Received: 25 January 2018 | Revised: 12 July 2018 | Accepted: 17 July 2018
DOI: 10.1002/ajp.22904

RESEARCH ARTICLE

WILEY AMERICAN JOURNAL OF PRIMATOLOGY

An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*)

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Funding information
Fonds de Recherche Québec-Nature et Technologies; Robert Bosch Stiftung; Max-Planck-Gesellschaft

Demographic factors can strongly influence patterns of behavioral variation in animal societies. Traditionally, these factors are measured using longitudinal observation of habituated social groups, particularly in social animals like primates. Alternatively, noninvasive biomonitoring methods such as camera trapping can allow researchers to assess species occupancy, estimate population abundance, and study rare behaviors. However, measures of fine-scale demographic variation, such as those related to age and sex structure or subgrouping patterns, pose a greater challenge. Here, we compare demographic data collected from a community of habituated chimpanzees (*Pan troglodytes verus*) in the Taï Forest using two methods: camera trap videos and observational data from long-term records. By matching data on party size, seasonal variation in party size, measures of demographic composition, and changes over the study period from both sources, we compared the accuracy of camera trap records and long-term data to assess whether camera trap data could be used to assess such variables in populations of unhabituated chimpanzees. When compared to observational data, camera trap data tended to underestimate measures of party size, but revealed similar patterns of seasonal variation as well as similar community demographic composition (age/sex proportions) and dynamics (particularly emigration and deaths) during the study period. Our findings highlight the potential and limitations of camera trap surveys for estimating fine-scale demographic composition and variation in primates. Continuing development of field and statistical methods will further improve the usability of camera traps for demographic studies.

KEYWORDS
biomonitoring, camera trap, demography, *Pan troglodytes*, party size, seasonal variation

1 | INTRODUCTION

Demographic factors play a key role in the structures and behavioral patterns of animal societies. Group density, size, and structure affect diverse behaviors including dispersal (Aars & Ims, 2000; VanderWaal, Mosser, & Packer, 2009), infanticide (Watts, 1989), mating (Goldizen, 1988), and ranging (Markham, Gesquiere, Alberts, & Altmann, 2015). Patterns of behavioral variation can also be understood better by incorporating demographic variation with other factors like ecology, phylogenetic constraints, and individual and social learning (Mitani, 2006).

In social species like primates, demographic patterns are typically studied through direct observations of individual groups, with longitudinal data spanning seasons, years, or even decades (Clutton-Brock & Sheldon, 2010). Such data are challenging to acquire and rely on the habituation of subjects to researcher presence, a process that may require years of investment before all group members are identifiable and accustomed to direct observation (Williamson & Feistner, 2003). In rare and elusive species, habituation may be entirely unfeasible. Further, researchers have noted ethical implications of habituation, given the potential to influence study subjects' behavior or induce stress, in addition to the potentially increased risks of poaching or disease transmission in some species (Fedigan, 2010; Gruen, Fultz, & Pruetz, 2013; Williamson & Feistner, 2003).

Noninvasive research and monitoring approaches offer alternatives or supplements to direct observation. These methods include well-established survey techniques (e.g., line transects) as well as recent advances in biomonitoring, such as the use of drones (Koh & Wich, 2012), passive acoustic monitoring (Kalan et al., 2015), noninvasive biological sample collection for genetic, hormone, or pathogen analyses (McCarthy et al., 2015), and camera trapping (Head et al., 2013). Camera traps allow particularly for the study of rare and elusive species and are effective for monitoring a wide array of taxa (Burton et al., 2015). Studies often extend beyond single species to examine ecological diversity and community structure (Ahumada et al., 2011; Meyer et al., 2015; Rovero et al., 2017). Camera trap-based methods also allow the study of rare and interesting behaviors, including predation (Leimgruber, McShea, & Rappole, 1994), geophagy (Galvis, Link, & Di Fiore, 2014), nocturnal activity (Boyer-Ontl & Pruetz, 2014; Tan, Yang, & Niu, 2013), and tool use (Bluff, Troscianko, Weir, Kacelnik, & Rutz, 2010; Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016; Torralvo, Rabelo, Andrade, & Botero-Arias, 2017). Additionally, camera traps have the critical advantage of allowing researchers to avoid the aforementioned logistical and ethical issues associated with habituating animals to researcher presence. Such noninvasive methods are particularly valuable given the need to survey and monitor ecosystems and populations threatened by the ongoing global biodiversity crisis (Butchart et al., 2010).

Broad population assessments, such as measures of distribution and relative abundance, are among the most common objectives of camera trap studies (Burton et al., 2015). Population dynamics, including measures of birth and death rates, can also be estimated (Karanth, Nichols, Kumar, & Hines, 2006). However, sampling with adequate temporal and spatial intensity to produce sufficiently precise estimates of group or population dynamics is often costly and time-intensive (Karanth et al., 2006). Finer demographic assessments, such as individual residence status, grouping patterns, and age structure, while highly informative, often require individual recognition and have been reported only rarely (Galvis et al., 2014; Karanth et al., 2006). Camera traps offer the potential to collect valuable data on demographic variation within and among populations and present an efficient alternative to traditional studies of demography and behavior, yet remain largely untested for estimating fine-scale demographic variation.

Chimpanzees (*Pan troglodytes*) are an apt model in which to test the degree of demographic variation detectable by camera traps. They live in social groups termed "communities" that range in size from about 20 to over 200 individuals (Langergraber, Watts, Vigilant, & Mitani, 2017; Stumpf, 2011). Within these communities, chimpanzees have a fission-fusion social structure in which individuals cluster in fluid parties of varying size and composition (Goodall, 1986). Chimpanzee party size and composition vary based on numerous factors including food availability and the presence of estrous females (Anderson, Nordheim, Boesch, & Moermond, 2002; Mitani, Watts, & Lwanga, 2002; Stanford, Wallis, Mpongo, & Goodall, 1994). The high degree of temporal and spatial variation in chimpanzee party size and composition provides the opportunity to examine the extent to which such variation can be reliably detected and quantified using camera traps.

Our aim was to assess the effectiveness of camera trap-based demographic measures in a community of western chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d'Ivoire, whose demography was already known through years of close observation and whose party compositions are recorded on a daily basis by observers. In a previous study, Després-Einspenner, Howe, Drapeau, and Kühl (2017), demonstrated that camera traps could be used for accurate measurements of chimpanzee density in this region using spatially explicit capture-recapture models. Here, we directly compared party compositions obtained from systematic follows with those obtained from camera trap videos recorded during the same period. We examined the degree to which camera trap data provided accurate assessments of party size, seasonal variation in party size, community demographic changes (births, deaths, emigrations, immigrations), and community composition (age/sex structure). We also examined whether changes in capture probability occurred over the study period since these could indicate decreasing trap shyness through habituation to camera traps and lead to improvements in estimating party size and composition over time.

A better understanding of both the potential as well as the limitations of camera traps for studying demographic variation can inform future research. For example, since camera traps do not require study subjects to be habituated to observer presence, their use could be applied to study an increased number of social groups across larger spatial scales. This would allow for more refined studies of intraspecific demographic variation and habitat use. Such studies could be useful particularly for conservation planning in threatened populations; however, before demographic assessments can be made using camera trap data, it is critical to understand better the degree to which such data can provide accurate and precise estimates of demographic parameters.

2 | METHODS

2.1 | Study site

We collected data in the Taï National Park, Cote d'Ivoire, (5°08′N to 6° 07′N, and 6°47′W to 7°25′W) from June 2014 to June 2015, which included both camera trap and long-term observational data. There are two annual dry seasons: one major dry season (November to February) and one minor dry season (July to August). Rainy seasons occur annually from September to October and from March to June (Doran, 1997). Among four habituated chimpanzee communities in the study area, this study focused on the East Group, which had been habituated for over a decade (Wittig, 2017). During the study period, the East community initially comprised 36 chimpanzees, with several demographic changes over the course of this period (see section 4).

2.2 | Camera trap placement and sampling

Camera traps were deployed from June 2014 through March 2015. In total, 83 camera traps (Bushnell Trophy Cam™; Model #119576C) were placed throughout the home range of the East community (mean = 64 cameras at a time; range = 13–80; Després-Einspenner et al., 2017). Each camera was placed either at a systematic location (*N* = 23), defined by 1 × 1 km grid system laid over the home range of approximately 40 km^2 (Després-Einspenner et al., 2017), or at a targeted location (*N* = 107 total locations across the study period) in the home range (Figure S1). Systematic cameras were placed in open areas within 30 m of the intersection points of grid cells and were not moved throughout the study, with the exception of two cameras that were relocated <3 m because one was damaged by a leopard and the other invaded by termites. Targeted locations were those frequently visited by chimpanzees (e.g., nut cracking sites, trails, natural bridges, or fruiting trees). If a targeted camera did not record chimpanzees for one month, it was moved to a different location in the same grid cell. In addition to camera placement, the habitat type, camera location (e.g., trail, fruiting tree), UTM coordinates, camera height, orientation, and camera coverage area were recorded. Camera coverage area, the camera trap field of view, was calculated per camera location as detailed in the Supporting Information (SI). Camera traps recorded for a duration of 1 min per video, once triggered. If an animal remained in front of the camera trap for >1 min, the camera was re-triggered again until motion was no longer detected, with a minimum 1-s interval for re-triggering following the end of each 1-min recording. Camera trap effort (total no. of cameras active × weeks active) was 1,720 trap-weeks for targeted cameras and 760 trap-weeks for systematic cameras. Camera trap data collection adhered to animal care regulations and legal requirements of Côte d'Ivoire, as well as to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

2.3 | Video analysis of chimpanzee party composition

For each chimpanzee video recorded, one of two observers, each of whom had studied the chimpanzees for several years, viewed the video and recorded the identities of each individual chimpanzee captured on the video. Both observers independently viewed a subset of 25% of these videos, and their Cohen's Kappa score for inter-observer reliability for individual identification was high (Cohen's Kappa = 0.814; Després-Einspenner et al., 2017). With subsequent viewing, any disagreements on individual identification were resolved or the identity of the chimpanzee was recorded as "unidentified."

We recorded camera trap party size in units of temporal events, with the camera trap party size equaling the total number of distinct chimpanzees recorded in a given event. We defined an event as any videos recorded at the same camera location on the same day, with videos occurring within 15 min of another, as detailed in the SI.

2.4 | Observational party composition data

Observational party composition data were obtained during daily focal animal follows of chimpanzees in the study community (Altmann, 1974), which included systematically recording the composition of parties to which the focal belonged, and were extracted from the Taï Chimpanzee Project's long-term database. These data comprised a 12-month period, July 2014 to June 2015 (*N* = 228 focal days), which included all full months of camera data collection as well as three additional months, to allow us to examine patterns of seasonal variation in observational party size over a full year (see below). For party compositions, observers recorded all weaned individuals visible to them, and continuously updated the data as any changes in composition occurred. Camera trap data included infants as well as weaned individuals, so to make observational data comparable, we subsequently added dependent infants to observational party compositions when their mothers had been recorded in parties. We sampled only the first observational party composition per hour to avoid biases related to repeated, non-independent observations from the same parties. From these, we extracted the number of individuals in each demographic (age/sex) class (infants: 0–5 years; juveniles: 5–10 years; adolescents (F/M): 10–13/10–15; adults (F/M): >13/>15; Boesch & Boesch-Achermann, 2000) and the total observational party size.

3 | DATA ANALYSIS

3.1 | Party size

First, we assessed the degree to which camera trap videos produced similar estimates of chimpanzee party size as compared to observational data. To this end, we directly compared the size and composition of chimpanzee parties captured on camera to corresponding observational data on party size and composition. We matched camera trap party data with concurrent observational data that were collected: (i) during the same minute as the camera trap video; (ii) within a 100-m radius of the camera, which allowed for potential error in GPS location data as well as accounting for diffuse spatial associations among individuals in a single party; and (iii) with at least one identified individual on camera also recorded by observers, as further confirmation that the same parties were being directly compared. We used Spearman correlations to assess the direction and strength of the relationship between camera trap party size and observational party size (Siegel & Castellan, 1988).

3.2 | Seasonal variation in party size

Next, we modeled the effect of seasonality on party size in both data sets. We included party size as the response in the models and used date and time of day as predictors, as described in the SI. In the camera trap model, we included party size for all chimpanzee parties recorded on camera during the study period as the response variable. In the observational model, we included party composition data for one full year (July 2014 to June 2015), which included the period during which camera traps were installed. We used Generalized Linear Mixed Models (GLMMs) fitted in R (version 3.4.0, R Core Team, 2017) with the functions “glmer” or “glmer.nb” of the lme4 package, version 1.1–12 (Bates, Mächler, Bolker, & Walker, 2015).

To account for the potential for particular chimpanzees or camera locations to influence variation in party size and composition, we included the random effect of focal follow subject or camera location in the observational and camera trap model, respectively. Moreover, to minimize Type I error rates (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) we included in each model the random slopes of date and time within the random effect. Further, to account for forest visibility influencing the probability of activating camera traps, we included the log of camera coverage area as an offset term in the camera trap model.

To fit the observational model, we first fitted a GLMM with a Poisson error structure, but due to overdispersion (dispersion parameter = 5.50) we instead fitted a GLMM with a negative binomial error structure using the function “glmer.nb” which did not show overdispersion in either model (observational model: 0.97; camera trap model: 0.87).

To test for significance, we used likelihood ratio tests (LRT) to compare the full model to a null model that lacked the fixed effects test predictors of date while retaining all other terms present in the full model. All model assumptions were met and model stability did not reveal influential cases (detailed in SI). The camera trap model comprised 317 events at 76 total camera locations with chimpanzee detections while the observational model comprised 3,509 party composition observations with 23 focal subjects.

We also examined whether reducing camera effort would lower our ability to detect seasonal variation in party size. To this end, we conducted a simulation programed in R in which we reduced the number of camera locations ($N = 76$ in original data) to 60, 50, 40, and 30 over the same study duration, and simulated 1,000 data sets for each number of camera locations by randomly sampling from the camera locations. We determined the likelihood of finding significant results for the effect of season at each number of camera locations.

3.3 | Demographic composition and changes

We examined the degree to which community demographic composition could be inferred based on the demographic composition obtained from the number of unique individuals captured on video during the study period, including infants. Doing so requires individual recognition, which was feasible in this data set due to the video observers' high degree of prior experience with identifying these chimpanzees. However, when unhabituated or unfamiliar chimpanzees are studied, individual identification, though possible, is a more time-consuming and challenging process (Head et al., 2013). Therefore, we examined whether, even in the absence of known individual identifications, we could infer community demographic composition by: (i) analyzing the size and composition of the largest party to appear on camera and (ii) calculating 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), then aggregating the maximum number of distinct individuals seen in each category as a proxy for total community composition. We compared the age class structure obtained using these methods to the true age class structure of the community during the study period, obtained from observational data, and tested whether they were significantly different using Fisher's exact tests.

Similarly, we studied whether demographic changes could be detected over the course of the study period by examining whether appearances (births and immigrations) and disappearances (deaths and emigrations) were detected in both the observational and camera trap data sets. We also examined whether there were false positive “appearances” (erroneously confirmed video captures of chimpanzees known to be absent or deceased) and “disappearances” (prolonged absences of video captures of individuals recorded as present in the observational data).

3.4 | Trap shyness

The ability to measure party size and composition accurately may be influenced by “trap shyness,” the tendency for some or all individuals to avoid camera traps, leading to the potential failure to detect chimpanzee parties and an underestimation of party size. With increasing exposure to camera traps, however, chimpanzees may habituate to them, thereby attenuating any such effects. To examine this possibility, we fitted two models. In the first, we tested whether higher proportions of the members of parties were captured on camera as the study progressed, which may indicate that fewer individuals avoided camera traps over time ($N = 68$ matched camera trap and observational parties, as described above). In the second model, we tested whether the likelihood that a camera trap would capture chimpanzees on a given day increased over the course of the study period, since this would indicate that parties were less likely to avoid camera traps altogether as the study progressed.

To fit both models, we again used GLMMs fitted in R with the function “glmer” of the lme4 package. We fitted both models with a binomial error structure. In the first model, the response was whether a given individual present in a party was captured on camera as a function of day of the study period and observational party size (fixed effects), and included event, individual ID, and location (as well as the combination of individual ID and location) as random effects (intercepts). As random slopes we included day of the study period and party size within individual ID and location. In the second model, the response was whether a camera trap was triggered by chimpanzees on a given day as a function of the time since the study began and the time since the camera trap was installed at a given location (fixed effects). As a random effect (intercept) we included the camera trap location and also random slopes of both fixed effects within camera trap location. As above, all model assumptions were met and model stability did not reveal influential cases (as detailed further in SI). Sample size for the first model was a total of 1,042 combinations of event and individual, nested in 68 events, 37 individuals, and 36 locations, and for the second model, a total of 13,063 camera days nested in 76 camera trap locations.

4 | RESULTS

A total of 595 chimpanzee videos were recorded during the study period. These comprised a total of 317 events, with a mean of 1.8 videos per event (range: 1–34).

4.1 | Party size

Camera trap party size and observational party size showed a weak positive correlation overall (rho = 0.31, $p = 0.01$, $N = 68$; Figure 1) and in each demographic class (Table S1). Camera trap party size (mean = 7.3 ± SD = 4.7) tended to underestimate observational party size (mean = 15.4 ± SD = 8.7; Figure 1), and, in general, observational party size was not accurately predicted based on camera trap party size (estimate ± SE: 0.5670 ± 0.1699, $t_{66} = 3.34$, $p = 0.01$).

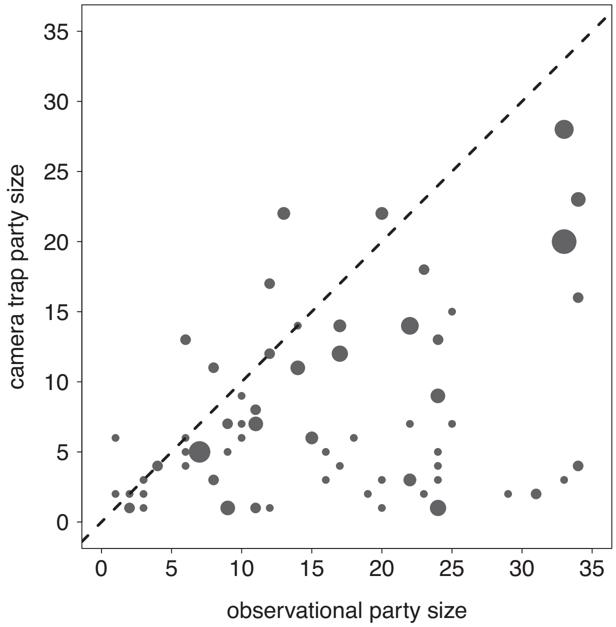

FIGURE 1 Correlation between camera trap party size and observational party size in matched parties ($N = 68$ matched events). The dotted line indicates a hypothetical perfect relationship (rho = 1) between observational and camera trap party size. Point size indicates the number of videos comprising the camera trap event ($N = 1–12$)

4.2 | Seasonal variation in party size

In the observational data, the full model as compared to the null model showed significant seasonal variation in party size (LRT: $\chi^2 = 19.723$, df = 2, $p < 0.001$). Time-of-day predictors had no significant effect on party size variation (Table S2).

In the camera trap data, we also found significant seasonal variation in party size (LRT: $\chi^2 = 7.595$, df = 2, $p = 0.022$). Also similarly, time-of-day predictors were not significant (Table S2). Camera trap data again indicated lower party sizes across the study period than observational data (Table S3), but the patterns of variation in the two models were highly similar, with both data sets indicating a peak in average party size during the major dry season, November to February (Figure 2 and Table S4). Reduced camera effort in the simulated data led to a lower likelihood of finding a significant effect of seasonal variation (Table 1).

4.3 | Demographic composition and changes

Of 37 total chimpanzees present over the course of the study period, 36 were captured on camera (while one not captured was born near the end of the study period; see below). The largest party captured on video in a single event, in January 2015, comprised 28 chimpanzees.

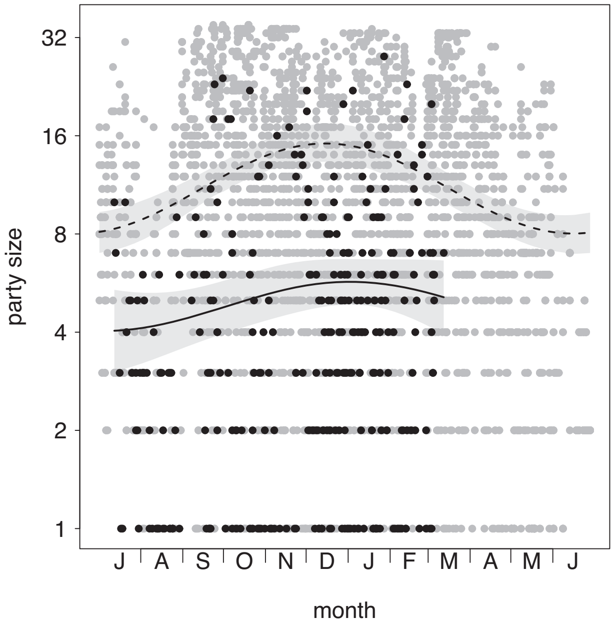

FIGURE 2 Seasonal variation in party size, as measured using observational and camera trap data. Model prediction lines for both camera trap (solid line) and observational (dashed line) models are indicated, with 95% confidence intervals for each. Gray points indicate observational model data while black points indicate camera model data. Camera traps were used over a 9-month period while observational data were extracted from a full year that included the camera trap study period

TABLE 1 Results of reduced camera effort on the number of events in simulated data and the probability of finding significant seasonal variation in party size in camera trap data

Camera locations[a]	Events[b]	Prob. seasonal variation[b]
60	251	0.54
50	208	0.38
40	167	0.28
30	125	0.20

[a] Randomly sampled from $N = 76$ total camera locations with 317 independent events in original data.

[b] Mean of 1,000 simulations.

Across all events, the aggregated maximum numbers of chimpanzees in each demographic class provided an estimate of 29 distinct chimpanzees. Demographic composition as inferred from these measures was very similar to the true demographic composition of the East Community (Figure 3). Age class structure did not differ significantly from true community age class structure in either the largest party captured (Fisher's exact test: $p = 0.872$) nor for the aggregated maximum values per age class category (Fisher's exact test: $p = 0.982$).

There were three deaths, one emigration, and one birth during the study period. For the three deaths, individuals were last captured on camera a maximum of 10 days prior to last being recorded in the observational data. The emigrating female chimpanzee was last recorded on camera on the same date she was recorded to emigrate, and not subsequently in the remaining 3.5 months of the study period. The single birth occurred 17 days prior to the de-installation of the final cameras during the study period, and this infant was the only individual who was never captured on camera during the study period.

It took 15 days following the first camera installations until chimpanzees were captured on camera, and required a maximum of 49 days for all individuals to be captured (Figure 4). Three chimpanzees (one juvenile female plus one adult female and her infant) were not captured on camera during the first month of data collection, but subsequently were all captured at least once per month. Of the 32 chimpanzees present continuously throughout the study period, 23 (72%) were captured at least once per month on camera. The maximum absence from camera trap data for an individual in the study community was 57 days, for an adolescent female. During this period, she was also not recorded in the observational data for 29 days.

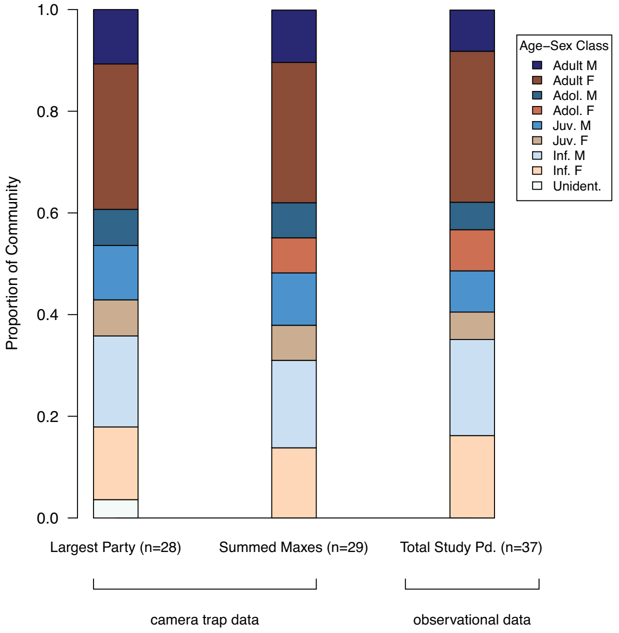

FIGURE 3 Demographic composition of the Taï East Community, inferred from proxy measures of the largest party size recorded in a single camera trap event (left) and the summed maximum numbers of individuals seen in any demographic class across events (center), compared with the true demographic composition during the study period (right), assessed from observational data records

4.4 | Trap shyness

In the first model, which assessed changes in individual capture probability in parties over time, an increased observational party size appeared to affect detection probability negatively. We found no obvious effect of camera trap habituation, however; day during the study period did not affect capture probability (Table S5). In the second model, which assessed whether an individual camera trap was more likely to be triggered as the study period progressed, neither time since study onset nor time since camera installation appeared significant (Table S6).

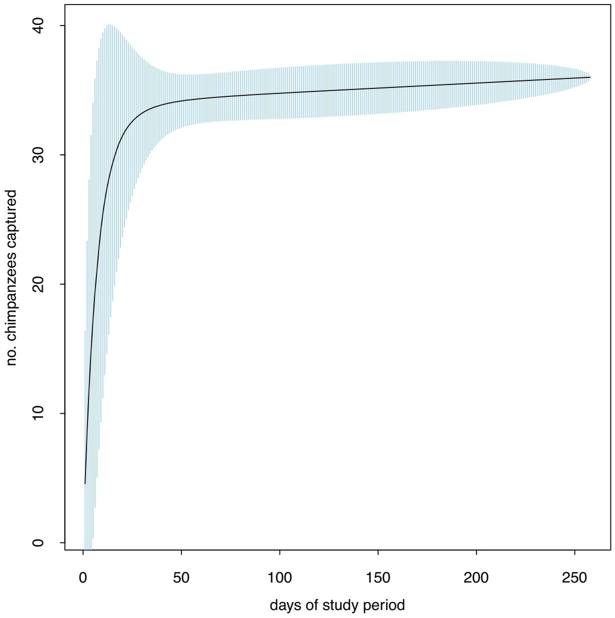

FIGURE 4 Accumulation curve for the number of individual chimpanzees captured on camera over the study period. Light blue lines indicate 95% confidence intervals. All chimpanzees were confirmed as captured on camera traps at 49 days following the beginning of the study period

5 | DISCUSSION

We found that camera trap data on chimpanzee party size considerably underestimated party size recorded by observers in the field, but provided a minimum estimate that could be useful for relative measures of party size variation (Figure 1). Indeed, we found significant and similar patterns of seasonal variation using both observational data and camera trap data (Figure 2). Both data sets revealed seasonal peaks in party size during the major dry season, a period of higher food availability (Boesch & Boesch-Achermann, 2000). These results conform to the pattern found previously at Taï (Boesch & Boesch-Achermann, 2000) and to the positive relationship between food availability and chimpanzee party size observed at other sites (Matsumoto-Oda, Hosaka, Huffman, & Kawanaka, 1998; Mitani et al., 2002). In comparison with other chimpanzee populations, the Taï chimpanzees demonstrate relatively high cohesion and experience somewhat lower seasonal variation in food availability (Boesch & Boesch-Achermann, 2000; Doran, 1997), both of which may lead to lower levels of party size variation throughout the year compared to many other sites. Therefore, these results suggest promising potential to detect seasonal variation in party size associated with ecological variation in other chimpanzee populations as well.

We also found that camera trap data allowed for a reasonably accurate approximation of community demographic composition and changes. All but one individual, an infant born near the end of the study period, were captured on camera during data collection (Figure 4). Further, we found that—even without relying on data regarding individual identities—we could approximate demographic composition with relatively high accuracy (Figure 3). Demographic changes (three deaths and one emigration) were detected in both observational and camera trap data via individual disappearances during the study period, but one birth near the end of the study period was not detected in the camera trap data. Chimpanzee births are typically difficult to observe directly, even in habituated communities. Female chimpanzees often isolate themselves socially when giving birth, a strategy that may help decrease the risk of infanticide (Nishie & Nakamura, 2017). In this case, the timing of the birth was confirmed by observers via direct observations of the female on successive days prior to and following the birth. Similarly, deaths and emigrations are rarely observed directly and must be inferred following prolonged absences. The emigration in this study was directly observed and so the timing could be confirmed. One death in this study was directly confirmed and the body found on the day of occurrence, while the other two deaths—of an adult female and her infant—were inferred when, following their absence from direct observations for 11 days, the female's juvenile daughter was first observed without her mother and sibling. Therefore, our results reflect a comparison of data obtained using two methods while acknowledging that—even in well-habituated study groups under direct observation—it can be difficult to acquire precise information regarding primate births, deaths, and emigrations.

Gaps in individual detection also occurred in the camera trap data, with one adolescent female being undetected for 57 days. However, she also was not detected in the observational data for 29 days during this period, suggesting she may have been absent or peripheral in the territory and hence absent from both data sets as a result. Indeed, gaps in individual detection also occur even in observational data on well-habituated chimpanzee communities, and may be particularly likely in large or widely distributed groups or for individuals who are more elusive or less habituated (Langergraber et al., 2014).

The variation detected in party size in this study might be attributable to factors such as high chimpanzee density or intensive sampling effort. However, chimpanzee density in this study area (0.67 indiv/km^2; Després-Einspenner et al., 2017) is rather low in comparison to many other chimpanzee study sites (range: 0.1–4.81 indiv/km^2; reviewed in Poulsen & Clark, 2004). In contrast, simulation data suggested that intensive sampling effort allowed detection of seasonal variation, with reduced sampling intensity leading to a lower probability of this outcome (Table 1). Després-Einspenner et al. (2017) previously examined the effects of reduced sampling intensity on the accuracy and precision of density estimates for this study community and found that reduced sampling intensity (though not reduced duration) still produced relatively accurate and precise estimates. Using a subset of the data from widely distributed camera trap locations across the home range (ensuring similar effort and spatial coverage using both systematic and targeted camera trap placement), they found that most individuals could be detected and density could be measured accurately with as few as five camera traps. In contrast, precisely estimating fine-scale measures of party size and group dynamics may require greater sampling effort than required to estimate density and abundance. Therefore, it is important to consider research goals and desired data output carefully when designing camera trap studies. Irrespective of the aims, more broadly distributed camera placement within an estimated territory is likely to yield more accurate measures, particularly for study groups with heterogeneous habitat use (e.g., eastern chimpanzees: Kahlenberg, Thompson, & Wrangham, 2008).

Although our results suggest promising potential for using camera traps to estimate demographic composition and variation within and among social groups, we note several limitations as well. The relatively weak positive correlation between camera trap party size and observational party size indicates that camera trap party size should be considered a minimum estimate and should not be used as an indicator of the true number of individuals present in a given party. Because of the fluid nature of parties, they cannot be "recaptured" in the same way stable social groups can; what is captured on camera in a given event is the only available estimate for true party size, despite the potential for stochastic variation in detection. In this study, party size negatively predicted individual capture probability, indicating that with increasing numbers of chimpanzees in a party, the likelihood of capturing any given individual decreased. In addition, Després-Einspenner et al. (2017) previously found that detection probability in this community varied based on other factors including prior detection at the same camera, individual heterogeneity (varying trap shyness among individuals), sex, season, and understory vegetation density. Heterogeneity in capture probability and trap shyness also pose challenges to obtaining accurate and precise demographic measures in other camera trap studies (Harmsen, Foster, & Doncaster, 2010; Sequin, Jaeger, Brussard, & Barrett, 2003; Treves, Mwima, Plumptre, & Isoke, 2010; Wegge, Pokheral, & Jnawali, 2004). Nonetheless, overall trap shyness may be expected to attenuate over time as individuals habituate to camera traps. In the current study, we found that several chimpanzees were not observed on camera during the initial month of data collection but subsequently appeared, suggesting a potential effect of trap shyness on the likelihood of appearing on camera when present in a party. However, time elapsed over the study period neither led to a higher likelihood of chimpanzees triggering the camera, nor to a higher proportion of members of observational parties being captured on camera, suggesting trap shyness did not attenuate substantially over time. A longer study period than used here may be necessary to detect attenuated trap shyness over time. Alternatively, some individuals may never fully habituate to camera traps irrespective of exposure length. To overcome limitations in capture probability, future research could focus on the potential for improvements in: (i) field methods that would allow parties to be captured more fully on camera (e.g., paired cameras recording from different angles at a given location, potentially leading to more individual captures per event) or (ii) analytical methods that would allow accurate party size estimation by using detection histories at sampling locations, thereby correcting for missed individuals despite heterogeneous capture probabilities.

Caution is also warranted in interpreting camera trap measures based on individual recognition (e.g., capture-recapture models, as well as measures of demographic structure and changes), given that video coder experience (in addition to factors such as illumination, vegetation density, and individual orientation toward the camera) may affect recognition and therefore the associated estimates. This may be the case particularly for studies of nonhuman primates, which often lack distinct markings used for individual identification in other species (e.g., tiger stripes: Karanth et al., 2006). The video observers in this study had years of prior experience studying these habituated chimpanzees, and their knowledge was essential for accurately assessing individual identities and for the resulting measures that relied on them. Without this knowledge, such estimates may be less accurate and precise. However, other demographic measures presented here, such as our estimates of camera trap party size and proxy measures for demographic structure, do not rely on individual recognition and are unlikely to be affected by observer knowledge of individual chimpanzees. These results suggest it would be feasible to obtain estimates of relative or minimum social group size and demographic structure for unhabituated primate groups, even in the absence of individual identification. This would allow comparative studies across numerous social groups in addition to studies of temporal demographic variation within groups and populations. For example, seasonal variation in food availability affects local population density in primates such as Japanese macaques (Hanya et al., 2006) and Bornean orangutans (Kanamori, Kuze, Bernard, Malim, & Kohshima, 2017); camera trap-based methods therefore may offer a myriad of opportunities to examine the role of seasonal variation in demographic patterns in primates.

Indeed, despite the caution warranted when using camera trap data to estimate fine-scale demographic variation, there are many promising applications of these data. They may potentially provide more accurate and precise measures of fine-scale group abundance than relying on indirect signs such as nest group size, thereby aiding behavioral studies as well as conservation monitoring efforts. Camera trap data can also be useful to supplement data obtained using other methods. For example, camera trap data can elucidate nocturnal activity and capture rare behaviors that would otherwise be difficult to observe. These data could also be used to provide baseline measures of abundance and composition prior to habituating a new study group. Such methods may also facilitate and supplement the efficient and accurate collection of direct observational data (e.g., Sirianni et al., 2017).

Noninvasive methods like camera trapping, when used carefully and in complement with other monitoring approaches, can provide a wealth of information regarding species presence, abundance, and key behaviors of interest (Ahumada et al., 2011; Foster & Harmsen, 2011; Galvis et al., 2014). Our findings illustrate applications for demographic research in primates as well. Given the threat of extinction faced by great apes and many other species, there is an urgent need to understand the usefulness of such approaches to maximize their potential effectiveness for studying remaining populations.

ACKNOWLEDGMENTS

The authors thank the Max Planck Society in Germany, Robert Bosch Foundation, Centre Suisse de Recherches Scientifiques, Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, Ministère de l’Environnement et des Eaux et Forêts, and the Office Ivoirien de Parcs et Reserves in Côte d’Ivoire, as well as the Taï Chimpanzee Project (TCP) for the opportunity to conduct research in Côte d’Ivoire. Camera trap data collection was possible through the financial support of the Centre for Forest Research—Fonds de Recherche Québec Nature et Technologies International internship program (MSc scholarship to Després-Einspenner). We thank Appollinaire Gnahe Djirian, Oulaï Landry, and Frédéric Yehanon Oulaï for providing party composition data extracted from the long-term database of the TCP, as well as Frédéric Yehanon Oulaï for identifying chimpanzees in the camera trap videos. We also thank Marina Cords and two anonymous reviewers for helpful comments that improved this manuscript. Field protocols, data collection, and data analysis complied with animal care regulations and applicable national laws in Germany and Côte d’Ivoire.

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How to cite this article: McCarthy MS, Després-Einspenner M-L, Samuni L, et al. An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). *Am J Primatol*. 2018;80:e22904. https://doi.org/10.1002/ajp.22904