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A population Estimate of Chimpanzees (*Pan troglodytes schweinfurthii*) in the Ugalla Region Using Standard and Spatially Explicit Genetic Capture–Recapture Methods

DEBORAH L. MOORE[1,2]* AND LINDA VIGILANT[2]
[1]*Department of Anthropology, University of Texas at San Antonio, San Antonio, Texas*
[2]*Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*

Population parameters such as size, density, and distribution of a species across a landscape are important metrics that inform conservation science and are key to management strategies. In this study, we used genetic capture–recapture methods to estimate the population size and density of the little-studied chimpanzees in the Ugalla region of western Tanzania. From 237 fecal samples collected non-invasively over a 10-month period, we identified a minimum of 113 individuals. Based on the two-innate rate method (TIRM) modeled in the software *capwire*, we obtained a maximum-likelihood estimate of 322 (CI 227–373) individuals over the 624 km^2 area surveyed. Using a spatially explicit capture–recapture (SECR) method, we estimated a population density of 0.25 (CI 0.16–0.38) individuals/km^2. Observations of nests and search effort data revealed areas of more intense usage. The findings of this study are an important step in the characterization of the Ugalla chimpanzees, and substantially improve our understanding of the number of chimpanzees that occupy this savanna-woodland region at the easternmost extent of the geographic range of this endangered subspecies. Am. J. Primatol.

Key words: population estimate; chimpanzees; genetic capture–recapture; spatially explicit capture–recapture; population density; conservation

INTRODUCTION

One of the most important first steps in designing conservation management strategies is the assessment of population parameters such as size, density, and distribution of a species across the landscape. These are vital baseline data, which can be utilized to assess conservation status and to measure success of conservation efforts over time. Population size and density are important for long-term monitoring, and the distribution of individuals and their use of space are informative in targeting key areas of protection. For example, in an investigation of Sumatran orangutan ranging, Buij et al. [2002] found that this Critically Endangered [IUCN, 2012] great ape foraged at different elevations during different seasons, and thus required a larger and more diverse habitat than originally thought. In a striking example of the importance of regular censuses to determine population size, the catastrophic decline by more than half of the numbers of chimpanzees and gorillas in Gabon would not have been recorded without regular monitoring of the great ape populations in that country [Walsh et al., 2003].

Population estimates can be difficult to obtain, due to the elusiveness and/or rarity of a species, or due to the remoteness of its habitat. Beginning in the 1940s, researchers estimated population sizes by repeatedly setting traps to capture a proportion of the population over several trapping sessions [Zippin, 1958]. Since these early "removal" studies, trapping methods now involve capturing and marking the animal, and then releasing it back into the population. These capture–mark-recapture (CMR) estimates have been based on how many marked animals are captured in subsequent trapping sessions, compared to how many unmarked animals are

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*Correspondence to: Deborah L. Moore, 5266 Long Island Rd., Ottawa, Ontario, Canada K4M 1E7.
E-mail: deborah.moore97@gmail.com

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captured [Darroch, 1959; Jolly, 1965; Leslie, 1952; Seber, 1965].

For many species including the great apes, it is neither logistically feasible nor ethical to trap individuals and alternative methods are necessary [Fedigan, 2010]. Chimpanzees construct nests to sleep in each night, and nest surveys have been the method most often used to obtain chimpanzee population estimates [Beck & Chapman, 2008; Devos et al., 2008; Hashimoto, 1995; Kuhl et al., 2008; Marchesi et al., 1995; Morgan et al., 2006; Plumptre et al., 2010; Pruetz et al., 2002]. The determination of a population estimate from nest surveys also can be problematic, however, due to the information needed to make such calculations, and the survey design required. For example, the nest decay rate must be known, and this figure varies widely between vegetation types, climate, and season [Kuhl et al., 2008]. Further, line transects should be randomly distributed throughout the survey area to avoid bias, and a minimum of 60–80 observations should be made for reliable population estimates [Kuhl et al., 2008]. Bias may also be introduced by inter-observer error, nest reuse, nest construction rates, and transect reuse [Kuhl et al., 2008; Tagg & Willie, 2013]. Given all of these critical elements necessary for obtaining reliable results, population estimates derived from nest surveys may often over- or underestimate the true population size [Boyko & Marshall, 2010; Kuhl et al., 2008; Plumptre & Reynolds, 1996; Stewart et al., 2011].

Modeled on mark-recapture methods, non-invasive recapture methods have been developed, and have demonstrated more accurate estimates for gorilla populations than those determined through nest surveys [Arandjelovic et al., 2010; Guschanski et al., 2009]. Rather than trap and mark individuals, non-invasive recapture methods instead utilize the "marks" that individuals leave behind. In genetic capture-recapture methods, the feces, hair, feather, or other tissue is collected without disturbing the animal, and the individual's DNA is extracted from the sample. Each collection of genetic material from an individual becomes a "capture" of that individual, and subsequent collections are "recaptures." Beyond the logistical and ethical advantages to this method, genetic capture-recapture avoids the issue of "trap-response" in traditional MCR methods, wherein the animals become either wary of or attracted to the traps, and also more closely approximates the assumption of a closed population due to the decreased time span necessary for sampling [Kohn et al., 1999]. Another important difference is that the collection of genetic material approaches a true "sampling with replacement" model, and individuals may be captured several times in one sampling session. Miller et al. [2005] developed a method in the software program *capwire* to deal with these kinds of data. For the analysis, one assumes that each "capture" is independent, and the data collected are a "capture history" for each individual [Miller et al., 2005]. There are two capture models; even-capture (ECM), wherein each individual has an equal chance of being captured, or the more flexible two-innate rate model (TIRM), wherein individuals are assigned a "high" or "low" probability of being captured. Based on a multinomial probability distribution model, a maximum likelihood estimation of population size is calculated [Miller et al., 2005]. In several studies, *capwire* has provided similar population estimates to those obtained by the traditional methods of accumulation curves (ACs) and Bayesian estimators (BE) [Arandjelovic et al., 2010; Perez et al., 2006; Puechmaille & Petit, 2007], although the AC and BE methods, as well as the ECM method in *capwire*, may underestimate the population size when there is capture heterogeneity among individuals [Arandjelovic et al., 2010; Miller et al., 2005; Perez et al., 2006; Petit & Valiere, 2006; Puechmaille & Petit, 2007]. When tested on capture data of European badgers (*Meles meles*) and red wolves (*Canis rufus*), wherein the population size was approximately known, the population estimate obtained using *capwire* was accurate for both species [Miller et al., 2005].

The size of a population is an important baseline metric; however, population density is an important indication of the richness of resources and of population dynamics [Isbell, 1991]. Population density is commonly calculated by dividing the population estimate determined in capture-recapture methods by the "effective trapping area" (ETA), which is ill-defined and varies across studies [Borchers & Efford, 2008; Efford, 2004]. In addition, traditional genetic capture–recapture methods do not take into account the movement of individuals between deposits of genetic samples (i.e., captures), nor the bias that may be introduced by a predetermined search area with borders that may not be biologically meaningful [Efford, 2011]. As such, a spatially explicit capture–recapture method (SECR) which addresses these issues may be preferable [Efford, 2004, 2011]. By incorporating a spatial function defined by the probability of capture as distance increases from an assumed home range center, accurate population densities have been obtained from populations of small mammals with known densities [Efford, 2004]. While the original method was designed for trap data, SECR methods have been updated to permit the analysis of a variety of capture data, including those data derived from genetic capture-recapture (i.e., feces) [Efford, 2011]. By considering a survey area (a concave polygon) the "trap," the SECR method calculates the probability of an animal leaving a "cue" (i.e., defecating) inside the polygon based on its spatial relationship with the assumed home range [Efford, 2011]. The spatial detection data are then fitted to spatial models of the population and the detection process in order to

obtain a maximum-likelihood estimate of the population density.

Density estimates are clearly vital, and yet they still do not provide information regarding local distribution of populations. Most animals use space heterogeneously, and identification of high-usage areas within a species' range also is important to developing conservation management strategies. In a test of the validity of nest count methods to estimate population size of chimpanzees in the Taï Forest, Ivory Coast, researchers found that a higher number of nest encounters was correlated with greater ape density, suggesting that "core" areas may be detected by observation of high levels of nest density [Yao Kouakou et al., 2011].

The great apes represent excellent subjects for the application of both traditional and spatially explicit genetic capture–recapture approaches, as they present all of the challenges these methods were designed to accommodate. In particular, chimpanzees are elusive, mobile, and occupy large home ranges. Given their great strength, and high level of intelligence, trapping is difficult and unethical. All four subspecies of chimpanzee are Endangered [IUCN, 2012], and population estimates are lacking across much of their distribution [Oates, 2006]. Although the majority of long-term studies are focused on the eastern subspecies (*Pan troglodytes schweinfurthii*), these study sites are located in habitats that are much more heavily forested than Ugalla and hence do not incorporate the full range of chimpanzee habitats. Given that socioecological theory predicts that the distribution of food resources plays a key role in influencing the size and ranging patterns of chimpanzee groups, the very limited knowledge regarding the population size and density of chimpanzees occupying savanna-woodland habitats is notable.

The chimpanzees living in the Ugalla region of western Tanzania occupy one of the driest and most open chimpanzee habitats [Moore, 1994; Ogawa et al., 2007], and Ugalla represents the easternmost range of this subspecies. It is expected that populations occupying savanna-woodland regions such as this will exhibit low population density, as female distribution and social organization are predicted to be determined by resource distribution and abundance in a given habitat [Isbell, 1991; Wrangham & Smuts, 1980]. Surveys to determine population estimates and test such socioecological predictions are challenging and have been limited in number in remote, expansive regions such as Ugalla ($\sim$3,350 km^2). The area was first investigated in 1961 by the Kyoto University African Primatological Expedition [Moore, 1992], and brief surveys were conducted in 1975 [Nishida, 1989] and in 1985 [Moore, 1986] to assess chimpanzee presence, rather than to estimate population size or density. More recently, Ogawa et al. [2007] combined several nest-site surveys spanning the period from 1995 to 2003; based on sightings of almost 2,000 nests, these authors estimated a population of 200–300 individuals in the entire Ugalla region. Those data yield a low approximate estimate of population density of 0.07–0.09 individuals/km^2. In a report on the biodiversity of western Tanzania, Moyer et al. [unpublished data] estimated 329 individuals occupied the Ugalla region, and designated areas of "suitable" and "unsuitable" chimpanzee habitat within the region. Recent intensive genetic sampling from a small portion of Ugalla (85 km^2) identified 67 individuals from the 375 samples collected [Rudicell et al., 2011]. The purpose of that study, however, was to estimate the frequency of SIV infection in the chimpanzees, and the sampling methodology was not designed to generate a population estimate. Although representing a different subspecies, it is interesting to note that at a savanna study site with habituated chimpanzees, that of Fongoli, Senegal, the community of 28–36 western chimpanzees (*Pan troglodytes verus*) occupies a minimum home range of 85 km^2 [Pruetz & Lindshield, 2012], supporting socioecological models that predict low population densities and large home ranges in these environments.

The purpose of this study was to conduct a noninvasive genetic survey of a large portion of the Ugalla region and apply the most recent genetic capture-recapture methods to determine an informative population size and density estimate for this area at the eastern edge of chimpanzee distribution. As this may be an important population for conservation of the Endangered species [IUCN, 2012], such data are of significance to the developing conservation focus in this area.

METHODS

Study Site

The Ugalla region is approximately 65 km east of Lake Tanganyika, in western Tanzania. Much of the region falls within the East Tongwe Forest Reserve and is not part of the national park system of Tanzania. The area was named by Kano [1971] and defined as the region bordered by the Mpanda–Uvinza road to the west, the Malagarasi river to the north, the Ugalla river to the east, and the Ilumba basin to the south [Moore, 1994].

Ugalla covers approximately 3,350 km^2 and is one of the most seasonal, dry, and open chimpanzee habitats [Hernandez-Aguilar et al., 2007; Kano, 1971; Moore, 1994; Ogawa et al., 2007]. The region is classified as savanna-woodland due to the extensive grassy groundcover, an extended drought season between May and October, and minimal rainfall. The majority of the region is composed of "miombo woodland," characterized by the tree genera *Brachystegia* and *Julbernardia*. Small strips of forest

occur around the ephemeral rivers of Ugalla, and comprise the 2% forest cover. The surveyed area is part of the East African Plateau, ranging in elevation from 1,095 to 1,919 m above sea level and carved by deep valleys. With <1,000 mm of rainfall per year [Hernandez-Aguilar, 2006], most rivers in this region are ephemeral [Moore, 1994].

Study Subjects

As is the case for each of the four subspecies of chimpanzees, eastern chimpanzees (*P.t. schweinfurthii*) are considered Endangered [IUCN, 2012], with as few as 200,000–250,000 remaining in the wild [Plumptre et al., 2010]. They are the subjects of Goodall's [1986] and Nishida's [1968] long-term studies, and are found from the western border of the Democratic Republic of Congo, in central Africa, to western Tanzania in East Africa. The chimpanzees in Ugalla are unhabituated to human presence.

Survey and Collection Methods

Between July 2009 and May 2010, DLM spent approximately 767 hr conducting searches over 101 days, logging over 1,440 km of reconnaissance walks ("recces"). Surveys were conducted from the one permanent research camp (5.3927S, 30.5844E) in Ugalla, and from an additional five temporary camps which were established; duration at each camp was 15–33 days. Prior to the initiation of fieldwork, a survey grid was established over an area of the Ugalla region. The location was decided based on previous nest surveys, remote sensing data, and ease of access [Moyer et al., unpublished data; Ogawa et al., 2007]. Rather than employ a strict transect survey method, a decision-based sampling method was used to increase detection probability (Fig. 1), while recording search effort for each $4\,km^2 \times 4\,km^2$ quadrat. This method compensated for the intentionally biased search effort, which maximized the resampling of individuals' feces necessary for a capture–recapture population estimate, by providing a weighted search effort across each grid that could provide data on relative abundance of chimpanzees in the area.

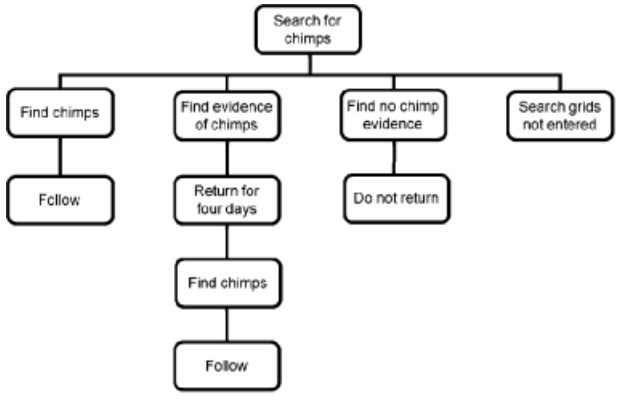

Fig. 1. Flow chart of survey design decision protocol.

Search effort was recorded using the Garmin eTrex Legend H "track log" feature set at 2 min. After a suitable camp site was established within the survey area, the surrounding area was searched for signs of chimpanzee presence based on the knowledge of the field assistant, Halufani Mulalelwa, who was born in this area and has spent over 50 years as a honey collector across the entire Ugalla region. If chimpanzee presence was inferred in an area based on fresh nests, observations, vocalizations, or fresh feces, this area would be searched again for four consecutive days. If a searched area did not contain any recent evidence of chimpanzee presence, the area would not be searched again. Whenever chimpanzees were seen, heard, or detected by tracks, they were followed. Track logs were uploaded to a laptop each evening to assess coverage of the survey area, and all surrounding quadrats in a minimum 4 km radius were searched prior to leaving a camp site.

DLM collected all samples using the two-step ethanol-silica preservation method [Nsubuga et al., 2004]. Approximately 5 g of fecal matter was placed in a 50 ml tube containing 30 ml of ethanol; after 24–36 hr, the ethanol was poured out and the sample was transferred to another 50 ml tube containing silica gel beads. For each sample collected, GPS location, time, temperature, vegetation type (open woodland, open woodland/slope, forest edge, closed forest, dry riverbed/closed forest, grassland, grassland/open woodland, clearing, thicket forest), bolus size (preestablished scale), and collection circumstances (following party, following trail, found under fresh nests, found on trail) were recorded. Each sample was assigned a number and was stored up to 5 months in the field prior to shipment from Kigoma, Tanzania, to the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, where they were stored at 4°C for up to 18 months prior to extraction of DNA.

Relative Population Abundance

To determine areas of high usage, or "hotspots" of chimpanzee activity [Yao Kouakou et al., 2011], we combined nest data with search effort to present a picture of relative abundance in the Ugalla region. We recorded every nest observed from our walking path, and for each nest, we recorded approximate distance from the path and estimated age of nest based on a standard scale [Tutin & Fernandez, 1984]. Nests were recorded only when first observed, and nest data were recorded from temporary camps, only, and not from the permanent research camp at Ugalla. We transformed our survey grid into $1\,km^2 \times 1\,km^2$ quadrats to obtain a more fine-scaled resolution, and

totaled meters walked for each of these quadrats as a proxy for search effort. We then divided number of nests found in each 1 km × 1 km square by search effort to portray relative abundance of chimpanzees in the Ugalla region. We plotted these results in ArcGIS version 10.1 to depict areas that may be more frequently used by chimpanzees.

Genetic Analysis

DLM conducted all laboratory work in the genetics laboratory in the Department of Primatology at Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. DNA was extracted from samples using the QIAmp DNA stool kit (Qiagen, Hilden, Germany) according to manufacturer's instructions and amendments, as per Nsubuga et al. [2004]. For the non-fecal samples (i.e., food wadges and sperm plug), the same extraction method was used, including the use of approximately 0.1 g of material. All extracts were first amplified in four independent polymerase chain reactions (PCRs) at the X–Y homologous amelogenin locus to assess presence or absence of amplifiable DNA and to determine sex [Bradley et al., 2001]. Extracts which produced products were then amplified in a two-step multiplex procedure [Arandjelovic et al., 2009], using unlabeled primers for 19 autosomal microsatellite loci in the first amplification, and fluorescently labeled forward primers and nested reverse primers for a subset of 12 loci in the subsequent single locus PCR reactions (Table I). Depending on amplification success, between 3 and 12 independent amplifications were performed for each extract at these 12 loci. Extracts that did not yield confirmed alleles at 8 or more loci were not used in further analyses. A genotype at a locus was considered heterozygous when each allele was observed in two or more independent reactions and homozygous when the single allele was observed in three to five independent reactions, depending on the amount of template DNA in the sample [Arandjelovic et al., 2009].

Extracts from males were amplified in a two-step multiplex procedure at 13 microsatellite loci on the Y-chromosome (Table I). PCR products were electrophoresed on an ABI PRISM 3100 Genetic Analyser. Allele sizes were determined using an internal size standard (ROX labeled HD400) and Genemapper Software version 3.7 (Applied Biosystems, Grand Island, NY).

TABLE I. Microsatellite Loci Amplified and Genotyped in This Study

Microsatellite	No. of alleles	No. of individuals typed
Autosomal		
D11s2002	5	110
D2s1326	10	107
D7s817	7	112
D5s1470	6	110
D6s1056	6	105
D5s1457	6	112
D1s1622	6	93
D2s1329	6	110
D3s2459	11	106
D7s2204	8	108
D14s306	9	107
D16s2624	5	94
Y-chromosome		
DyS392	1	52
DyS439	2	59
DyS469	1	57
DyS502	1	55
DyS510	2	61
DyS517	2	61
DyS520	1	61
DyS533	1	57
DyS562	1	60
DyS588	1	59
DyS612	1	62
DyS630	2	61
DyS632	1	66

Identification of Individuals

We used the software program *cervus 3.0* to ensure that matching genotypes from different extracts were not from different individuals, including full siblings. Based on allele frequencies of each locus amplified for the Ugalla population, we determined the number of loci necessary to confidently ($P_{\mathrm{IDsibs}} \leq 0.001$) assign consensus identifications to extracts with the same genotype. Genotypes that mismatched at one or two loci were examined for genotyping errors, and re-amplified in cases of ambiguity.

Population Estimation

Once consensus identifications were assigned to each extract, we used the software program *capwire* [Miller et al., 2005] to estimate the population size of the surveyed area, since it performs as well as estimates obtained with Bayesian estimators and ACs [Arandjelovic et al., 2010]. Additionally, this program is specifically designed for the analysis of genetic data, which differ from traditional mark-recapture data in that an individual may be "captured" many times in a sampling session, thereby approximating true sampling with replacement [Miller et al., 2005]. We grouped all samples into a single sampling session from July 2009 to March 2010, as the assumption of a closed population with few additions or losses of individuals over this time span is permissible for a long-lived species with a relatively slow life history. Samples from the same individual collected at the same time and location were considered one capture. This model assumes a

closed population and the probability of recapture equal to capture, and can either assume equal capture probability for all individuals (ECM) or can allow for capture heterogeneity in the sampled population by assigning individuals to low or high capture probability (TIRM) [Miller et al., 2005].

For the SECR analysis, we also grouped all samples into a single sampling session ("occasion") and included a buffer of 5,000 m of suitable chimpanzee habitat around our search area. Polygons ("traps") were defined as each quadrat searched in our survey grid, and "captures" were each collection of successfully identified feces (as above, if an individual's feces were collected more than once at the same time and place, this was counted as one "capture"). This model has an assumed heterogeneous capture probability, but rather than assign a "high" or "low" likelihood, capture probability decreases with distance from an individual's home range center. To compare these results to the estimate of population size, we simply multiplied the density estimate by the area surveyed ($N = DA$). The application of a population density to determine a population estimate ($N = DA$), where "A" is the area surveyed, however, may be inaccurate due to the mosaic of suitable and unsuitable habitat incorporated by "A" [Efford & Fewster, 2012]. For this study, therefore, population densities were estimated separately for the areas determined as "suitable" and "unsuitable" chimpanzee habitat in a 2006 biodiversity report of western Tanzania [Moyer et al., unpublished data] (Fig. 2). The models were run in the freely available statistical software package "R" [R Development Core Team, 2008].

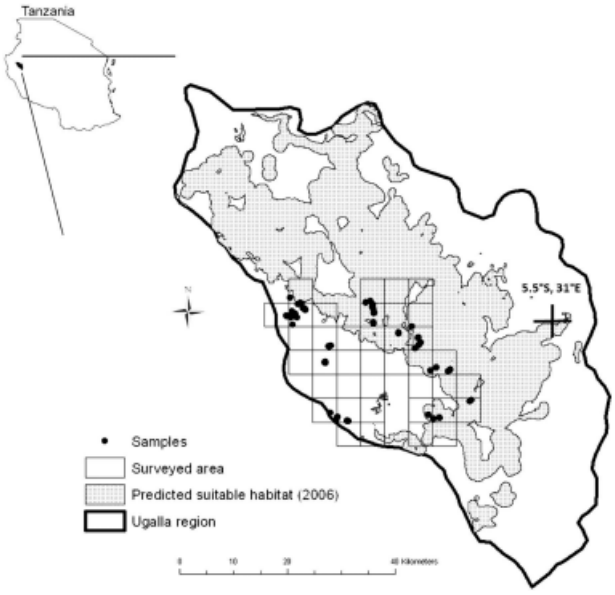

Fig. 2. Map of Ugalla region showing "suitable habitat" per Moyer et al. [2006], with area surveyed and sample locations from this study.

Ethics

This study complied with protocols approved by IACUC at the University of Texas at San Antonio (#PA001-05/14A0), and was approved by the appropriate Tanzanian government authorities (COSTECH Permit No. 2009-143-ER-2009-05). This research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

RESULTS

We collected 237 samples, including 228 fecal samples, eight food wadges (the discarded bolus of chewed seeds/leaves/fruit pulp left once the juice has been sucked out of it), and one sperm plug, and recorded the presence of 1,525 nests. The area surveyed totalled 624 km^2; 39 $4\,km^2 \times 4\,km^2$ quadrats were searched.

We determined that genotypes must be complete at a minimum of eight loci to confidently ($P_{IDsib} \leq 0.001$) assign consensus identifications. Two of the extracts that were complete at seven loci mismatched all other samples at a minimum of four loci; we thus could be confident that they represented unique individuals and each was assigned a consensus ID (U008 and U046). An additional two extracts that were complete at six and seven loci matched each other at five loci and one allele of three other loci. These had no mismatched loci, were assigned a P_{IDsib} value of 0.01, and mismatched all other extracts at a minimum of four loci. Because these also were from samples collected together, we felt confident that these two extracts represented one unique individual, and consensus identification was assigned (U075). The 237 samples yielded 237 extracts, of which 197 provided genotypes successfully amplified at an adequate number of loci to assign consensus identifications, representing an 83% (197/237) success rate. The 197 genotypes were on average 95% complete, with 137 (70%) of the samples successfully amplified at all 12 loci. These 197 extracts represent 113 individuals, including 69 males and 44 females.

Of the 113 individuals genetically identified, 28 were detected more than once (Table II). Assuming no capture heterogeneity, we obtained a population estimate of 245 (CI_{ECM} 193–313) individuals; using the TIRM option, the estimated population was 322

TABLE II. Sample Captures and Recaptures of Individuals in Ugalla Region

Times captured (N)	Individuals (N)	Males/females (N)
1	85	48/37
2	21	14/7
3	5	5/0
4	1	1/0
5	1	1/0

(CI_{TIRM} 227–373) individuals. These estimates are for the surveyed area of 624 km^2, which produces population density estimates of 0.39 (CI 0.31–0.50), assuming even capture probability, and 0.52 (CI 0.36–0.60) individuals/km^2, assuming capture heterogeneity. Using the SECR method, the population density for the Ugalla region is estimated at 0.25 (CI 0.16–0.38) individuals/km^2. For the separate estimates of density based on habitat types, we obtained a population density of 0.39 (CI 0.20–0.73) individuals/km^2 in suitable chimpanzee habitat, and in the habitat not considered suitable, the population density estimate was 0.32 (0.22–0.46) individuals/km^2.

To gain a clearer picture of the distribution of individuals across the Ugalla region, we mapped the relative abundance of nests ((total nests observed/total meters walked) × 100) using ArcGIS 10.1, allowing identification of areas of more intense usage. To compare this calculation to actual nest counts, we superimposed actual number of nests observed over the relative abundance grid (Fig. 3). Quadrats with high nest counts and high relative abundance were largely coincidental, although the two quadrats with the highest measures of relative abundance did not also have the highest nest counts, and the one quadrat with the highest nest count was not an area with the highest relative abundance (Fig. 3).

DISCUSSION

In this study, we employed two approaches for inferring chimpanzee population size and density across a 624 km^2 area of the Ugalla region. From the 237 samples collected and extracted, we determined that there is a minimum of 113 individuals living in this area of the Ugalla region. Based on genetic capture-recapture analysis conducted in the software program *capwire*, we calculated a population estimate using two models, both of which use a maximum likelihood estimator. Under the even capture model, the population estimate is 245 (CI_{ECM} 193–313) individuals, and assuming capture heterogeneity, there are approximately 322 (CI_{TIRM} 227–373) individuals in the surveyed area of Ugalla. These estimates translate to 0.39 and 0.52 individuals/km^2, when the estimated number of individuals is divided by the area surveyed.

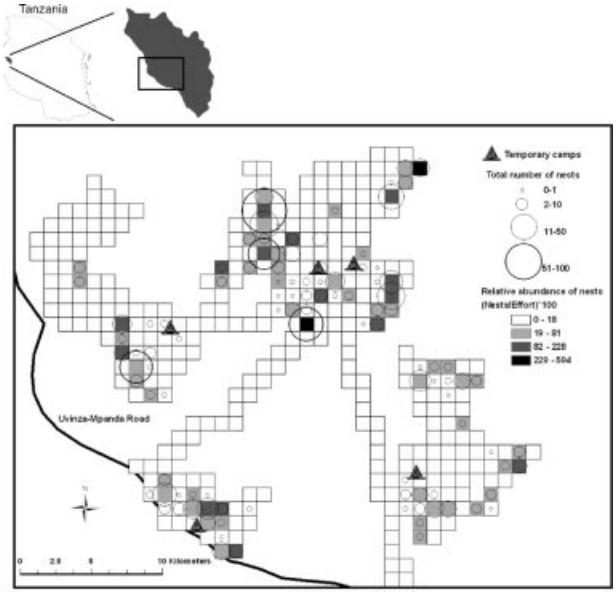

Fig. 3. Map of surveyed area showing relative abundance of nests ((nests/effort) × 100) per 1 km^2 × 1 km^2 grid, with embedded circles indicating the observed number of nests.

Estimating population density by extrapolating the population estimate over the area surveyed, however, may not be appropriate. These simple density estimates do not consider the movement of individuals and the edge effects of our surveyed area (i.e., how far a home range may extend outside of the search area); we therefore used a spatially explicit capture–recapture (SECR) method to estimate a population density of 0.25 (CI 0.16–0.38) individuals/km^2. The density obtained by SECR is lower than that obtained by simply dividing the number of individuals by the area surveyed, and generates a population estimate of 156 individuals in the survey area, which is lower than both the ECM and TIRM models obtained in *capwire*. This disparity between the two methods may indicate that we did not incorporate the entire range of the individuals captured in our survey area, and emphasizes the error that may occur when population estimates are used to estimate densities without ranging information.

When we calculated separate densities for "suitable" and "unsuitable" habitat, we obtained higher density estimates of 0.39 and 0.32 individuals/km^2, respectively; however, the confidence intervals of all three density estimates largely overlap, and the higher estimates may be due to the lower sample sizes. This discrepancy between the population density estimates of the entire survey area and the separate estimates according to chimpanzee habitat may also highlight important issues regarding data sets. In any genetic capture-recapture study, higher ratios of recaptures to captures improve the accuracy and precision of the maximum-likelihood estimate [Miller et al., 2005]. For the entire survey area, 38 of the 151 captures were recaptures, which is a recapture–capture ratio of 0.25. For the suitable habitat, the recapture rate was much lower, with only 12 of the 70 captures representing recaptures (0.17). The low number of recaptures is likely responsible for the relatively high density estimate (0.39), and for the wide confidence interval (0.20–0.73). In contrast, 26 of the 81 captures in the unsuitable habitat were recaptures (0.32), resulting in a relatively narrow confidence interval (0.22–0.46) and a more precise

population density estimate of 0.32 individuals/km^2. These findings also demonstrate that chimpanzees may occur at relatively high densities outside of areas previously identified as suitable chimpanzee habitat. It should also be noted that the habitat designations from Moyer et al. [unpublished data] were based on chimpanzee presence data from surveys conducted prior to 2006, and are known to not incorporate all of the variables that may predict suitable chimpanzee habitat in this region, such as elevation. Further, the division between "suitable" and "unsuitable" habitat should not be considered a definitive boundary, but as an approximate midpoint in a continuum. Modeling of chimpanzee habitat in the Greater Mahale Ecosystem (GME) is ongoing, and is continuously updated as new data, such as those collected in this study, become available.

The population size and density estimates determined here are higher than previous inferences for Ugalla [Moyer et al., unpublished data; Ogawa et al., 2007]. A series of nest surveys conducted between 1995 and 2005 produced an estimate of 200–300 individuals across the entire Ugalla region of approximately 3,350 km^2, representing a population density of 0.07–0.09 individuals/km^2 [Ogawa et al., 2007]. In a study of chimpanzee distribution across Tanzania, Moyer et al. [unpublished data] combined previous nest surveys with environmental variables to predict suitable chimpanzee habitat, and estimated that 1,645 km^2 of the Ugalla region met this criterion. The authors determined that population density within this area was 0.2 individuals km^2 (based on an estimate of 0.14 within Ugalla, and an estimate of 0.2 for the neighboring Masito region), and calculated a slightly higher estimate of 329 chimpanzees across the Ugalla region [Moyer et al., unpublished data]. Our estimates of 322 individuals within 624 km^2, and a density of 0.25 individuals per km^2, are higher than these previous estimates. If we extrapolate across only the area considered to be "suitable" chimpanzee habitat using the density estimate of 0.25, we obtain a minimum population estimate for Ugalla of approximately 411 chimpanzees. Based on the density estimate obtained for "unsuitable" habitat, we may realistically extrapolate this density estimate to a much larger area of the Ugalla region, and suggest that the population estimate may be as high as 837 individuals (0.25 km $\times$ 3,350 km of the Ugalla region).

Nest count surveys of chimpanzees are known to vary widely in precision and accuracy [Bradley et al., 2008; Morgan et al., 2006]. It is implausible that the number of chimpanzees in the region increased dramatically in the last decades, although it is likely that the nest survey counts systematically undercounted chimpanzees [Mathewson et al., 2008; Plumptre & Reynolds, 1997; Yao Kouakou et al., 2009]. In Ogawa et al. [2007] study that estimated a population density of 0.07–0.09 individuals/km^2, many different nest surveys conducted over 10 years were used in their calculations. Except for those conducted by JM, none of these transects were randomly determined, and many were "walks" rather than strict line transects. Further, approximately half of the surveys did not meet the minimal number of observations necessary for a reliable estimate [Kuhl et al., 2008]. Besides the survey design issues, the calculations may have been biased by the nest decay rate used [Stewart et al., 2011]. It was recently demonstrated that the nest decay rate in Ugalla is highly variable, ranging from a mean of 83.3 days in the small strips of forest during the dry season, to a mean of 185.5 during the dry season in the savanna woodland [Stewart et al., 2011]. Ogawa et al. [2007] used a nest decay rate of 260 days, which would result in an underestimation of the true population density. Nest site reuse is another factor that would result in an underestimate, as the nest count then underrepresents the number of nests. In the Ugalla region, nest site reuse is a common phenomenon, occurring at 48% of nest sites after 18 months [Stewart et al., 2011]. Thus the combination of survey design issues, overestimation of nest decay rate, and lack of accounting for nest reuse, may have contributed to the relatively low-density estimate obtained by Ogawa et al. [2007].

The population density estimate obtained here is also consistent with the population density of the only study site in a savanna-woodland with habituated chimpanzees, namely that of Fongoli in Senegal, West Africa. Researchers there have reported a minimum home range of 85 km^2 for a community that has ranged between 28 and 36 individuals [Pruetz & Lindshield, 2012], representing a maximum population density of approximately 0.32–0.42 individuals/km^2. In contrast, population densities across forested sites are higher and varied, ranging from 2.5 to 9 individuals/km^2 [Boesch & Boesch-Achermann, 2000; Chancellor et al., 2012; Chapman & Wrangham, 1993; Nishida, 1990; Pusey et al., 2008; Watts et al., 2006].

The occurrence of relatively low population densities of chimpanzees in savanna-woodland habitats with widely dispersed resources supports socioecological models that predict changes in distribution of animals with variation in distribution of resources [Isbell, 1991; Wrangham, 1980]. Specifically, chimpanzees are ripe fruit specialists, and such resources are expected to be scarce and/or sparsely distributed in a savanna-woodland environment, certainly relative to tropical forest. Indeed, in a study of the ecology of the Ugalla region, fruit was found to be unavailable in the small strips of forest during the long dry season, but was continuously available from different areas of the woodland throughout the year [Hernandez-Aguilar, 2006]. Of the 75 plants identified in the feces of the Ugalla chimpanzees, over 60% were fruit, suggesting that the Ugalla chimpanzees are as highly

frugivorous as their conspecifics elsewhere [Hernandez-Aguilar, 2006]. High consumption of fruit also is reported for chimpanzees at Fongoli [Pruetz, 2006], where the prediction of low population density also is supported.

In addition to obtaining estimates of population size and density, it also is important to assess patterns of landscape usage, as animals are never evenly distributed across an area [Yao Kouakou et al., 2011]. This is particularly relevant for territorial species with distinct home ranges, such as chimpanzees. Yao Kouakou et al. [2011] conducted nest transect surveys across the home ranges of four habituated or semi-habituated chimpanzee communities at Taï National Park, finding higher nest densities in the core areas of each community. Although transect surveys were not conducted for the present study, by weighting nest counts with survey effort (i.e., meters walked), the relative abundance of nests was obtained, and clear areas of nest concentration were visible. The areas of high relative concentrations (i.e., nests/search effort) also are approximately coincident with areas of higher absolute nest counts, and may suggest possible core areas of Ugalla communities. Of note, one of these potential core areas is located very near the Uvinza–Mpanda road, which although unpaved and narrow is the main road through this remote region of western Tanzania. This nest concentration also is close to a cluster of small tobacco farms, supporting findings that chimpanzees may be somewhat resilient to low levels of human disturbance [Plumptre et al., 2010]. A much higher human concentration, however, is located approximately 20 km northeast of this putative chimpanzee community, at the Burundian refugee settlement of Mishamo established in 1972. Mishamo and the other two settlements created at this time have been officially closed, and residents were given the opportunity to return to Burundi or become naturalized Tanzanian citizens and integrated into communities [Thomson, 2009]. Not surprisingly, many have elected obtain citizenship, and the village of Mishamo that began as a refugee settlement remains heavily populated (Moore, pers. obs.). According to local Tanzanians, much of the poaching that occurs in Ugalla is carried out by these "refugees," and while chimpanzees are not specifically targeted, they may be injured when accidentally caught in the poacher's snares. The high chimpanzee usage areas identified in this study, therefore, represent important concentrations of this Endangered [IUCN, 2012] species, and should be considered potential targets for future investigations of the Ugalla chimpanzees and key areas important in conservation efforts.

Feeding ecology is fundamental to group organization, as resource distribution drives the population density and ranging patterns of a species, with consequent effects on group structure [Isbell, 1991; Sterck et al., 1997; Wrangham, 1979]. Due to their dietary dependence on ripe fruit, chimpanzees have adopted a highly flexible strategy of fission-fusion, wherein foraging party size is fluid and frequently changes [Goodall, 1986; Nishida, 1968]. While individuals fission into smaller foraging parties, they remain part of a coherent community which occupies a spatially discrete home range that is defended by predominantly male coalitions against neighboring communities [Boesch & Boesch-Achermann, 2000; Hiraiwa-Hasegawa et al., 1984; Tutin et al., 1983; Watts & Mitani, 2001]. The fission–fusion social structure is seen as an adaptive strategy, which defrays the costs of group living while maintaining the benefits of group membership [Dunbar et al., 2009; Lehmann & Boesch, 2004; Lehmann et al., 2007]. Lehmann et al. [2007] investigated the relationship between ecological variables, time budget variables, and party size of 14 chimpanzee populations across Africa, to determine whether the putative increased time required for feeding and travelling imposed by living with a group is the likely driver of the evolution of fission–fusion social systems, and to create a predictive model of chimpanzee presence given certain ecological conditions. In support of their hypothesis, the authors found that feeding time was positively correlated with party size, and also determined that party size was best predicted by the ecological variables of rainfall and forest cover [Lehmann et al., 2007]. Of particular interest regarding the chimpanzees of Ugalla, the amount and seasonality of rainfall was the most important ecological variable in the prediction of time spent feeding and travelling, and in the prediction of chimpanzee presence [Lehmann et al., 2007]. In fact, their model predicted that when rainfall falls below 1,000 mm, as is the case in Ugalla, the time spent travelling for a party size >10 individuals was "prohibitively high" [Lehmann et al., 2007]. In a further study, Lehmann et al. [2008] incorporated body mass into their model, and similarly concluded that the increased time requirement for feeding and moving in marginal environments, such as Ugalla, may force chimpanzees to live in prohibitively small groups. In contrast to these modeled predictions, a recent study suggested that the chimpanzee community at Issa Valley in Ugalla may contain a minimum of 64 individuals [Rudicell et al., 2011], which far exceeds the modeled group size for chimpanzees at the margin of their biogeographical range [Dunbar et al., 2009; Lehmann et al., 2008]. Thus, chimpanzees in the Ugalla region may be extending the behavioral flexibility of this species in ways not yet observed in the wild.

The low population density of Ugalla, determined in this study, should be expected to have some effect on the social structure and organization of this population, and these effects could characterize other communities of savanna-woodland chimpanzees.

Population densities 10 times lower than that of forested communities could suggest the presence of home ranges that are 10 times larger. In response to the more widely distributed and more seasonally variable resources that are found in a savanna-woodland habitat [Hernandez-Aguilar, 2006] and in contrast to modeled predictions [Lehmann et al., 2007], perhaps communities adopt a "fluid," extensive ranging style, in which the entire community moves together, utilizing different portions of their home range during different seasons [Tutin et al., 1983]. Alternatively, low population densities must present a challenge to community coherence, and perhaps smaller, fissioned foraging parties are more permanent, experiencing little contact with other parties and resulting in very small effective communities. Additional research will be required in order to assess whether one or more of these potential variants in social structure and organization characterize chimpanzees living in savanna-woodland environments.

In sum, this study applied two analytical methods in the context of a noninvasive genetic survey to derive robust estimates of population size and density for an understudied chimpanzee population living in a resource-limited environment, which is atypical for the species. The confidence intervals surrounding both the population size and density estimates would be significantly narrowed with higher rates of individual recaptures. This could be accomplished by spending more time at each location, revisiting locations, or by employing several teams to collect samples simultaneously. Locating unhabituated chimpanzees in a savanna-woodland habitat is extremely difficult, and the employment of local people who are familiar with the area is fundamental to the success of a project of this nature. The findings of this study also provide baseline data altering our understanding of the number of chimpanzees in the region and are an important first step in the characterization of the conservation status of the Ugalla chimpanzees, and finally, this study also demonstrates the feasibility of obtaining reliable population parameters from elusive primates and other mammals, without the enormous effort of habituation [Bertolani & Boesch, 2008; Doran-Sheehy et al., 2007] or the invasiveness of trapping, and with a reasonable amount of effort and planning.

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