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Research Article

Evaluating Genetic Capture-Recapture Using a Chimpanzee Population of Known Size

ANNE-CÉLINE GRANJON,[1] *Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*

CAROLYN ROWNEY, *Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*

LINDA VIGILANT, *Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*

KEVIN E. LANGERGRABER,[2] *School of Human Evolution and Social Change and Institute of Human Origins, Arizona State University, 900 Cady Mall, Tempe, AZ 85287, USA*

ABSTRACT Genetic capture-recapture (CR) estimates of population size have potential for aiding the conservation and management of rare or elusive animals. To date, few studies have explored the performance of genetic CR estimates by implementing them in a population of known size. We evaluated the accuracy and precision of genetic CR estimates by genotyping fecal samples collected opportunistically over the territory of a well-studied group of approximately 190 previously identified and genotyped eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Kibale National Park, Uganda. We compared the performance of genetic CR estimates based on 3-month and 3-year sampling periods to explore the impact of lengthened sample periods, which are expected to increase accuracy and precision of estimates but also increase the chances of violating population closure assumptions. We compared the effects of using spatial and non-spatial models and equal or heterogeneous detection probabilities upon estimates. Over the 3-year period, we detected 54% of the group members and produced population size estimates with more accuracy and narrower confidence intervals than the 3-month sampling period. The population remained effectively closed over the 3 years and detection heterogeneity was linked to age but not sex. Non-spatial methods estimated group size more accurately than spatially explicit methods, which had a stronger tendency to underestimate population size. This study suggests that genetic CR may produce accurate and precise population size estimates if substantial effort is allocated to sample collection and genotyping. © 2016 The Wildlife Society.

KEY WORDS capwire, genetic census, genotyping, microsatellites, *Pan troglodytes*, population size estimators, spatially explicit.

Reliably estimating the size of an animal population, and detecting changes in population size over time, are essential for assessing a population's conservation status and the effectiveness of protective measures. The difficulty or inadvisability of capturing and marking individuals in certain species led to the increasing application of genetic capture-recapture (CR) approaches to estimate population size using individually distinctive multilocus genotypes derived from non-invasively collected source material including shed hair, feathers, and feces (e.g., elephants [*Loxodonta cyclotis*], Eggert et al. 2003, bears [*Ursus arctos*], Bellemain et al. 2005, wolves [*Canis lupus*], Caniglia et al. 2011). Although a number of increasingly sophisticated genetic CR models are available to estimate population size, all models depend on a set of assumptions, and the extent to which these assumptions are met with empirical data from the wild will determine the model's performance. Simulations of genetic CR estimates have investigated the effect of violating models' assumptions on the estimates (Miller et al. 2005, Petit and Valière 2006, Efford 2011, Blanc et al. 2013), but the extent to which assumptions are violated in natural conditions, and the magnitude of any resulting biases, is largely unknown. Empirical evaluations of CR population size estimates using natural populations have been limited to comparisons with estimates of population size derived from other methods (e.g., min. population size [Bellemain et al. 2005], transects [Zhan et al. 2006, Arandjelovic et al. 2010], visual count [Puechmaille and Petit 2007], tracking [Hájková et al. 2009], camera-traps [Janečka et al. 2011], trapping sessions [Gerber and Parmenter 2014]). However, the use of such comparisons is limited if these other methods are themselves imprecise (Bellemain et al. 2005, Puechmaille and Petit 2007, Stenglein et al. 2010, Gerber and Parmenter 2014).

Wild great apes, including chimpanzees (*Pan troglodytes*), gorillas (*Gorilla* spp.), orangutans (*Pongo* spp.), and bonobos (*Pan paniscus*), are typically wary of humans and occur at low

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[1]*E-mail: celine_granjon@eva.mpg.de*
[2]*E-mail: kevin.langergraber@asu.edu*

density. These features, in combination with their endangered status (International Union for the Conservation of Nature 2008), make the use of indirect population size estimation methods (e.g., genetic CR) useful to avoid direct contact and possible disturbance of social behaviors. Population size estimates for great apes have traditionally been based on counts of signs of individual presence (e.g., nests built each night for sleeping; McNeilage et al. 2006, Kouakou et al. 2009). But recent studies have reported that estimates based on such data have such low precision that they may detect only very dramatic changes in population size (Wanyama et al. 2010, Piel et al. 2015). There is some evidence that genetic CR gives more precise estimates of great ape population size than do traditional ape census methods, but the accuracy of the genetic CR results and the best manner of implementing such studies are unclear (Arandjelovic et al. 2010, 2011; Chancellor et al. 2012; Moore and Vigilant 2014; Roy et al. 2014; McCarthy et al. 2015). A challenge in estimating population size with genetic CR is how to model the heterogeneous detection probabilities among individuals. Although researchers often consider how detection heterogeneity may be influenced by factors including age and sex, the true detection probabilities remain unknown. Statistical tests are routinely implemented to determine the best fitting model, but validation studies using known populations are lacking.

In Kibale National Park, Uganda, members of the Ngogo group of eastern chimpanzees (*Pan troglodytes schweinfurthii*) have been individually recognized and studied for years, making the population size and age and sex composition during the sampling period precisely known. Chimpanzees have a fission-fusion social system, whereby all of the members of a group (termed community in the primatological literature; Sugiyama and Koman 1979) are never found in the same place at the same time but instead associate in temporary parties that vary in size, duration, and composition. Especially in the east African chimpanzee subspecies considered here, adult males tend to associate in larger parties than do adult females (Gilby and Wrangham 2008, Langergraber et al. 2009). The easier detection of multiple than lone fecal samples may lead to a sex difference in detection probabilities. Age may also create biases in detection probabilities in great apes, as previous studies on paternity and behavior reported that fecal samples from individuals $\leq$3 years old are difficult to obtain even with intense research effort involving direct observations of habituated individuals (Vigilant et al. 2001, Inoue et al. 2008, Wroblewski et al. 2009, Langergraber et al. 2013).

Our objective was to evaluate the performance of several commonly employed genetic CR methods by using them to estimate the number of individuals present in a group of chimpanzees in Kibale National Park, Uganda. Using data collected over a 3-month and a 3-year sampling period, we compared the accuracy and precision of 3 different types of CR methods of population size estimation, including 1 non-spatial Bayesian model (Petit and Valière 2006, Arandjelovic et al. 2010), 3 non-spatial maximum likelihood (ML) models (Miller et al. 2005), and 5 spatially explicit capture-recapture (SECR) maximum likelihood models (Efford 2011). The Bayesian model, 1 non-spatial ML model, and 2 spatially explicit models assume equal detection probability. The 5 other ML models, both non-spatial and spatially explicit, assume detection heterogeneity, and 1 of these models specifically assumes sex-dependent detection heterogeneity.

Because we predicted male-biased and age-dependent detection probabilities, we expected underestimation of the population size from the 4 equal-detection models (Miller et al. 2005, Efford 2011). We also expected SECR models to underestimate population size because SECR considers individuals sampled at low frequency and at the edge of the sampling area to have their home range center outside the sampling area instead of belonging to the study population, whereas our sampling area corresponded exactly to the home range (territory) of this chimpanzee group. We expected the population to have membership changes over 3 years but not 3 months; thus, we expected overestimation of population size for the 3-year sampling period. Alternatively, we predicted the 3-year sampling period could produce more accurate and precise population size estimates because the longer sampling period would likely provide an increased number of detections.

STUDY AREA

We used samples collected from 2011 to 2013 in the 35.2-km^2 territory of the Ngogo group of chimpanzees, located in the 795-km^2 Kibale National Park of southwestern Uganda (Fig. 1). The territory of the Ngogo chimpanzee group was surrounded on all sides by neighboring groups of chimpanzees. The Ngogo territory is at 1,400–1,470 m in altitude and typically experiences about 1,500 mm of annual rainfall, mostly during March to May and September to December. Kibale lies at the intersection of montane and lowland rainforest and has a temperate climate (range = 16–23°C). The Ngogo chimpanzees predominately use old-growth forest in an area that also

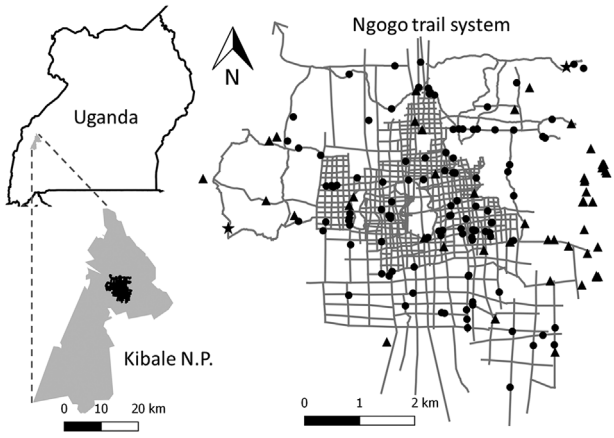

Figure 1. Sampling area in Kibale National Park (N. P.), Uganda. Lines represent trails in the Ngogo territory, circles and triangles represent chimpanzee fecal samples collected during the 3-month (2012) and 3-year (2011–2013) sampling periods, respectively. Stars represent the 2 locations where samples from 3 chimpanzees belonging to non-Ngogo groups were collected.

includes colonizing forest regenerated from anthropogenic grassland (Lwanga 2003).

METHODS

This research was reviewed by the Institutional Animal Care and Use Committee (IACUC) of Boston University and deemed not to require official IACUC approval due to it consisting only of non-invasive behavioral observations and sample collection. This research was reviewed and approved by the Uganda Wildlife Authority and Uganda National Council of Science and Technology to meet all animal welfare laws of the country in which data collection occurred (Uganda).

Known Group Size and Composition

The Ngogo group has been the subject of year-round, continuous study since 1995 (Watts 2012). All individuals are individually identified, named, and habituated to close (5–10 m) observation by researchers. The group is monitored on a daily basis by 2–3 local Ugandan field assistants who conduct focal follows of individuals (Altmann 1974) from 0700 to 1600. At 15-minute intervals they record the identities of known, previously identified individuals, and newly identified individuals (i.e., births and females that have immigrated into the community) that are associating in the same party as the focal individual. If the presence of a known, identified individual has not been recorded for 3 months, we consider them to have left the community (i.e., either by death or for ~13-yr-old females, by emigration) on the day after they were last observed. The majority of individuals are observed $\geq$1 time/month, allowing accurate determination of group size at any given point in time.

Age classes are defined as infants (from birth to 5 yr), juveniles (5 yr to adolescence), adolescent females (first appearance at ~10 yr of an anogenital sexual swelling associated with increased fertility, until first birth), adolescent males (having descended testes, which typically occurs at 10 yr, until 16 yr), adult females (having given birth, which typically occurs around 15 yr), and adult males ($\geq$16 yr). For this study, we used the ages of individuals as of 1 June of the relevant year(s).

Sampling Design

We collected fecal samples along an extensive grid-like trail system that was slightly larger (47.1 km^2) than the territory of the Ngogo group (Fig. 1). One intensive sampling period of 3 months was extended by prior and subsequent opportunistic sampling to create a sampling period of 3 years. For the 3-month sampling period, each day we collected samples from a predetermined route along the trails with a north-south orientation. We began our sampling routes with the easternmost north-south trail and moved steadily west until all north-south trails had been included in our sampling routes. We then conducted sampling routes along west-east trails and trails with an irregular, non-grid-like directionality, in the areas of the trail system where north-south trails were absent. Our sampling routes were thus evenly distributed over the entire territory and predetermined rather than influenced by the daily locations of chimpanzees. Our sample collection routes during the 3-month sampling period totaled 293.4 km and covered an average of 9.8 km/day (range = 0.1–19.5 km). We collected 368 fecal samples on 30 days between 2 February and 27 May 2012.

The 3-year sampling period (5 Jan 2011–8 Aug 2013) encompassed the 3-month period and included an additional 85 samples collected opportunistically by a 3-person team whose main focus was to search the Ngogo territory for illegal hunting snares. These samples were all collected from the same area as in the 3-month sampling period but were not as evenly distributed, with relatively more samples collected from the edges of the Ngogo territory where hunting snares are more likely to be found (Fig. 1).

We employed the ethanol-silica 2-step fecal sample collection and storage procedure described in Nsubuga et al. (2004). Briefly, we immersed a small pellet (~5 g) of fecal material in 30 mL 95% ethanol. After about 24 hours, we transferred the pellet into a 50-mL tube filled with desiccating silica beads. We collected only samples estimated to be <3 days old based on shape, color, and desiccation. We stored samples in silica at room temperature for up to 6 months until they reached the lab, where they were stored at 4°C and used for DNA extraction after 2 weeks to 3 years.

Sample Extraction and Amplification

We extracted DNA from samples using the QIAamp DNA Stool Mini Kit (QIAGEN, Hilden, Germany) with slight modifications of the manufacturer's protocol (Nsubuga et al. 2004) and stored extracts at −18°C. For each extract we amplified the amelogenin locus on the sex chromosomes in 4 replicates for sex determination using polymerase chain reaction (PCR) methods following Bradley et al. (2001). Because we expected some proportion of extracts to contain little or no amplifiable amounts of DNA, we did not further use extracts that failed 4 attempts at amplification of the amelogenin locus.

We next simultaneously amplified each usable extract in triplicate at 19 autosomal microsatellite loci following the first step of a 2-step multiplex PCR method described in detail elsewhere (Arandjelovic et al. 2009). This first multiplex reaction mix contained 10 μL of Type-it Multiplex PCRMaster Mix® (QIAGEN), 0.15 μM of each forward and reverse primer for all of the 19 loci, 3.86 μL of water, and 5 μL of template DNA for a total volume of 20 μL. Instead of subsequently amplifying each locus separately as in Arandjelovic et al. (2009), we re-amplified a subset of 12 of the 19 loci in 3 smaller multiplex PCRs containing 4 loci each, using 2.5 μL of 1:100 diluted first-step multiplex product as template DNA, 5 μL Multiplex PCRMaster Mix® (QIAGEN), 0.15–0.35 μM primer, and 0.5–2 μL water for a volume of 10 μL (Tables S1 and S2, available online in Supporting Information).

Genotyping and Identity Analysis

We electrophoresed products from the amelogenin PCR and the 3 sets of second-step multiplex PCRs in an ABI PRISM 3130XL Genetic Analyzer and scored allele sizes with the software GENEMAPPER version 3.7 (Applied Biosystems, Foster City, CA) using HD400 size standard. We required

that alleles in heterozygous genotypes were each observed from a minimum of 2 replicate PCRs. We compared the rate of allelic dropout at confirmed heterozygous loci to the concentration of respective DNA extracts as inferred using SYBR® Green I quantitative PCR (ThermoFisher Scientific, Waltham, MA, USA) at the c-myc Exon3 locus on Stratagene MxPro3005P in 25-μL volume containing 1 μL of template DNA, 0.75 μL of forward and reverse primers, 12.5 μL of Maxima® SYBR Green qPCR Master Mix (2X), and 10 μL of ultrapure water. This suggested that 4 and 2 replicates were sufficient for extracts under and above 30 pg/μL, respectively, to confirm a homozygote genotype with 99% certainty. We discarded genotypes from 40 extracted samples that produced genotypes at ≤3 loci. We conducted additional genotyping on the remaining samples as needed to achieve validated homozygous genotypes. We next used the program CERVUS (Kalinowski et al. 2007) to determine that a minimum of 8 matching loci between 2 samples was required for the probability of identity for siblings ($P_{ID_{sib}}$) to be <0.001 (Waits et al. 2001). Thus, we used only sample extracts that were successfully typed at a minimum of 8 loci for subsequent analyses. We then compared all multilocus genotypes to one another using the identity function in CERVUS and gave a unique identification (ID) to matching genotypes. We re-examined genotypes of samples mismatching at ≤4 loci to check for genotyping errors and as recommended performed re-genotyping when genotypes mismatched at just 1 or 2 loci (Kalinowski et al. 2006, Arandjelovic et al. 2009). This process clarified all putative mismatches, and all genotypes that we classified as representing different individuals differed at ≥5 loci.

A unique multilocus microsatellite genotype generated in the same laboratory using the same loci is available for each habituated individual from previous genetics research on the Ngogo group (Langergraber et al. 2007, 2009, 2011, 2013). After constructing our final list of individual genotypes, we used again the identity function in CERVUS to find matches with genotypes from Ngogo individuals whose ages and sexes were known from long-term observational research.

We considered matching genotypes from samples collected on the same day within 50 m to be multiple piles of a single-occasion deposit by an individual and therefore did not represent independent redetections (Miller et al. 2005). We constructed a consensus genotype using DNA from these multiple samples but afterwards removed all but 1 sample from the dataset to represent it as a single detection event. We defined the sampling intensity for each sampling period as the number of genotyped samples/number of unique individuals (Miller et al. 2005).

Detection Probabilities

We considered the first appearance of a unique genotype as the detection of an individual, and every subsequent appearance as redetections. We tested for the effects of age and sex on detection probability with a generalized linear model (GLM) in R (version 3.1.2, www.r-project.org). We modeled the binomial response (i.e., detected yes or no) with a binomial error structure and logit link function (McCullagh and Nelder 1989). We tested the significance of the full model with a likelihood ratio test (LRT; Dobson and Barnett 2008) by comparing it with a null model containing only the intercept. To test for an interaction between sex and age, we used an LRT to compare the deviance of the full model with that of a reduced model with the interaction term removed. To test for a non-linear effect of age, we used an LRT to compare the deviance of models with and without the squared age term.

We tested the assumption that detection probability is equal to redetection probability for members of different age classes and members of different sexes using repeated random sampling with replacement in R. For each sex and age category (i.e., infants, juveniles, adolescents, and adults), we randomly sampled as many samples from the known population as we collected during the study (e.g., if we collected 24 samples from adolescents, we selected 24 random samples from the adolescent population present at the time of sampling, 1,000 times). We then examined whether the proportion of redetections in our samples was significantly different from that expected by chance.

Population Size Estimation

We used Bayesian and ML methods to estimate the number of individuals in the Ngogo group, assuming 1) demographic population closure (i.e., no deaths, births, or migrations) and 2) detection probability (i.e., proportion of individuals detected from the total population) equal to redetection probability (i.e., proportion of individuals detected more than once from the sampled population). Both the Bayesian credible intervals and the ML confidence intervals are hereafter abbreviated CI. We used 9 models (Table 1) described below.

For the Bayesian model, we used a sequential Bayesian algorithm written by Arandjelovic et al. (2010) based on Petit and Valière (2006) and implemented in R. We implemented the non-spatial ML models using the R package capwire (Miller et al. 2005, Pennell et al. 2013), which computes 3 ML models (equal capture model [ECM], two innate rates model [TIRM], and partitioned TIRM [TIRMpart]) to estimate population size (Table 1). Like the Bayesian model, the ECM assumes equal detection probability. The TIRM assumes 2 categories of individuals, with either low or high detection probability (Table 1). We used an LRT in capwire to compare the goodness-of-fit of ECM and TIRM to the data. We considered the null model (i.e., equal detection probability, ECM) rejected when the likelihood ratio (LR) <0.1 rather than LR <0.05 because this test is often insensitive (Miller et al. 2005, Puechmaille and Petit 2007). We used the data partitioning (Pennell et al. 2013) function of capwire to split the data into 3 detection probabilities. If partitioning is statistically supported ($P < 0.05$), the data violate the TIRM's assumption of 2 detection probabilities. Therefore, the third model, TIRMpart, applies the TIRM on a partitioned dataset excluding any individual detected a large number of times. The number of excluded individuals is then added to this partitioned estimate to obtain the final TIRMpart estimate.

For spatially explicit models, we used an ML method that accounts for spatial heterogeneity of detection in density

Table 1. Models used for chimpanzee population size estimates in Kibale National Park, Uganda, 2011–2013.

Model	Type[a]	Spatially explicit	Assumptions
BS	Bayesian	No	Equal detection probability
ECM	ML	No	Equal detection probability
TIRM	ML	No	Two detection probabilities
TIRMpart	ML	No	Three detection probabilities
SE1	ML	Yes	Constant density, equal detection probability
SE2	ML	Yes	Constant density, 2 detection probabilities
SE3	ML	Yes	Sex-dependent density, equal detection probability
SE4	ML	Yes	Sex-dependent density, 2 detection probabilities for each sex
SE5	ML	Yes	Sex-dependent density and detection probability

[a] ML = maximum likelihood.

estimations (SECR; Borchers and Efford 2008, Efford 2011) and implemented it in the R package secr (version 2.9.5). The SECR method assumes that each individual in the population has a circular home range, which may be centered in or outside the sampling area, and estimates the location of individuals' home range centers, assuming that the density follows a homogeneous Poisson distribution. The assumptions of homogeneous Poisson distribution and home range centers located outside the sampling area were unlikely to be met because we restricted our sampling to the known home range of the Ngogo group. We set the buffer (i.e., distance outside the sampling area in which sampled individuals may have their home range center) at 5 km, which is more applicable for chimpanzees than the default 100 m (Efford 2011, Moore and Vigilant 2014). Models SE1 and SE2 (comparable to ECM and TIRM, respectively) assume 1 or 2 detection probabilities among individuals. Models SE3, SE4, and SE5 allow for sex-dependent densities, which is suitable for chimpanzees considering their female-biased sex-ratio (Nishida et al. 2003), and only SE5 allows for variation in detection probability by sex (Table 1). We determined the statistical support for each SECR model using Akaike's Information Criterion corrected for small sample size (AIC_c) and considered a model to be supported when $\Delta AIC_c < 2$ (Burnham and Anderson 2002). Finally, we multiplied the density estimate (individuals/km^2) by the searched area (47.11 km^2) to obtain an estimate of the population size.

For each of the 9 models discussed above, we compared the point estimates to the true number of chimpanzees in the Ngogo group at the time of sampling and described their performance using 3 criteria: 1) accuracy, defined as the extent of bias (either positive or negative) from the true population size; 2) relative CI width (CI width/population estimate); and 3) whether the CI included the true population size. Finally, we examined whether the statistically best fitting models within Capwire and SECR also were the most accurate.

RESULTS

Known Group Size and Composition

During the 3-month sample collection period, the Ngogo population consisted of 189 individuals, including 34 adult males, 59 adult females, 15 adolescent males, 20 adolescent females, 21 juveniles, and 40 infants. Two of the 40 infants were born during this sampling period. A third infant was born but died within 2 weeks and was therefore not included in the true population size for this study. One adolescent female immigrated from a neighboring group into the Ngogo group, but no emigrations out of the Ngogo group or any deaths occurred during this sampling period. The population size was 189 for the majority of the 3-month period (75 of 115 days), varied by only 0.02% during this time, and was therefore considered demographically closed.

During the 3-year sampling period, 26 infants were born (not including the one that was born and died within 2 weeks), 2 individuals died (1 adult F and 1 infant), 4 adolescent females immigrated into Ngogo from another group, and 1 adolescent female emigrated from Ngogo. The population size on 1 June was 173 in 2011, 190 in 2012, and 195 in 2013. This represented a 12.7% increase from 2011 to 2013. Thus, the population was not demographically closed during the 3-year sampling period. We considered the true population size to be 186 for the 3-year sampling period, which is the average of the 3 yearly population sizes.

Genotyping and Identity Analysis

Of the 368 samples collected during the 3-month sampling period, we genotyped 144 (39.1%) samples at the minimum 8 loci required to differentiate individuals with high confidence ($P_{IDsib} < 0.001$). Thirteen of these genotypes matched genotypes from other samples collected within 50 m on the same day, and hence represented multiple single-occasion deposits by an individual that we consequently removed from the dataset because they did not represent true redetections. The final sample size was therefore 131 genotyped samples representing 77 individuals (i.e., 75 genotypes from 38 M and 56 genotypes from 39 F), for a sampling intensity ($\bar{x}$ no. observations/sampled individual) of 1.7 with unique genotypes sampled 1–7 times.

We attributed 96% ($n = 74$) of these genotypes to known individuals from the Ngogo group. Three female genotypes, which all came from samples collected toward the edges of the Ngogo territory (i.e., 1 in the west and 2 in the same location in the northeast; Fig. 1), did not match the genotype of any Ngogo chimpanzee but did match genotypes from chimpanzees belonging to neighboring groups (data not shown), making the true population size in our sampling area slightly larger than the number of Ngogo group members.

The increase of the sampling period from 3 months to 3 years added 73 genotyped samples corresponding to 49

individuals, which all matched Ngogo group members and included 22 that were not sampled during the 3-month period. Thus, the 3-year sampling period included 204 genotyped samples derived from 104 individuals. The sampling intensity in the 3-year sampling period was 2.0, with unique genotypes sampled 1–10 times. We detected 54% ($n = 101$) of the population members over the 3 years.

Detection Probabilities by Age Class and Sex

We detected 39.1% ($n = 74$) of the 189 individuals present during the 3-month sampling period. The 74 detected individuals included 7.5% ($n = 3$) of the infants, 23.8% ($n = 5$) of the juveniles, 42.9% ($n = 15$) of the adolescents, and 54.3% ($n = 51$) of the adults. Chronological age had a significant quadratic effect on detection probability, with infants and old individuals having low detection probability (LRT: $\chi^2_1 = 17.9$, $P < 0.001$; Fig. 2; Table S3, available online in Supporting Information). Although more males (43.9%, $n = 36$) were detected than females (35.9%, $n = 38$), detection probability did not significantly differ by sex (LRT: $\chi^2_1 = 3.2$, $P = 0.07$; Fig. 2 and Table S3). The interaction between age and sex was not significant (LRT = $\chi^2_1 = 0.01$, $P = 0.9$).

The proportion of detections to redetections in the dataset was not significantly different from the random simulations among age categories (random sampling simulations: infants: $P = 1.00$, juveniles: $P = 1.00$, adolescents: $P = 0.95$, adults: $P = 0.99$) or by sex (F: $P = 0.94$, M: $P = 0.82$), thereby meeting this assumption of CR models.

Population Size Estimation: 3-Month Sampling Period

Underestimation of the true population size was more frequent (7 of 9 models) than overestimation (Fig. 3 and Table 2). The most accurate model was TIRMpart, with an estimate of 180 individuals that was quite close to the true population size (189). We found TIRM was supported over ECM (LR = 27.34, $P = 0.02$) and TIRMpart over TIRM ($P < 0.001$). Approximately half (5 of 9) of the models had CIs that contained the true population size, and all of the models with CIs excluding the true number of individuals underestimated the true population size (Table 2). The widths of the CIs relative to the point estimate ranged from 41% to 211%, and the model with the narrowest CI that still included the true population size was TIRM with 55.2% relative width.

Model SE5, which assumes that the sexes differ in density and in detection probabilities, had the highest AIC_c relative weight (67%, >3.5 times higher than the second supported model, SE1; Table 2; Table S4, available online in Supporting Information). However, our GLM suggested no difference in detection probability by sex in our data, which is more compatible with the assumptions of SE2 and SE4 (i.e., detection heterogeneity independent of sex), both of which were more accurate than SE5 (Table 2).

Population Size Estimation: 3-Year Sampling Period

Compared to the 3-month period, data from the 3-year period produced more accurate estimates for all non-spatial models, and for 2 of the 5 spatially explicit models (Fig. 3 and Table 2). Underestimates of the true population size (8 of 9 models) were again more frequent than overestimates. All 9 models had narrower CIs in the 3-year than in the 3-month period and the model with the narrowest CIs that still included the true population size was again the TIRM (35.9% relative CI width). However, more than half of the models excluded the true population size in the 3-year sampling period (5 of 9; Table 2 and Fig. 3).

As in the 3-month sampling period, TIRM was supported over ECM (LR = 46.38, $P < 0.001$), TIRMpart over TIRM ($P < 0.01$), and SE5 had the highest AIC_c support (95% weight), although TIRM and SE4 (not TIRMpart and SE5) were the most accurate non-spatial and spatial models, respectively.

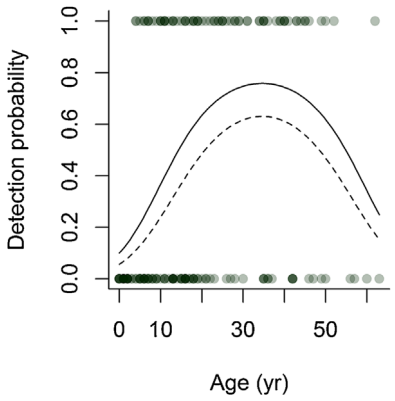

Figure 2. Detection of chimpanzees as a function of their age and sex in Kibale National Park, Uganda, 2011–2013. Circles indicate individuals either detected (detection = 1) or not detected (detection = 0). Darker circles indicate more individuals of that age. Curved lines represent the detection probability functions for males (solid line) and females (dotted line).

DISCUSSION

In this study, we examined the performance of several commonly used genetic CR models for estimating population size using a population of chimpanzees whose size ($N = 186$–189) and age and sex composition was precisely known (Langergraber et al. 2007, 2009, 2011, 2013; Watts 2012). We evaluated 9 different models employing different assumptions regarding detection probabilities (Table 1), home range locations, and sex-dependent densities. Genetic CR estimates were generally lower than the true population size, which was often not even included within the CI (Table 2 and Fig. 3). These underestimates were not surprising in the cases of the Bayesian, ECM, SE1, and SE3 models because these models assume equal detection probabilities (Table 1). Equal capture models typically underestimate population size when heterogeneity is present (Miller et al. 2005, Caniglia et al. 2011). However, even models that accounted for the detection heterogeneity present in our data tended to underestimate population size (i.e., TIRM, TIRMpart, SE2, SE4). Although our true population size was itself slightly lower than the number of individuals using the area, the sampling and inclusion of genotypes from 3 individuals from neighboring communities using the periphery of the Ngogo territory were too few to inflate the estimates.

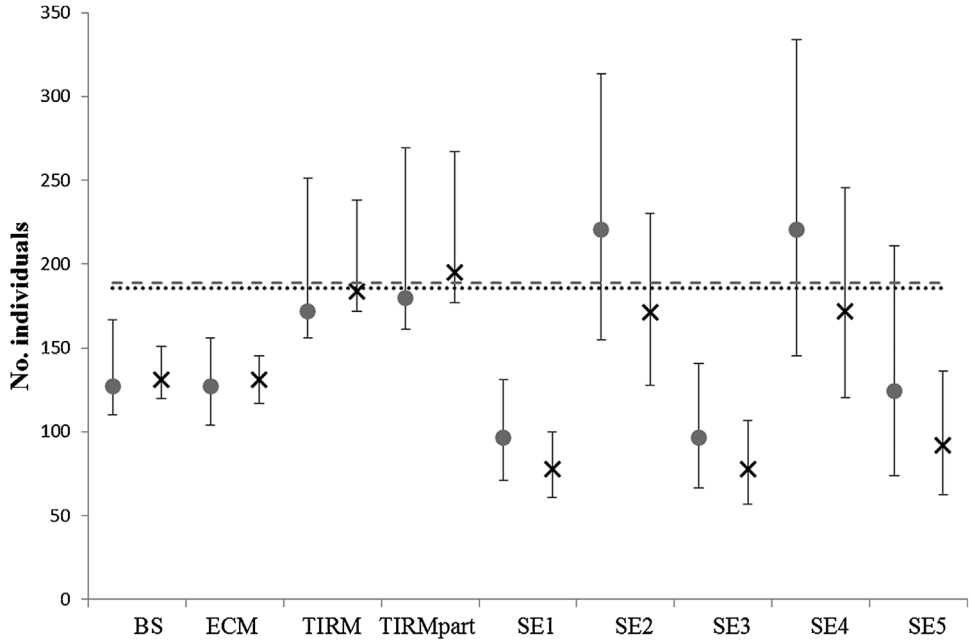

Figure 3. Chimpanzee population size estimates in Kibale National Park, Uganda, with the 3-month dataset (gray circles; 2012) and the 3-year dataset (black crosses; 2011–2013). The symbol (circle or cross) and the vertical lines indicate the point estimates and confidence intervals or credible intervals of each model. The dashed gray horizontal line indicates the true number of individuals in the population in the 3-month period ($N = 189$). The dotted black horizontal line indicates the true number of individuals in the population in the 3-year period ($N = 186$). BS = Bayesian model assuming equal detection probability. ECM = non-spatial maximum likelihood (ML) model assuming equal detection probability. TIRM = non-spatial ML model assuming 2 detection probabilities. TIRMpart = TIRM with high detection probability individuals excluded (partitioned dataset). Maximum likelihood spatially explicit models have the following assumptions: SE1 = constant density and equal detection probability; SE2 = constant density and 2 detection probabilities; SE3 = sex-dependent density and equal detection probability; SE4 = sex-dependent density and 2 detection probabilities for each sex; SE5 = sex-dependent density and detection probability.

Despite the overall tendency of the models to underestimate population size, some models performed reasonably well with regard to accuracy, relative CI width, and inclusion of the true population size within the CIs. Importantly, TIRM and TIRMpart performed well according to these 3 criteria in both the 3-month and 3-year sampling periods. This is encouraging considering that previous research has emphasized TIRM when using multiple genetic CR approaches to estimate population size (Puechmaille and Petit 2007; Arandjelovic et al. 2011, 2015; McCarthy et al. 2015). Also encouraging was the result that, in contrast to the general pattern for the models overall, TIRM and TIRMpart had higher overall performance in the 3-year versus the 3-month sampling period, with notably narrower confidence intervals in the former. The superior performance of these 2 models was also correctly detected by the LRT associated with the capwire package (Pennell et al. 2013). Although in our study TIRMpart produced an accurate population size estimate, reports of inconsistent results using TIRMpart in simulations suggest that use of this approach should be carefully evaluated (Stansbury et al. 2014).

We expected that SECR models would not provide accurate estimates of population size because we sampled only within the home range of the Ngogo group, which violates one of the main assumptions of the SECR models (Efford 2011). Nevertheless, SE2 and SE4, which assumed heterogeneous detection probability and equal or sex-biased density, respectively, had an accuracy in the 3-year sampling period comparable to the non-spatial models TIRM and TIRMpart (Table 2). Their relative CI width also decreased from the 3-month to the 3-year sampling period, although the CIs remained very large (>50% of the estimate; Table 2). The SECR estimates of population size should incorporate prior information on species-typical home range sizes and sample broadly enough such that several are likely to be included in the sampling area, a strategy implemented by Moore and Vigilant (2014) and McCarthy et al. (2015) for chimpanzees. A recent CR study with live traps covering several home ranges reported that SECR models gave accurate and precise estimates of a squirrel (*Tamiasciurus hudsonicus*) population of known size (Van Katwyk 2014).

A concern in planning a long-term genetic census is that longer study periods may increase the chance that individuals enter or leave the population via births, deaths, or migration. Indeed, with a few individuals leaving and 30 individuals joining the population during the sampling period, the Ngogo population was not demographically closed. However, the majority of changes in population membership during this time were due to the birth of infants, which are very unlikely to be detected. Of the individuals who were detected during the 3-year sampling period, 98% ($n = 101$) were present for its entire duration. Thus, with regard to individuals belonging to age classes that were likely to be detected, the population was effectively closed. This explains why the 4 models accounting for detection heterogeneity (i.e., TIRM, TIRMpart, SE2, SE4) gave an accurate estimation of population size.

Table 2. Results of all chimpanzee population size estimates in Kibale National Park, Uganda, for the 3-month (2012) and the 3-year (2011–2013) sampling sessions.

Model[a]	$\hat{N}$	Relative bias (%)	CI[b]	CI width (% of estimate)
3 months (true population size = 189)				
BS	127	−32.8	110–167	44.9
ECM	127	−32.8	104–156	40.9
TIRM	172	−9.0	156–251†	55.2
TIRMpart[c]	180	−4.8	161–269†	60.1
SE1	97	−48.93	71–131	62.3
SE2	220	16.59	155–314†	72.1
SE3	97	−48.80	67–141	76.6
SE4	220	16.62	145–334†	85.6
SE5[d]	125	−34.11	74–211†	110.2
3 years (true population size = 186)				
BS	131	−29.6	120–151	23.7
ECM	131	−29.6	117–145	21.4
TIRM	184	−1.1	172–238†	35.9
TIRMpart[c]	195	4.8	177–267†	46.2
SE1	78	−58.11	61–100	50.7
SE2	171	−7.89	127–230†	60.1
SE3	78	−58.12	57–107	64.4
SE4	172	−7.66	120–245†	72.8
SE5[d]	92	−50.56	62–136	80.0

[a] BS = Bayesian model assuming equal detection probability. ECM = non-spatial maximum likelihood (ML) model assuming equal detection probability. TIRM = non-spatial ML model assuming 2 detection probabilities. TIRMpart = TIRM with high detection probability individuals excluded (partitioned dataset). Maximum likelihood spatially explicit models have the following assumptions: SE1 = constant density and equal detection probability; SE2 = constant density and 2 detection probabilities; SE3 = sex-dependent density and equal detection probability; SE4 = sex-dependent density and 2 detection probabilities for each sex; SE5 = sex-dependent density and detection probability.

[b] CI = confidence or credible interval; CIs that contain the true number of individuals are indicated by †.

[c] Indicates the non-spatial model with strongest statistical support with a likelihood ratio test.

[d] Indicates the spatially explicit capture-recapture model with strongest statistical support based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Other census research on great apes assumed that infants do not really belong to the detectable population, and estimated the number of undetected infants based on the average ratio of infants/adult females in other habituated and demographically monitored populations (Roy et al. 2014). However, this appears inadvisable for several reasons. First, adjusting the population point estimates with an estimated number of undetected individuals prohibits the continued use of the CIs, which provide essential information about the precision of the estimate. Second, demographic research on habituated chimpanzee populations shows that the proportion of the population that is composed of infants can substantially vary between groups (e.g., 0.12–0.33, R. M. Wittig, Max Planck Institute for Evolutionary Anthropology, personal communication), making it problematic to find a universally applicable adjustment factor. Third, infant detection probability is low but not null (Fig. 2), and they are included in the category of low detection probability as shown by the high accuracy of population size estimates of TIRM and TIRMpart (Table 2).

Our results provide provisional support for the International Union for Conservation of Nature's (IUCN) recommendation that genetic CR be used alongside or instead of traditional census methods to estimate chimpanzee population size (Kühl et al. 2008). For example, in a census of large mammal species throughout Kibale National Park, Wanyama et al. (2010) used sightings of chimpanzee nests and feces along a 4-km transect (repeated 3 times) to estimate a density of 2.7–3.6 chimpanzees/km^2 at Ngogo. Their confidence interval excluded the true population density at this time (4.9, long-term records; K. E. Langergraber, Arizona State University, unpublished data), and the closest confidence limit underestimated the true population density by 36%. Although the genetic CR estimates in the current study also tended to underestimate population size, even the worst performing genetic CR estimators did not perform this poorly in regard to relative CI width. However, with the sampling intensity obtained in the current study, even our best performing genetic CR estimates (i.e., TIRM, TIRMpart) would detect a population decrease of only 21–47%—although this is somewhat more sensitive than the transect method of Wanyama et al. (2010), which requires 49–60% change for detection at the same confidence level.

The accuracy of our best performing population size point estimators, most notably TIRM and TIRMpart, coupled with the large confidence interval associated with all estimates lead us to conclude, in common with previous authors (Roy et al. 2014), that high sampling intensity is the key element to consider in designing great ape census studies capable of detecting small (5–10%) changes in population size. Our sampling intensity of 2.0 genotyped samples/individual for samples collected over the 3-year period is at the low end of the suggested value of 2–2.5 (Miller et al. 2005, Arandjelovic et al. 2010). Also, only about 40% of our collected samples produced usable genotypes, and such low success rates may be typical of samples collected from unhabituated animals and must be taken into account.

MANAGEMENT IMPLICATIONS

Our study illuminates the efficacy of sample collection as a primary focus, contrasting to sample collection as an ancillary goal of other tasks, such as patrolling for snares and other illegal hunting activities. Not surprisingly, the majority of our successfully genotyped samples were collected in a 3-month period dedicated to systematic surveying for fecal samples, but the additional samples collected over the longer term also proved valuable. This suggests that a combined strategy is viable but may be more effective when including repeated short-term sessions of intense sampling. All species of great apes are listed on the IUCN Red list of endangered species and necessitate intensive conservation and monitoring efforts. Although large-scale population estimates with non-genetic methods may ring the alarm of dramatic population decline (Plumptre et al. 2015), they remain extremely imprecise and genetic CR can help provide more accurate, precise, and fine-scale population trends, even over a longer period of time. In our study, the TIRM provided the

best model when both accuracy and precision of the estimate were considered.

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