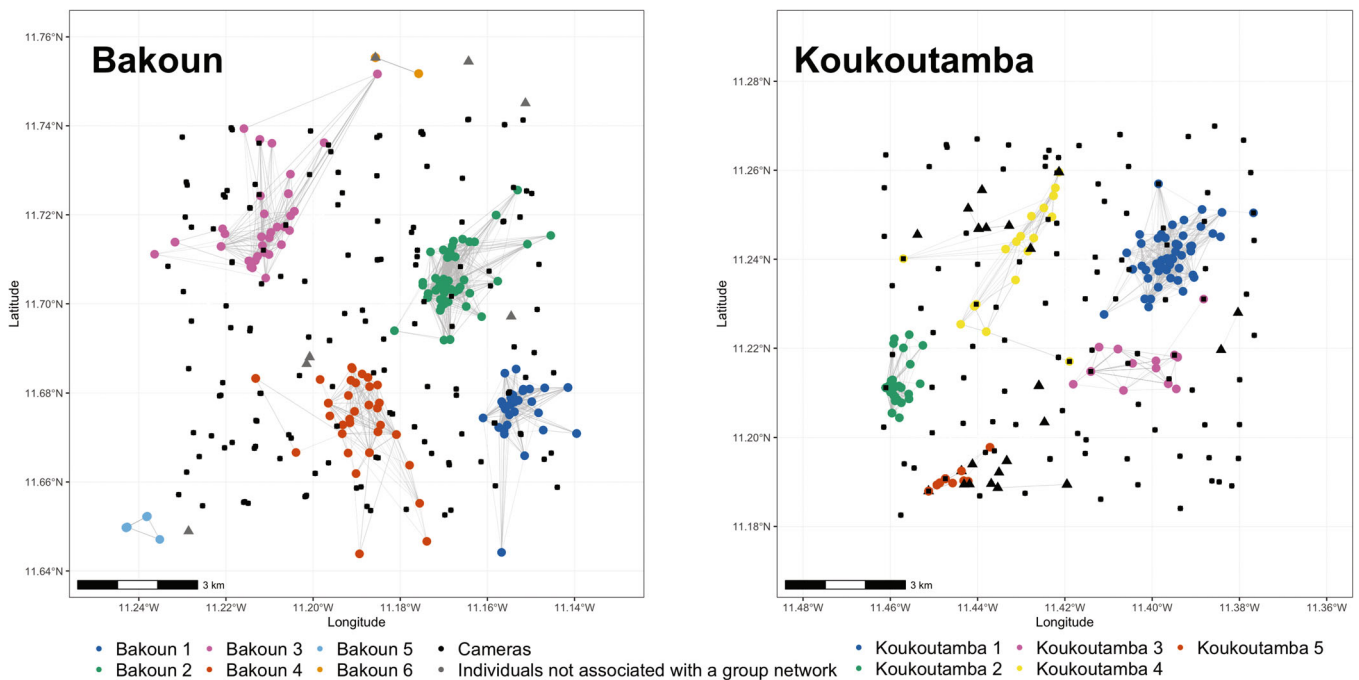


FIGURE 2 Social network based on individual association among all identified chimpanzees in Bakoun and Koukoutamba. Black squares correspond to the locations of the cameras, and colored dots represent different individuals associated with each group. Dots have been positioned at the average coordinates of their detections using the *secr* package in R (Efford, 2022, version 4.4.5). Gray lines indicate when individuals have been seen together. Triangles denote individuals that could not be associated to a group.

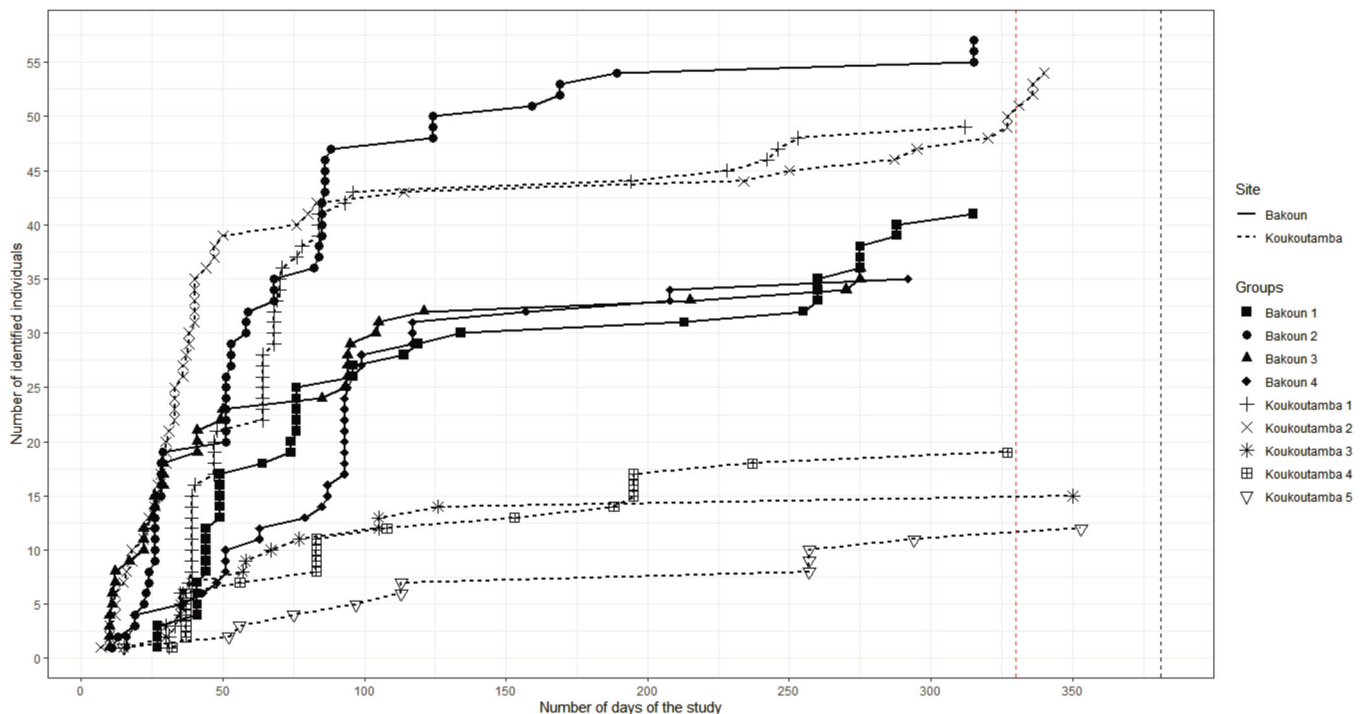


FIGURE 3 Cumulative curves of the number of identified chimpanzees over the data collection period. These curves are calculated separately for each group. Each point is the result of a new identified individual. Identification is dated as the date of the second video where the individual has been recognized (as one recapture was necessary to identify an individual). The red and black dotted vertical line delimits the end of the study period for Bakoun and Koukoutamba, respectively.

slowly increased in size without a clear change of slope during the study period.

3.3 | Age and sex structure of chimpanzee associations from camera trap data

From the descriptive data of the social networks (Table 2), we note that the number of events with recognized individuals was at least 100 for all groups, except for Koukoutamba 3, 4, and 5. This difference in data quantity could explain why the cumulative curves

TABLE 1 Number of individuals identified by sex and age class in January 2019 for Bakoun groups (B), in March 2020 for Koukoutamba groups (K). Inf is for infants, Juv for juveniles and A for adults.

Age and sex class	B1	B2	B3	B4	K1	K2
Adult male	10	13	11	11	17	13
Adult female	10	13	7	8	8	14
Adolescent male	4	6	3	5	6	6
Adolescent female	4	5	5	5	5	1
Adolescent unknown	0	1	0	0	0	0
Juvenile male	4	2	3	0	2	0
Juvenile female	2	4	2	1	1	5
Juvenile unknown	0	2	1	1	4	5
Infant unknown	9	12	7	6	6	11
Total	43	58	39	37	49	55
Sex ratio (A♂/A♀)	1	1	1.57	1.37	2.1	0.93
Ratio (Inf+Juv/A♀)	1.5	1.53	1.85	1.14	1.62	1.5
Ratio (Inf/A♀)	0.9	0.92	1	0.75	0.75	0.79

TABLE 2 Descriptive data on the data collected and the social networks for the groups in Bakoun (B) and Koukoutamba (K) sites.

Variables	B1	B2	B3	B4	K1	K2	K3	K4	K5
#Individuals	43	58	39	37	49	55	14	21	24
#Events	104	136	102	113	145	144	24	38	17
Mean/median #observation by individual (range)	7.9/6 (2-27)	7.4/6.5 (2-18)	7.3/6 (1-18)	6/5 (1-16)	7.6/7 (2-15)	6.3/5 (1-20)	2.9/2 (1-8)	4.3/3 (1-10)	1.8/1.5 (1-6)
#Observed associations	2142	3036	1058	612	1672	1350	-	-	-
Density ^a (%)	2.28	1.35	1.4	0.81	0.98	0.63	-	-	-
Transitivity ^b	0.83	0.72	0.64	0.69	0.67	0.66	-	-	-
Mean degree ^c (range)	26 (6-40)	29.9 (5-47)	14.2 (1-25)	11.8 (1-21)	19.5 (1-37)	17.24 (1-39)	-	-	-

^aThe higher the density, the more individuals are seen with each other.

^bHigh transitivity means that the network contains groups of individuals that are densely connected to each other.

^cIndividuals with high degree are more central to the network as they are connected to many individuals.

of those three groups were different (Figure 3). The lower network density of groups Bakoun 4 and Koukoutamba 1 and 2 (0.8%, 0.98%, 0.63% of all possible associations were observed, respectively) and the mean degree (i.e., individuals had, on average, 14, 19.5, and 17.2 associations) suggest that individuals in these groups were less connected than those in Bakoun 1 and 2. In all groups, individuals seemed to cluster in groups, with transitivity of 0.66–0.83. These descriptive results highlight that individuals tended to mix with many others and potentially formed parties with a diverse set of group members.

The network analyses suggested that sex influenced adult association patterns in various ways depending on groups (Figure 4). Generally, male–male adult associations were more common than mixed-sex adult associations in all groups but Koukoutamba 2. In Bakoun 1 and 3, male–male associations were more common than associations between adult females.

The network analyses further showed that there were reliable differences in how many times certain individuals were observed with others (Table S7), reflecting the large range in degree (0–40; Table 2). That is, certain individuals were observed many times with other chimpanzees, while other individuals were observed only once, with one other group member. Similarly, we found that certain pairs of individuals were more frequently observed together than others (Table S7).

3.4 | Home range estimate using camera traps

While we acknowledge potential under-estimation of home ranges (see Section 2), we observed nearly no overlap in group home range over the 11 months of data collection in Bakoun (Figure 5). However, three cameras captured members of two different groups (of all age and sexes) during different observation periods. The home ranges of the Koukoutamba chimpanzee

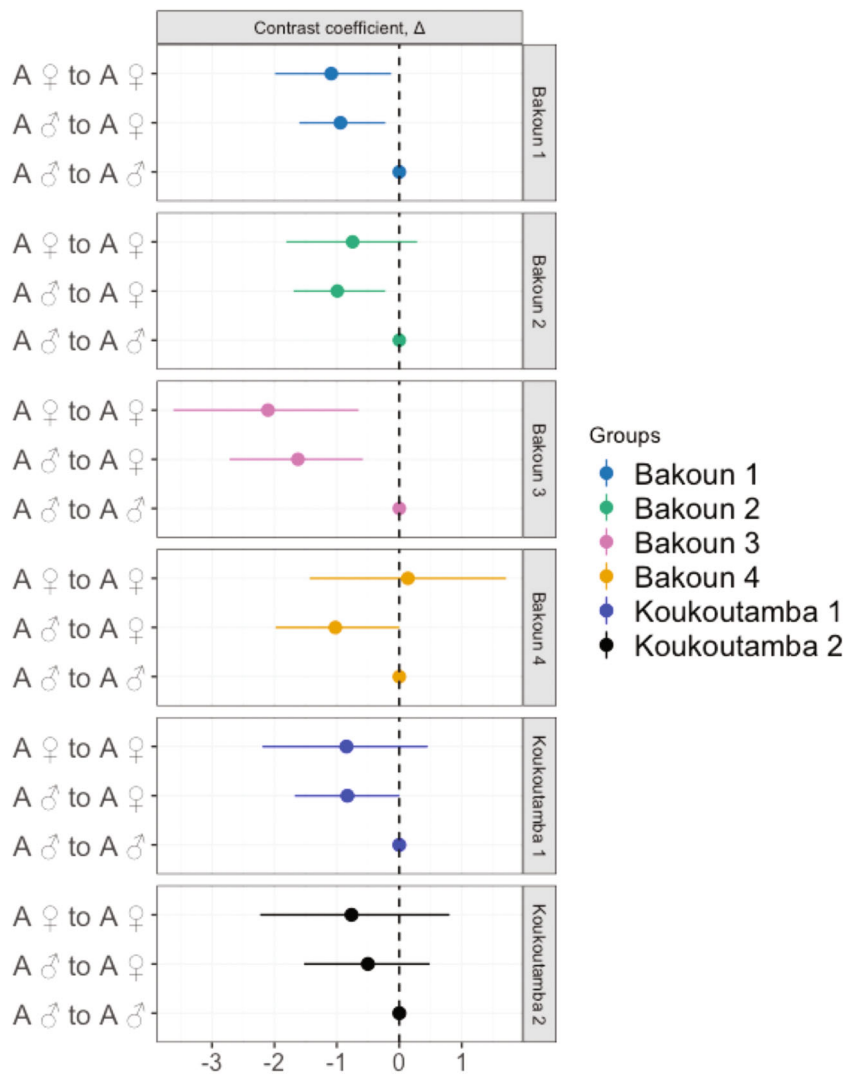


FIGURE 4 Probability of observing association between adults in six chimpanzee groups. Contrast coefficients, Δ (colored dots) and 95% highest posterior density intervals (HPDI) (colored error bars) assess the effect of sex on the probability of observing an association. Each dot represents the estimated change in the probability of observing associations between individuals of a given sex category in comparison to the probability of observed association between adult males (i.e., the reference group, on the dotted vertical line). Δ and HPDI below, and with no overlap to zero indicate that the probability of observed associations in this category is reliably lower than observing associations between adult males. The opposite is true if the Δ and HPDI are above zero.

groups are less clearly separated than for Bakoun (Figure 5), with some overlap of the MCP 100% (3.42 km² between Koukoutamba 1 and Koukoutamba 3, 1.32 km² between Koukoutamba 1 and 4, 0.78 km² between Koukoutamba 2 and 4 and even 0.57 km² overlap between three groups). The Bafing River seems to act as a natural barrier between groups. The portion of the home range of Koukoutamba 4 that was North of the Bafing River is an artifact of the MCP method, as it does not allow angles greater than 180°. Cameras at the edge of the grid captured members of Bakoun 1 and 3, which suggests that those groups' home ranges may extend beyond the grid. By contrast, Bakoun 2 is limited in the north by another group, as is Bakoun 4 in the south, meaning that we have probably not underestimated home range size much for these groups. Koukoutamba 4 is constrained by the Bafing River and the other groups, but the other Koukoutamba groups could have parts of their ranges beyond the grid, even though Koukoutamba 2 might be limited by the river and by Koukoutamba 5. Because of the uncertainty in home range size (Table S6), we estimated maximum chimpanzee density only for

the group (Bakoun 4) whose home range was least likely to extend beyond the camera grid as 2.52 ind/km².

4 | DISCUSSION

Our study suggests that camera trap surveys can provide a detailed understanding of unhabituated chimpanzee groups. We were able to distinguish multiple social groups in the MBNP landscape and produce minimum estimates of group composition (Question 1). We gained an understanding of the social structure of these groups, showing that sex appears to influence patterns of association between adults (Question 2). We were further able to delineate the minimum home range size for each group in the study area (Question 3). Overall, our findings show the potential of camera trap methods for understanding both the social and demographic features of previously unknown chimpanzee groups. While these methods do have great potential, it is important to note both their strengths and limitations in comparison to other methods used for biomonitoring.

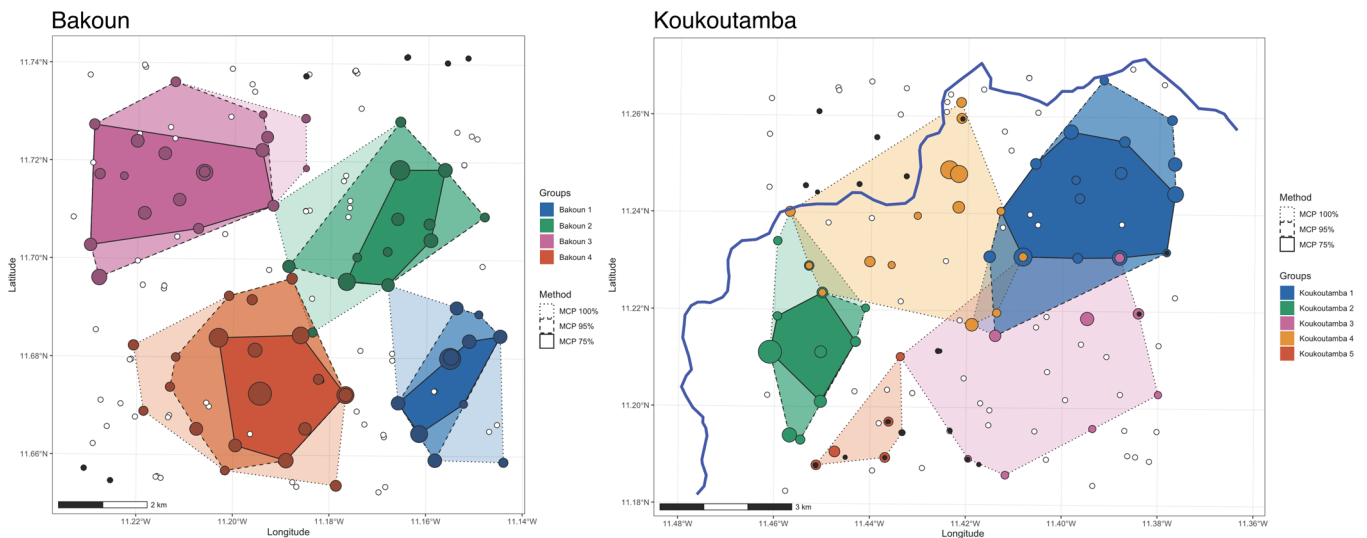


FIGURE 5 Home ranges using the Minimum Convex Polygons method (MCP 100%, 95%, and 75%). Dots (circles) represent camera locations and are white when they filmed individuals that could not be recognized or did not film chimpanzees, black if individuals could be recognized but not assigned to a group, or colored when individuals could be recognized and assigned to a group. The dots were sized proportionally to the capture rate. The different line styles indicate the boundaries of the MCP with varying percentages of data. The blue line crossing the design is the Bafing river.

4.1 | Misidentification

The present findings rely on the ability of observers to identify unfamiliar chimpanzees in videos. We found high interobserver reliability in the two tests we performed. However, these tests did not show perfect agreement, implying the possibility of misidentifications in the data set. It is important to note, however, that the tests are not a perfect representation of our recognition work. The first test compared the agreement between all analysts individually, but we used in our analysis the matches agreed to collectively. This discussion phase, when one team member could point out what might have been overlooked by another, lowers the possibility of misidentification but it was not captured in the first interobserver reliability test. The second test comparing citizen scientists and the WCF team was based on the results of the collective decisions. The difference in results between the two teams was never a mismatch. The citizen scientists however associated individuals not identified by WCF as one already identified, creating an extra observation for this individual. Another type of identification error that could occur is the creation of a ghost individual, i.e. creating a new ID for an individual already present. Alternatively, we could have merged two individuals that are different. The former would underestimate the group size, the latter overestimate it. However, with more data, the likelihood of errors would decline, as ghost and merged individuals are corrected. This is especially true for chimpanzees as the pool of individuals across time scarcely changes (except for immigrating females which can be easily spotted). Disagreements between the citizen scientists and WCF occurred because the WCF team had more information available, making the comparison between the two teams moderately uneven. In addition, when there is a highly unbalanced number of

entities in the various categories, the Cohen's Kappa coefficient tends to be biased towards low values (Feinstein & Cicchetti, 1990). Here, out of the 2732 possible pairs of individuals, only one percent of the pairs fell in the category “the pairs are the same,” which lowers the kappa value despite the two teams agreeing on 99.3% of the classification of the pairs. We cannot rule out the possibility of misidentification, but we believe that the performances of the WCF team members are high.

4.2 | Missing individuals

To provide meaningful and comparable results on demographic structure, we must be able to identify most individuals in a group. The cumulative curves provided insight into whether the groups within the study areas were close to being fully identified. While it is difficult to state with certainty that a curve is reaching an asymptote, we are confident that we were able to identify most individuals in four groups in Bakoun and two groups in Koukoutamba, as we found little change in the number of identified individuals after the first months of the study. However, we did identify a few individuals inside the home ranges of these groups that we could not assign to any group as they were captured alone. Additional data from 2020 to 2021 in Bakoun showed that those individuals were part of those groups. We confirmed that one adult male identified in 2018 belonged to Bakoun 4 while an adult female and her infant belonged to Bakoun 2. The supplemental data also allowed the recognition of new individuals, adolescents or young adults females that could have immigrated in the meantime, and new infants. In addition, in 2020 and 2021, we identified as part of Bakoun 4 two adult females (one

with an infant and one with an infant and a juvenile) that we did not identify and most likely missed in 2018. It seems, then, that the 2018 data underestimated some age classes in the demographic table, with missed individuals from two groups. These missed individuals would change the sex ratio for Bakoun 4 from 1.37 to 1.2 and for Bakoun 2 from 1 to 0.93, which are still high values compared to habituated groups in dense forest areas.

It could be possible that we also identified all individuals in the Koukoutamba groups 3, 4, and 5 even though the cumulative curves did not plateau after the first months. To investigate this possibility, we examined the largest number of individuals of a given demographic class appearing together in an event (e.g., the largest number of adult males observed together). Here, we knew that all individuals in one age/sex class were distinct as they were all captured in the same event, even though we could not identify them as we saw only their backs as they moved away from the camera. The largest tally of a given age/sex class per event can be interpreted as the minimum number of individuals in that age-sex class in the group. The minimum number of adult males obtained this way for Koukoutamba 3, 4, and 5 was bigger than the actual number of males we identified for those groups. Likewise, the minimum number of adult females in Koukoutamba 4 and 5 was also greater than the actual number of adult females identified. Accordingly, it appears that we were unable to identify all the individuals for the three remaining Koukoutamba groups.

4.3 | Social networks

Social networks are typically constructed using observational data (i.e., through focal follows or scan sampling), but they require a large time investment for researchers and are subject to several measurement biases (Castles et al., 2014; Hart et al., 2022). We took a different approach that does not require habituation and constructed social networks using observed co-occurrence of individuals in camera trap videos, which is less labor intensive (and likely to become even more efficient with the increased application of Artificial Intelligence algorithms, Schofield et al., 2019). We were able to assess group membership for each group observed in MBNP, suggesting that all these groups were closed. Social networks also differed in density across groups, with more associations observed in some groups than others, but the networks had similar transitivity, suggesting that individuals were forming parties with certain group-mates. Overall, the results tend to align with previous reports of network structure in habituated chimpanzee groups (e.g., Fox et al., 2023), suggesting that groups differ in their sociality, but preferentially associate with certain individuals.

Theory suggests that sociality and dispersal patterns are linked, with individuals of the non-dispersing sex likely to make stronger or more frequent bonds with each other (Cheney, 1992; Lehmann et al., 2007). Males are philopatric in all chimpanzee groups (Boesch & Boesch-Achermann, 2000). Evidence from habituated Eastern chimpanzees generally suggests that among adults, male-males

associations are the strongest (e.g., Whiten & Arnold, 2003). However, there are chimpanzee groups that do not match this pattern, for example in Taï, Côte d'Ivoire, where female-female associations despite being less strong than male-male associations, are stronger than what was described in Eastern Chimpanzees (Boesch & Boesch-Achermann, 2000). In the Moyen Bafing region, we found that females were less likely to be observed together than males in two groups, while there was no sex difference in the other four groups. Accordingly, the current results only partly align with the hypothesis of stronger male bonds in male philopatric systems, and hint at potential group differences in sex-biased association across the Moyen Bafing region. We did not consider effects of seasonality and food availability in the association patterns even though they are known to influence party size and group composition in some habituated groups (Satsias et al., 2022).

Nevertheless, the current study takes some first steps in understanding social structure using camera traps data. Although camera trap data underestimate the composition of parties as not all individuals are captured by the camera (McCarthy et al., 2018), previous research suggests that it is possible to create reliable social networks of chimpanzee groups (McCarthy et al., 2019). Biases caused by not capturing and recognizing all individuals in the party are likely to be equivalent for the different groups. As we used the same method for all the groups, we believe that the quantitative comparison of the social network metrics is informative.

4.4 | Home range estimation and camera trap data

Comparison of chimpanzees occupying different field-sites is difficult because studies often employ different data collection and home range estimation methods (Martínez-Íñigo et al., 2021; Vieira et al., 2019). MCP approaches for home range estimation are characterized by different biases depending on the methods used for data collection. Data collection approaches that use GPS tracking from focal follows of members of habituated groups may overestimate home range sizes—especially if using all track logs and drawing MCPs with 100% of data—because small incursions to less frequented areas (i.e., that are not in the home range) will be mapped (Worton, 1987). By contrast, data collection methods that rely on finding signs of chimpanzees' presence, such as non-invasive genetic monitoring, will likely miss areas that are less often used because the probability of finding samples will be low (Arandjelovic & Vigilant, 2018).

Data collected with camera trap share both limitations described above. Captures from camera traps are static, meaning that the estimated polygon will always be drawn with the camera locations as edges, which implies that the resolution of any home range estimate is dependent on the locations of the cameras. MCP estimates using camera trap data will, therefore, roughly map an area by drawing straight lines between cameras—at times encompassing areas that are not necessarily used by the animals. This issue is evident in Figure 5, where the estimated home range of Koukoutamba 4

includes a section of the opposite bank of the Bafing river. The MCP approach ignored the clear constraint of the Bafing River for this group, as no individuals in Koukoutamba 4 were captured on the other side of the river.

While this is an important limitation, the MCP are drawn within the grid of cameras and will therefore map minimal home ranges. Using this method, we found almost no overlap in home ranges among the Bakoun groups, a finding that differs from nearly all known chimpanzee groups, whose home range typically overlaps partly with neighbors (Goodall, 1986; Herbinger et al., 2001). In Koukoutamba, the results more closely resembled previous findings: Koukoutamba groups had overlapping home ranges when we used the MCP100. We cannot conclude confidently, however, that the groups in Bakoun had less home range overlap than groups in Koukoutamba. If mapping home range size is of interest, it would be important and easy to add cameras outside the current study area in directions where the groups could travel (no river barrier, no other groups present).

4.5 | Comparison with other methods through a conservation prism

The present study tested whether camera traps are an efficient tool for studying unhabituated chimpanzee groups. We find that camera traps are a promising tool for gathering information relevant to effective conservation actions and for monitoring their efficiency. We were able to provide detailed information on chimpanzee group composition from data gathered over only 12 months, which is much shorter than the time needed for sample collection in genetic studies (3 years in Arandjelovic et al., 2011, 19 years in Koops et al., 2023) and the minimum 5-year period for habituating chimpanzees (Crockford et al., 2019). Obtaining nearly complete data on group composition and monitoring for six groups in a 2-year period is a significant achievement, in comparison to habituation methods that result in data for at most one group within the first 10 years (Crockford et al., 2019; Goodall, 1986). The present study also offers opportunities for expanded data collection, as surveys may be repeated across years to detect demographic changes and to estimate vital rates, while also identifying the few individuals that may have been missed.

It is important to note that sampling six groups within a 200 km² area may not be fully representative for the 6600 km² MBNP. Nonetheless, monitoring methods need to be adapted to specific research questions (Conroy et al., 2012; Nichols & Williams, 2006). If a rapid estimate of population density is needed within a large area, then transect lines based on nest counts or distance sampling survey with camera traps may be the most appropriate methods (Buckland et al., 2001; Cappelle et al., 2019; Kouakou et al., 2009). Alternatively, if documenting population trends over a 5-year period is the objective, such large-scale methods will be too imprecise to provide reliable answers for chimpanzees because of their slow reproductive rate (Cappelle et al., 2021; Houa et al., 2022). Smaller-scale methods,

such as the camera trap approach presented here, can provide the level of precision needed to answer such questions. The complexity of population trend estimation for species with a slow life history forces conservation stakeholders to evaluate the trade-off between large scale studies with low precision and small-scale studies that have high precision (as shown in Table 3).

4.6 | Cross site comparison

The MBNP is a forest mosaic landscape, with few patches of denser forest along rivers, and a mean annual rainfall of 1585 mm/year (Leeuwen et al., 2020). On an environmental gradient from savanna mosaic to dense forest, the Moyen Bafing region would resemble the savanna mosaic in terms of forest cover, but it is less dry (Lindshield et al., 2021). Additionally, local communities inhabiting this area are tolerant towards chimpanzees, which benefit from a hunting taboo (Boesch et al., 2017; Heinicke et al., 2019). Accordingly, we predicted that we would discover more similarities with the chimpanzee groups inhabiting savanna mosaic environment than with groups living in denser forest (Boesch & Boesch-Achermann, 2000). We assumed that food availability was rather limited, as the forested surface is minimal within each home range of MBNP, and no active agricultural fields were present in the study areas. Chimpanzees inhabiting savanna mosaic landscapes form rather small groups compared to their home range size, resulting in low densities (Pruetz et al., 2017). With a median minimum home range size of 13.17 km² (N = 6), the results (Table S6) seem to contradict the expectation that home ranges will be larger in savanna-like habitats (Figures S2 and S3; Lindshield et al., 2021). The Bafing area may have higher food abundance than expected and there may be alternative sources of food than the ripe fruits that typify chimpanzee diets. Accordingly, in Fongoli, chimpanzees inhabiting savanna landscape endure periods of heat and dehydration stress, but do not experience stress related to a negative energy balance (Wessling et al., 2018). Low density in Fongoli might result from heat stress, which is less important in the cooler Moyen Bafing region. Additional studies on food availability will be necessary to understand how chimpanzees can persist at high densities. We already know that chimpanzees in the Bakoun area may buffer food shortages by using tools to fish for algae, which are a highly nutritious food source (Boesch et al., 2017).

As for sex ratio, we found a male bias in the MBNP we monitored. Male biased sex ratios are rather rare for chimpanzee groups living in dense forests, but are witnessed in groups inhabiting dryer environments, such as Fongoli, Senegal, where the sex ratio is 1.7 (Pruetz et al., 2017). Such male-biased sex ratios can occur in more forested areas but appeared to be contextual, for example resulting from group fission (Feldblum et al., 2018; Wilson et al., 2014). The Waibira group in the Budongo Forest Reserve in Uganda also exhibits a sex ratio close to one (0.92; Badihi et al., 2022). However, this group is one of the largest recorded with around 120 individuals and it seems to accommodate many males because of a flexible core-peripheral social structure that reduce male–male

TABLE 3 Advantages and disadvantages of the different methods for chimpanzee monitoring.

Method	Density/variation	Home range size and use	Social structure	Demography	Financial cost	Effort
Transect line based on nest counts	Useful for large areas/detect only large trend	No/No	No	No	Low	<1 year
Genetic data (capture-recapture)	Useful for medium area/detect medium trend	Yes/Only with large effort	No	Incomplete	High	>2 years
Direct observation after habituation	Single group/small trend	Yes/Yes	Yes	Yes	Very high	>5 years
Camera trap distance sampling	Large scale/detect only large trend	No/No	No	No	Medium	>1 year
Capture-recapture with Camera traps	Several groups/small trend	Yes/Yes	Yes	Yes	Medium	<2 years

intragroup competition (Badihi et al., 2022). Finding a male-biased sex ratio in the MBNP groups might suggest that it is common for chimpanzees inhabiting dryer environments. With a high density of chimpanzees in the area, it is possible that there is strong intergroup competition, which might favor a high number of adult males relative to females (Lemoine et al., 2020). However, more detailed data on home range and patrolling would be needed for a fuller understanding of how male chimpanzees in the MBNP manage intragroup competition.

4.7 | Conclusion

We have shown that a relatively dense camera trap design (one camera per km²) makes it possible to gather more detailed information from several chimpanzee groups than other monitoring methods like nest counts or genetic census. The camera trap method also provides an alternative time-effective approach to collecting demographic data, with less human disturbance than habituation methods. We were able to reliably recognize most individuals that ranged in the study site in a year-long study period and would recommend that future research is plan with a similar time frame and with a density of one camera per km². The present study also suggests that long-term non-invasive monitoring of unhabituated groups is feasible, if the design would be carried on over several years.

Through this design, we were able to characterize important features of the Moyen Bafing population, with the composition of six groups showing a male-biased sex ratio, and many dependent infants. The groups were of moderate size compared to other habituated groups, and they inhabited what seem to be rather small home ranges. This was surprising for the type of habitat the population inhabits, which is dryer and includes less forest than most parts of the chimpanzee range. Moyen Bafing may represent one of the last remaining strongholds for Western chimpanzees, perhaps even more so than already acknowledged (Kühl et al., 2017).

AUTHOR CONTRIBUTIONS

Benjamin Debetencourt: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing—original draft (lead); Writing—review & editing (lead). **Mamadou Moussa Barry:** Data curation (supporting); Investigation (supporting); Supervision (supporting); Validation (supporting); Writing—review & editing (supporting). **Mimi Arandjelovic:** Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (supporting); Writing—review & editing (supporting). **Colleen Stephens:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Visualization (supporting); Writing—review & editing (supporting). **Nuria Maldonado:** Data curation (supporting); Investigation (supporting); Supervision (supporting); Writing—review & editing (supporting). **Christophe Boesch:** Conceptualization (equal); Formal analysis

(supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing—original draft (supporting); Writing—review & editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the interobserver findings of this study are available in the Supporting Information material of this article. The other data that support the findings of this study are available from the corresponding author upon reasonable request. Supporting Information is provided in the eponym word document, and the pdf document "Cross_site_comparison".

ETHICS STATEMENT

All research was conducted following the American Society of Primatologists Code of Best Practices for Field Primatology, and in respect to the Guinean law.

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