Nest Counts Reveal a Stable Chimpanzee Population in Sapo National Park, Liberia

Clement G. Tweh[1,2], Célestin Y. Kouakou[3,4], Robert Chira[2], Benedictus Freeman[5,6], John M. Githaiga[2], Shadrach Kerwillain[5], Mary Molokwu-Odozi[5], Matthew Varney[5] and Jessica Junker[7]

[1]*Wild Chimpanzee Foundation, Oldest Congo Town, Monrovia, Liberia*
[2]*School of Biological Sciences, University of Nairobi, Kenya*
[3]*Unités de Formation et de Recherche (UFR), Université Jean Lorougnon Guédé, Daloa, Côte d'Ivoire*
[4]*Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, Abidjan, Côte d'Ivoire*
[5]*Fauna & Flora International, Oldest Congo Town, Monrovia, Liberia*
[6]*Biodiversity Institute, University of Kansas, Lawrence, Kansas, USA*
[7]*Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*

Abstract: Surveying and monitoring primate populations is key for conservation decision-making. The western chimpanzee (*Pan troglodytes verus*) has recently been up-listed to "Critically Endangered" on the IUCN Red List. Population status and trends of the remaining populations of chimpanzees almost always rely on counts of sleeping nests along line transects. In tropical forests, permanent line transects can facilitate survey work but may also be avoided by animals, complicating data analysis and possibly resulting in erroneous estimates. We conducted surveys in Liberia's Sapo National Park and its buffer zone along clear-cut ('permanent') and uncut ('temporary') line transects to estimate chimpanzee abundance and compare chimpanzee densities inside and outside the park. We recorded all indirect signs of chimpanzee presence and human activities on 16 permanent transects in Sapo and six temporary transects in the surrounding buffer zone. Our analysis revealed a population density of 0.83 individuals/km² across the park and its buffer zone. Compared to previous estimates, this suggests a relatively stable population over the past eight years of roughly 1,000 chimpanzees. It appears that poaching and habitat encroachment, which has persisted in the area since the first chimpanzee survey in 2009, did not have a significant negative affect on population growth over time. Possible reasons for this include local taboos against killing chimpanzees, poachers not targeting chimpanzees directly, and the chimpanzees' behavioral flexibility. Nest encounter rate inside the park was considerably lower than in the buffer zone and significantly fewer nests were found on or near permanent transect lines (19%) than temporary transects (44%), indicating an avoidance effect of chimpanzees towards the former. The study also shows that permanent transects were frequently used by illegal miners and poachers, providing direct evidence of the impact that humans have on chimpanzee habitat use and the potential negative implications of cutting permanent transect lines on wildlife in the park. We call for an increase in conservation and law enforcement efforts to protect depletion of wildlife resources from the park. We also stress the need for legal enforcement of the park's buffer zone, in order to effectively protect wildlife against poaching, habitat destruction and disease, to ensure the continued survival of chimpanzees in Liberia's oldest national park.

Key Words: Avoidance effect, chimpanzee nest survey, distance sampling, hunting, permanent line transect, Sapo National Park

Introduction

In 2016, it was reported that western chimpanzees had declined by more than 80%, from about 175,000 in 1990 to 35,000 chimpanzees in 2014, and the species was consequently up-listed to "Critically Endangered" on the IUCN Red List of Threatened Species (Humle *et al*. 2016; Kühl *et al*. (2017). Kühl *et al.* (2017) analyzed survey datasets from 20 sites across the entire West African region (A.P.E.S. Portal 2017), representing about 25,000 of the remaining 35,000 chimpanzees. This study demonstrated the importance of analyzing large datasets of wildlife populations over cross sections of protected areas to acquire a detailed scientific understanding of trends across local, regional and global scales, providing the wherewithal as such to identify the key conservation measures needed to prevent species' declines and extinctions.

Sapo National Park is a site of global conservation concern, comprising one of three remaining major blocks of the Upper Guinean Rainforest. It is one of the most intact ecosystems in Liberia (Kouakou *et al*. 2009). Until 2016, Sapo was Liberia's only national park. Since then, however, the government has created two more national parks, namely Gola Forest National Park and the Grebo-Krahn National Park (MFA 2016, 2017). Located in southeastern Liberia, Sapo National Park provides refuge to an important chimpanzee population numbering >1000 individuals (N'Goran *et al*. 2010) and is one of the last remaining forest blocks in the Guinean Forests of West Africa Hotspot (Mittermeier *et al*. 1998), a critically fragmented and highly threatened region of outstanding biological diversity (Mittermeier *et al.* 2004). It is situated between two of Liberia's most important conservation priority areas identified by Junker *et al.* (2015a) that includes Gbi Forest and Cestos-Senkwehn Proposed Protected Areas to the west, and Grebo-Krahn National Park to the east. In total, these three areas host about 2,500 chimpanzees, or about 35% of the country's chimpanzee population (Tweh *et al.* 2014). A 3-km buffer zone around Sapo National Park was proposed based on the Liberia National Forestry Reform Law (FDA 2006) that stipulates that a buffer zone be established around protected areas. This is intended to buffer wildlife populations inside the park against poaching, habitat destruction and disease (Freeman 2014). However, the buffer zone of Sapo has yet to be officially delineated and demarcated on the ground.

In 2012, Fauna & Flora International (FFI) established a long-term biomonitoring program in Sapo National Park to estimate population trends for chimpanzees, pygmy hippopotamuses (*Choeropsis liberiensis*), and elephants (*Loxodonta africana cyclotis*), as well as duikers, birds, reptiles and amphibians (Freeman 2014). As part of this program, 90 permanent line-transect trails were cut (hereafter 'permanent transects') that are surveyed once or twice each year by trained biomonitoring staff of Liberia's Forestry Development Authority (FDA) and community auxiliaries to obtain direct and indirect information on the presence or absence of the target species. Transects were first cut in 2011 and have been cleaned once a year since 2014. Results from the 2014 survey (FFI unpubl. data) suggested a probable decrease in nest encounter rate when compared to data collected on temporary uncut transects (hereafter 'temporary transects') during a survey in 2009, published by the Wild Chimpanzee Foundation (WCF) in collaboration with the FDA in 2010

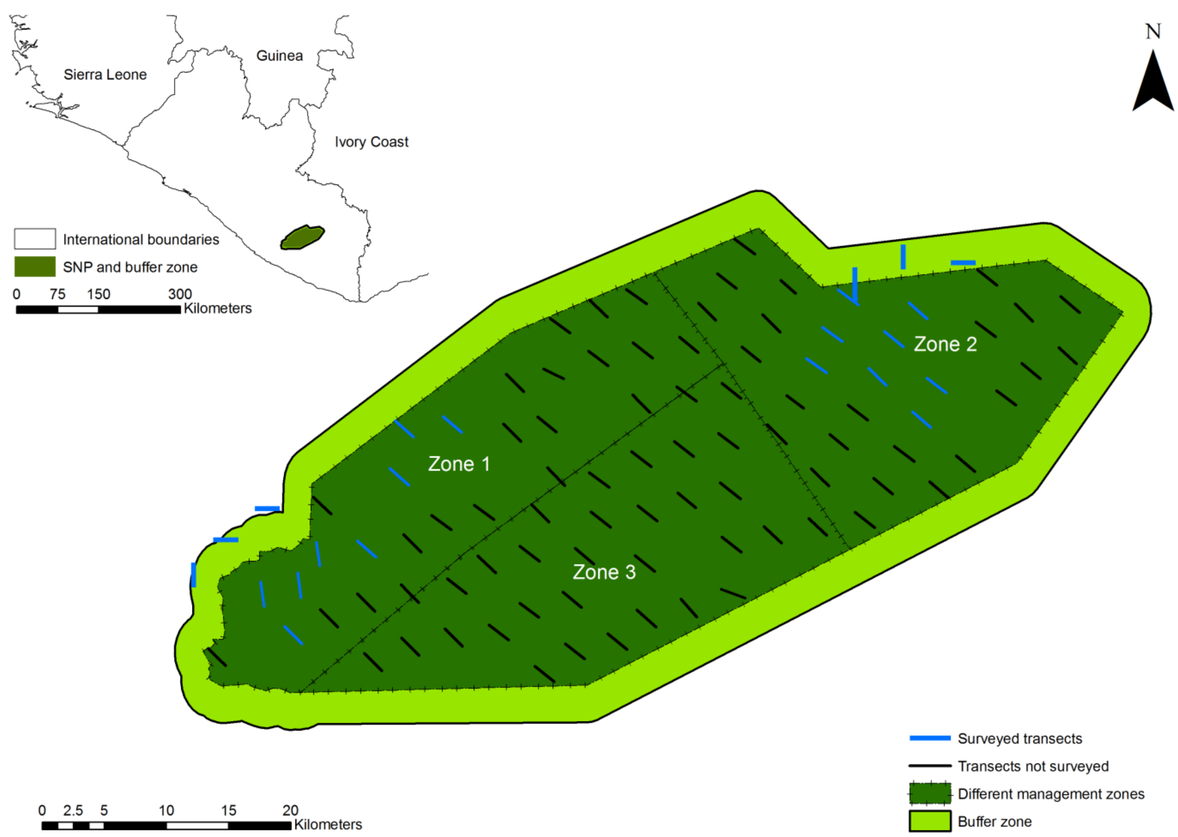

Figure 1. Map of Sapo National Park in southeastern Liberia, showing Fauna & Flora International's 90 systematically placed, permanent transects (black) in the three zones of Sapo National Park, 16 of which were randomly selected and surveyed in zones 1 (N = 8) and 2 (N = 8) for this study (blue). The buffer zone contained six strategically-placed temporary transects, of which six were randomly selected and surveyed for this study (blue).

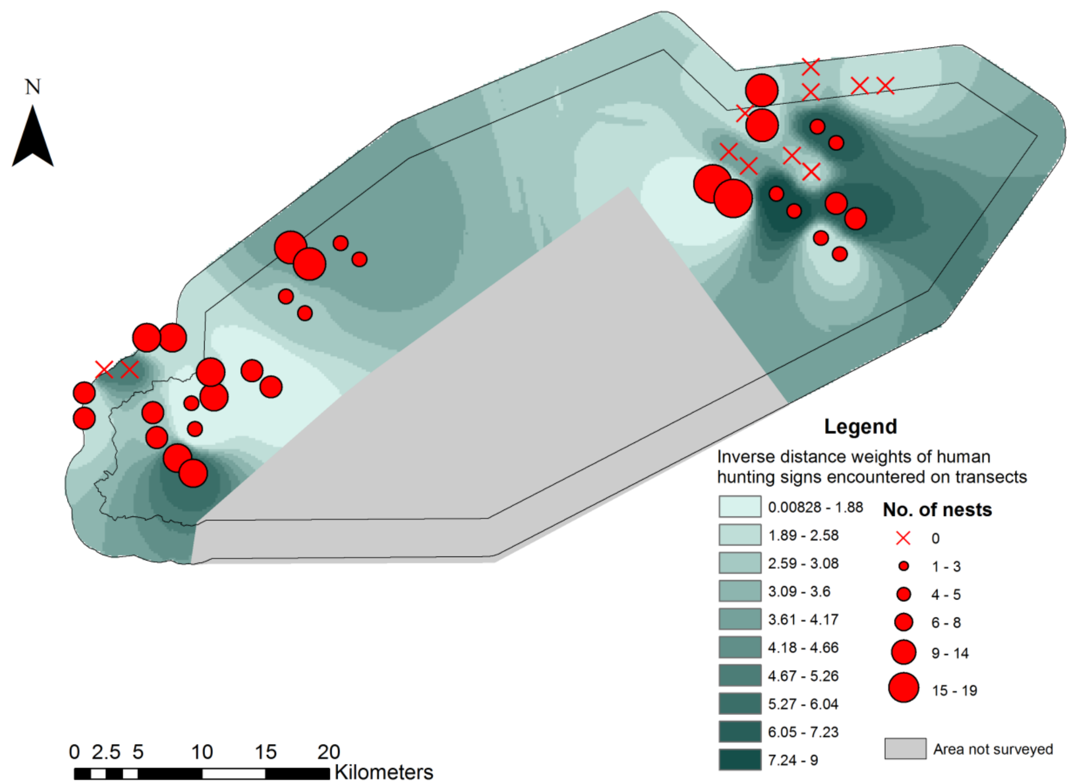

Figure 2. The distribution and density of hunting signs and the number of chimpanzee nests encountered in Sapo National Park and its buffer zone.

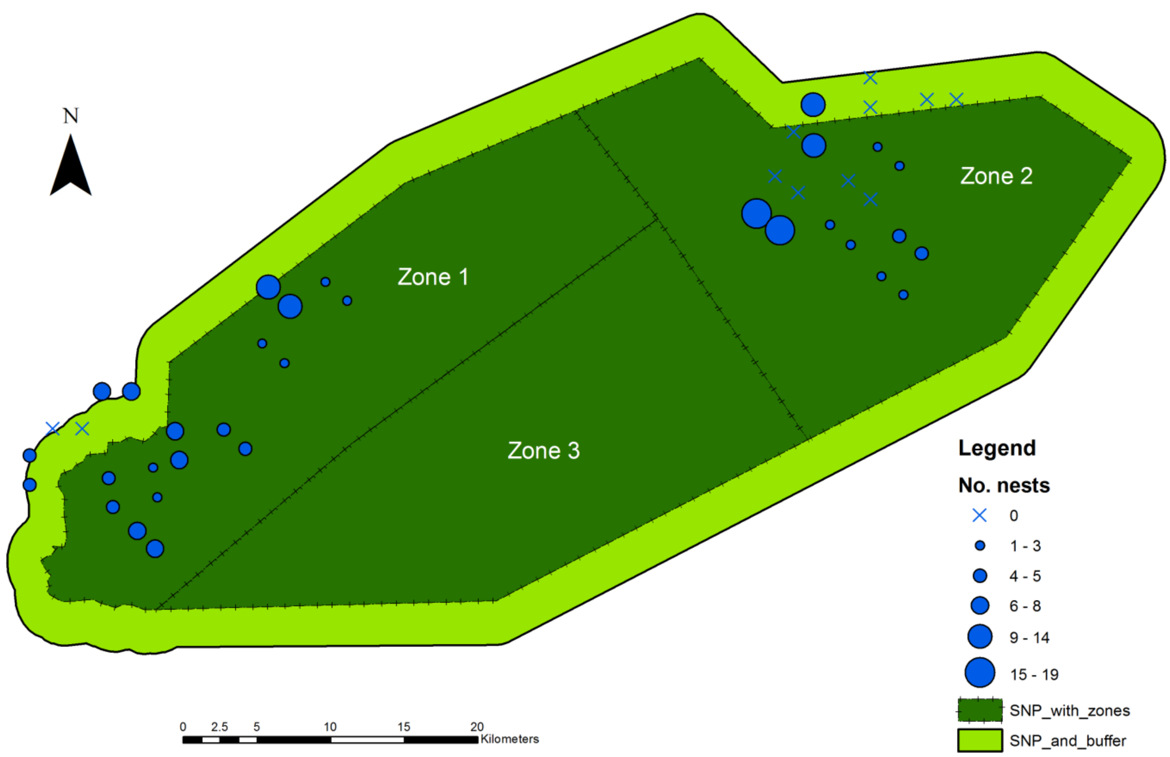

Figure 3. The distribution of chimpanzee nests detected on/near permanent transects in Sapo National Park and temporary transects in the buffer zone.

(N'Goran *et al*. 2010). Nest encounter rate was the number of nests observed per distance walked (Kouakou *et al*. 2009; Walsh *et al.* 2003).

Line transect surveys are frequently used to estimate the population abundance of chimpanzees and other primates in diverse terrestrial habitats (Campbell *et al.* 2016; Kühl *et al* 2008). Line transect survey techniques require adherence to a set of assumptions and a number of considerations derived from distance sampling methodologies (Buckland *et al.* 1993, 2001). For example, 1) objects, namely animals or signs of their presence (for example, dung or sleeping nests) directly on the line transect are always detected with certainty; 2) objects are detected at their initial location prior to any movement in response to the observer; and 3) distances are measured accurately. Major challenges while walking line transects to count the sleeping nests of chimpanzees in rainforest habitat include observer fatigue, detecting nests that are right above the observers at zero perpendicular distance, poor visibility due to dense vegetation or bad weather conditions, and travelling through dense vegetation (Buckland *et al.* 2001). Importantly, the last factor may motivate surveyors to cut the vegetation on transects, clearing the areas of dense vegetation, to facilitate access to observers. The risk of this, however, is that animals stay away from areas close to permanent transects in an attempt to avoid humans and the disturbance they cause (this has been observed in other species, for example, Griffiths and van Schaik 1993) resulting in an underestimation of population size. In contrast, when the vegetation is extremely thick, the observer's only clear line of view will be along cut transects and he or she will therefore tend to detect animals only as they cross the cut transect, resulting in overestimations of population size (Buckland *et al.* 2001). Likewise, where animals use permanent transects as pathways (see, for example, Tagg and Willie 2013), many direct sightings or signs of presence will likely be recorded along them. There may also be increased potential for repeated animal counts, especially for highly mobile species, which will lead to biases and possibly overestimations of population sizes (Glennie *et al.* 2015). Lastly, tracks and dung can be expected to be more visible and thus more easily detected in cleared than in densely vegetated areas.

In addition to the above-mentioned analytical concerns, permanent transects may be used by illegal miners or poachers as pathways to facilitate access to protected areas. Their actions may negatively impact wildlife populations through increased forest encroachment and hunting for bushmeat. This has been shown for roads and other linear clearings in tropical forests to have had a detrimental effect on wildlife populations (Laurance *et al*. 2009). It is therefore encouraged that every effort should be taken to minimize the effects of cutting transects. Not using permanent transects during field surveys effectively minimizes human impact and also prevents intruders from using transects to access protected natural resources illegally (for example, Griffiths and van Schaik 1993). However, open permanent transects may allow observers to increase sampling effort in tropical dense forest as it facilitates their travelling and decreases the frequency of habitat disturbance (Varman and Sukumar 1995). Surveillance (ranger patrols), tourists and research activities may efficiently benefit from those transects by allowing for the coverage of larger areas.

Given the apparent population declines of West African chimpanzees across most of their range over the past 25 years and the importance of reliable population trend data for informing effective conservation policy strategies, we used a combination of permanent and temporary line transect methods to estimate 1) chimpanzee abundance and temporal trends in abundance in Sapo National Park and its buffer zone, and 2) compare chimpanzee density between the core park and the area around the park, in the buffer zone. We hypothesized that: 1) nest detection probability at farther distances from permanent transect in Sapo would be significantly higher than from the temporary transects located in the buffer zone; 2) human presence has not affected the distribution of chimpanzees in the park and buffer zone; 3) vegetation types did not vary significantly along transect plots in the park and buffer zone. The last assumption was based on homogeneity in vegetation classified from Landsat TM imagery captured in 2012. The findings of this study were expected to play a critical role in ensuring the protection and conservation of the Western chimpanzee and its habitats in the Sapo National Park.

Methods

Study site

The park is in southeastern Liberia between 5°–6°N and 8°–9°W (Fig. 1). At the time of its creation in 1983, it encompassed roughly 1300 km² (Vogt 2012). In 2003, however, the northwestern part was extended, increasing the park's size to more than 1800 km², surrounded by an undefined buffer zone (Freeman 2014). Sapo National Park is divided into three management zones (hereafter 'zones'). Zone 1 is the southwestern section of the park (the headquarters are located there), Zone 2, the northern part, is adjacent to the town of Putu, and Zone 3, the southeastern section, extends to Dodoweken and other towns neighboring the park. Sapo National Park is Liberia's first protected area and an important center for biodiversity (Kouakou *et al.* 2009). Due to its abundant mineral resources, Sapo has faced a number of threats of illicit mining. In March 2005, the United Nations Mission in Liberia (UNMIL) reported that an estimated 5,000 illegal miners were living there (Freeman 2014). By 2010, this number had increased to 18,000; however, the majority of the miners were evicted by the government of Liberia by October of that same year (Freeman 2014). Recent socioeconomic studies (FFI unpubl. data) indicate that approximately 38,000 people currently live along the borders of the park.

Vegetation classification

Vegetation classification was based on a land-cover map derived from Landsat TM imagery captured in 2012, courtesy of the FFI database for Sapo National Park. An extensive field inventory was undertaken in 2012 using GPS and compasses to locate systematic points for the establishment of permanent line transects. These points were used to evaluate the consistency of land-cover types from the Landsat imagery, using Arc GIS computer program, by interpolating GPS data of physical vegetation observation and Landsat imagery of the park.

Data collection

The survey was conducted in the park and its buffer zone over a period of four months, from November 2016 to March 2017. We randomly selected 16 out of 90 systematically placed permanent line transects for our survey (Fig. 1). Permanent transects were clear-cut in 2011 by the FFI to survey 50 pre-identified indicator species and to quantify human threats (Vogt 2011). Each transect was 2 km long and traversed the three management zones. We were unable to survey Zone 3 because of a large influx of armed illegal miners that lead to the FDA's decision to suspend all research and biomonitoring in that area. The distance between these transects was approximately 3 km. We used Quantum GIS v. 2.1.4 (QGIS Development Team 2016) with the Geographic Resources Analysis Support System (GRASS) v. 7.0.4 (GRASS Development Team 2017) to strategically place another six temporary (uncut) line transects of equal length in the buffer zone surrounding zones 1 and 2 (Fig. 1). We excluded the buffer zone surrounding Zone 3 from our survey area because of the security reasons outlined above. Patrols of the FDA investigation teams were active in the buffer zone at the time of our survey and would likely have influenced our survey results, so we deferred from using a systematic random survey design there, and surveyed strategically placed temporary transects instead. Because of this, the temporary transects in the buffer zone had to be located close to permanent transects. All field data were collected in accordance with the survey procedures established by the *IUCN Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations* (Kühl *et al*. 2008). Whenever a chimpanzee nest was spotted, we accurately measured the perpendicular distance from the transect line to each nest and recorded its geographic location using a hand-held GPS device. We also recorded the presence and geographic location of all anthropogenic activities observed on and from the transect line.

Mapping of vegetation types

Vegetation was sampled every 500 m of each 2 km transect. A quadrat of 20×20 m was placed on either side of the transect (Manu and Cresswell 2007) using a 50-m measuring tape and rope to establish a quadrat. Every quadrat at 500 m was considered a transect plot. The vegetation structure in the transect plots were classified in one of four categories: sapling cover (smaller trees that are equal to or less than 10 m tall), lower cover (trees greater than 10 m tall and up to 20 m), mid-cover (trees more than 20 m and up to 30 m) and high canopy (all trees above 30 m) (Jones *et al.* 1995). The percent canopy cover of every classified variable in a plot was estimated due to limited time and resources and the lack of an experienced botanist in the survey team.

Data analysis

We used the Distance v.6.2 software (Thomas *et al.* 2010) to estimate chimpanzee abundance and QGIS to plot the distribution of chimpanzee nests and model inverse-distance weighted density of human signs across the study area. We estimated chimpanzee population size based on a nest production rate of 1.143, which is based on observations of habituated chimpanzees in Taï National Park (Kouakou *et al.* 2009), because there were no habituated chimpanzees in Sapo. For the proportion of nest builders, we used Plumptre and Cox's (2006) estimate of 83%. We used a nest decay rate of 100.69 days, which was based on the results of a nest decay study conducted in Sapo National Park in 2009 (N'Goran *et al.* 2010). Finally, we calculated chimpanzee abundance for the park, excluding Zone 3, which we did not survey for the reasons outlined above, but including the buffer zone. Our survey therefore covered an area of 1275.65 km². We also estimated chimpanzee density (/km²), 95% confidence intervals (CI) and the coefficient of variation (CV) for each estimate. We did not left-truncate our data and did not set predefined distance group intervals (S. T. Buckland pers. comm. 2017). Because chimpanzees avoided permanent transects, the detection probability plot did not show the desired "shoulder" (Fig. S1), which is typically expected for distance data sets (Buckland *et al.* 2001). We opted to ignore the poor fit of the probability function, as nests from within 6 m of the line appeared to have built up at just over 6 m, resulting in a higher density beyond 6 m than at an average locality. In this case, bias is expected to be lower when ignoring the poor fit than through left-truncation of the data, where Distance 'averages out' the low density within 0−6 m with a high density at, for example, 6−12 m (S. T. Buckland pers. comm. 2017). We fitted a half-normal model with simple polynomial adjustment to our frequency distribution of perpendicular distances as this model was identified as the model with the best fit from a set of alternative models, using Akaike's Information Criterion (AIC) (Akaike 1973; Sakamoto *et al.* 1986). To confirm the presence of an avoidance effect of permanent transects by chimpanzees, we compared the frequency distributions of perpendicular distances measured to nests encountered on permanent transects in the park with temporary transects in the buffer zone using a two sample t-test, assuming unequal variances (Sokal and Rohlf 2012).

We also conducted a Spearman's Rank Order Correlation Test in R v. 3.2.2. (R Core Team 2015) to test for the influence of human activities on chimpanzee distribution and abundance in the combined area of the park and the buffer zone. To do this, we grouped all anthropogenic activities related to farming (plantations, cleared forest patches), mining (mining camps), hunting (gunshots, empty cartridges, snares, hunting camps, poacher trails, human direct observation), logging (logging camps, logging road) and other human activities (human path/rangers patrol path, human tracks, human vocalizations, human waste, and extraction of non-timber forest products (NTFP)), and summed them for each transect.

A one-way ANOVA test was used to determine whether vegetation used by chimpanzees differed in percent canopy cover at every stratum with transect plots in the park and buffer zone, while the Chi-squared test was used to determine the distribution of chimpanzee nests stages across the survey area. Estimated percent data from transect plots were arc-sine transformed. We used the Tukey's Honest Significant Difference (HSD) (a *post hoc* test) to examine the level of significance in differences between transect plot variables in the park and buffer zone.

Results

Survey effort and chimpanzee abundance estimate

The estimate was based on the total survey effort L = 38.38 km, the average transect length l = 1744.5 m, the effective strip width ESW = 15.665 m, and the study area A = 1275.65 km². We surveyed 16 km in each zone inside the park and 6.38 km in the buffer zone surrounding zones 1 and 2. The majority of nests were seen in Zone 1 (N = 41), followed by Zone 2 (N = 29) and then the buffer zone (N = 25) (Fig. 2), resulting in a nest encounter rate (no. of nests encountered/km surveyed) for the three areas of 2.56 (Zone 1), 1.88 (Zone 2), and 5.80 (buffer zone). For a summary of the model results, see Table S1.

Based on 95 nest observations in zones 1 and 2 of the park and its buffer zone, we estimated the chimpanzee population at 1,055 individuals (95% CI = 595–1,870, CV = 0.29) with a density of 0.83 chimpanzees/km² (95% CI = 0.47–1.47, Table 1). This represents approximately 15% (9−27%) of the total chimpanzee population in Liberia as estimated by Tweh *et al.* (2014).

Avoidance effect

Chimpanzees appeared to avoid building their sleeping nests within 0−6 m of permanent transect lines inside the park, resulting in only 19% (n = 13) of nest detections from 0−6 m in these areas. Eighty-one percent of the chimpanzee nests were spotted more than 6 m away from permanent transects, as compared to only 44% on temporary transects. The two-sample t-test comparing perpendicular distances measured to nests in the park and the buffer zone clearly showed that nests in the Sapo National Park were detected at greater distances from the transect than those in the buffer zone ($t(2) = 4.06$, $p < 0.001$, df = 69).

Distribution of signs of chimpanzee presence

The survey area differed only slightly among the three areas surveyed (Zone 1, Zone 2 and the buffer zone) (χ^2 0.05, 6 = 22.23, $p<0.05$). The distribution of chimpanzee nests, however, differed significantly across the park and the buffer zone, with the majority of chimpanzee nests being found in Zone 1 of the park (see Fig. 3). One hundred and fourteen signs of chimpanzee presence were encountered in total, of which 38% (N = 43) were observed in Zone 1, and 39% (N = 44) and 24% (N = 27) in Zone 2 and the buffer zone, respectively (Table S2).

Distribution of signs of human presence

To control for survey effort, permanent transects in Sapo National Park were surveyed before the temporary transects in the buffer zone. Every transect was surveyed each day between 08:00 and 16:00. Routes we took in the buffer zone to reach the transects in the park were used just once, and the GPS tracking system was used to control for distance between transects. We found 83 signs of human presence on all transects combined, of which 30% were recorded in Zone 1 (N = 25), 46% (N = 38) in Zone 2, and 24% (N = 20) in the buffer zone. We found no signs of mining on either the permanent or temporary transects. We did, however, find signs of mining in the buffer zone while walking between transect lines. Signs of hunting (N = 63) were the most frequently encountered signs of human presence, accounting for 75.9% of all the signs of human presence detected and ranging from 1–3 observations per transect (Fig. 3). Hunting sign encounter rates for the park and the buffer zone were 1.7/km and 1.6/km, respectively. The most frequently encountered hunting signs during this survey were poacher trails (N = 33), followed by empty cartridges (N = 20) and snares (N = 2). While empty cartridges were only observed on/from permanent transects,

Table 1. Population estimate for chimpanzees in Sapo National Park in 2009 and in 2017.

Year	Study area (km²)	Chimpanzee abundance (CI)	Chimpanzee density (CI)	Chimpanzee nest encounter rate (signs/ km surveyed)	Human sign encounter rate (signs/ km surveyed)	Source
2009	1,248.11 km² (SNP excluding mining areas)	1,079 (713–1,633)	0.86 (0.571–1.308)	4.05	1.27	N'Goran *et al*. (2010)
2017	1,275.65 km² (SNP excluding Zone 3, but including the buffer zone)	1,055 (595–1,870)	0.83 (0.47–1.47)	2.48	2.16	This study

SNP = Sapo National Park

snares were seen only along the temporary transects in the buffer zone. Poacher trails were recorded on both, permanent (N = 23) and temporary transects (N = 10). All poacher trails were probably in use, as the markings on trees along these trails, typically made by the poachers to mark their way, were still fresh. Of the empty cartridges found, 70% (N = 14) were new (0−3 months), and 20% (N = 4) were recent (3−6 months). Signs of farming (N = 2), logging (N = 3), NTFP (N = 3), and OHA (N = 12) accounted for only 2.4%, 3.6%, 3.6%, and 14.5% of all human signs, respectively. Encounter rates for farming, logging, NTFP and OHA signs were 0.06/km, 0.08/km, 0.08/km and 0.31/km, respectively. Evidence of logging and farming was recorded only in the buffer zone, and not inside the park. Signs of NTFP were observed only in the park, whereas signs of OHA's were recorded in both the park (N = 9) and its buffer zone (N = 3). For a summary of these figures, please refer to Table S2.

The results of the Spearman test showed that there was no significant correlation between the number of chimpanzee signs and human signs detected on transects (Spearman's Correlation: ρ = -0.087, p >0.05, Fig. S2), the number of chimpanzee nests and hunting signs detected on transects (ρ = -0.246, p >0.05), or the number of chimpanzee signs and hunting signs detected on transects (ρ = -0.310, p >0.05).

Vegetation in the transect plots

The vegetation survey in transect plots revealed three vegetation types—primary forest, mature secondary forest, and young secondary forest. A one-way ANOVA was used to examine differences in the various vegetation variables (% canopy cover, % middle canopy cover, % lower canopy cover, % of sapling) in transect plots in Sapo National Park and its buffer zone. Our results showed there were significant differences for the estimated vegetation variables, % canopy cover (F 0.05, 2, 73 = 4.57, p <0.05(0.013)) and % middle canopy cover (F 0.05, 2, 73 = 11.82, p <0.05 (0.000) in Sapo National Park and the buffer zone; there was no significant differences for the percentage of vegetation variable for lower canopy cover (F 0.05, 2, 73 = 1.022, p >0.05(0.28)) and % of sapling cover (F 0.05, 2, 73 = 1.455, p >0.05 (0.21) in Sapo National Park and the buffer zone.

The Tukey HSD *post hoc* test was used to examine significant differences in vegetation variables between the park and the buffer zone. There were no significant differences for high canopy cover and middle canopy cover (Tukey *post hoc* p >0.05): the value for the high canopy cover in the park was 74.8% and for the buffer zone 66%. The park and buffer zone differed, however, in the percent lower canopy cover and sapling cover. The lower canopy was 66.5% in the park and 41% in the buffer zone. The sapling cover was very different—70.7% for the park and 100% for the buffer zone.

Discussion

Sapo National Park is a regional biodiversity hotspot and the second-largest area of protected primary tropical rainforest in West Africa after Taï National Park in neighboring Côte d'Ivoire (Junker *et al*. 2015a). Our study provides the first estimate of the chimpanzee population in the park and its buffer zone, data which can provide baseline for population monitoring that is important for informing effective conservation management decisions to ensure the long-term survival of chimpanzees in this region. Our analysis estimated a population of 1,055 chimpanzees in the park (excluding Zone 3) and buffer zone—a density of 0.83 individuals/km². This is similar to the population estimate published by N'Goran *et al.* in 2010 of 1,079 chimpanzees (excluding mining areas), equating to a density of 0.86 chimpanzees per km².

Our survey results therefore suggest that the population has remained relatively stable over the past eight years. This is remarkable given that the majority of western chimpanzee populations are declining (for example, Côte d'Ivoire (Campbell *et al*. 2008), Senegal (Galat *et al.* 2000), and Nigeria (Greengrass 2009)). However, human threats, especially poaching for bushmeat (Greengrass 2015), but also habitat encroachment and disturbance caused by illegal mining (Kayjay 2010), and possibly disease transmission (Ordaz-Németh *et al.* 2017) continue to exist around the park. Our encounter rate of evidence of human activity was double that from the surveys in 2009 (Table 1).

The apparent stability of the chimpanzee population in Sapo National Park over the past eight years, despite the persisting threats, may be explained by chimpanzees not being directly targeted by hunters, as has been observed elsewhere in Liberia (Junker *et al.* 2015) and other countries (for example, Equatorial Guinea (Brncic *et al.* 2010), Sierra Leone (Regnaut and Boesch 2012), Guinea (McCarthy *et al*. 2015), and Uganda (Watkins 2006)), and by their behavioral flexibility, enabling them to survive in human-modified landscapes (McLennan 2008; Brncic *et al.* 2010; Hockings *et al*. 2015). Many Liberian villages practice taboos against killing and eating chimpanzees (J. Junker unpubl. data), including those situated near the southwestern border (Zone 1) of the park (Greengrass 2011). However, it is likely that other large mammal populations inside the park, especially those of frequently consumed bushmeat species, experienced significant decreases in population size over the same time period. Multi-faceted surveys that could easily be combined with chimpanzee surveys in the future (for example, Tweh *et al.* 2014) would be able to provide more information to clarify this. Another reason for the park's chimpanzee population remaining stable over the past years could be partially related to the Ebola outbreak in West Africa in 2014/2015. It may have discouraged hunters from killing chimpanzees (and other species), it is possible that significantly less bushmeat was purchased and consumed during this time in Liberia (Ordaz-Németh *et al.* 2017).

In contrast to our results, a recent study by Kühl *et al*. (2017) indicated that the chimpanzee population in Sapo National Park underwent a significant decline from 2009–2014. A number of factors may explain this discrepancy. Temporal variation in nest decay due to variation in climatic conditions, which was not considered in this study, may have biased our estimate of chimpanzee population size (Laing *et al.* 2003). We used a nest decay rate that was estimated during a short-term nest decay study in Sapo in the rainy season from June–October 2009 (N'Goran *et al.* 2009). Our survey, however, was conducted mostly during the dry season (November 2016–March 2017), during which time nests may have decayed at a slower rate (Kouakou *et al.* 2009). Also, short-term studies of decay time for orangutan nests have shown to be prone to considerable variation (Laing *et al*. 2003). Although studies on the variation in chimpanzee and orangutan nest decay have shown that factors other than climate, namely tree type, tree size and nest height may considerably influence nest duration (Kouakou *et al.* 2009, Laing *et al.* 2003), we think that this did not affect our estimate because the area for which nest decay time was estimated (N'Goran *et al.* 2009) overlapped considerably with ours.

The sampling strategy of the two surveys used to calculate the population trend estimate for Sapo by Kühl *et al.* (2017), differed substantially from ours in that the 2009 study only surveyed temporary transects, whereas the 2014 study only surveyed permanent transects. We surveyed permanent transects inside the park in combination with temporary transects in the buffer zone and found a clear avoidance effect of chimpanzees towards permanent transects, where the percentage of chimpanzee sleeping nests detected on/near (0–6 m) permanent transect lines (19%) was more than two times lower than that on/near temporary transects (44%). And so, one might argue that our estimate of chimpanzee abundance inside the park grossly underestimates true population size and is not directly comparable to the estimate of the survey in 2009. However, although our encounter rate of 2.21 nests/km surveyed is lower than the nest encounter rate recorded by N'Goran *et al.* (2010) (4.05 nests/km surveyed), it is also almost 10 times higher than the nest encounter rate recorded by the Fauna & Flora International (FFI) teams in 2014 (0.23 nests/km surveyed, FFI unpubl. data). There are multiple estimates for the area, potentially caused by methodological differences. We believe that the results of this study produced an estimate that, despite possibly representing a slight underestimate of the true population due to the avoidance effect is nevertheless comparable to the 2009 estimate, indicating that Sapo's population has been relatively stable over the past eight years, thereby yielding a more accurate population trend than the one reported by Kühl *et al.* (2017). During the 2014 survey, only 35 chimpanzee nests were found on 154 km of transects distributed across the park. We speculate that the following three factors may have contributed to this low nest encounter rate. 1. Because of the clear-cutting of permanent transects in 2011 (M. Molokwu-Odozi pers. obs. 2017), the disturbance that this process created may have deterred chimpanzees from areas near permanent transect lines, resulting in very few nest detections during the survey in 2014. However, this disturbance effect may have weakened over time so that five years later during our survey in 2016/17, chimpanzees only avoided the area on or immediately next to the permanent transect lines at 0–6 m. 2. FFI surveys were multi-faceted surveys (teams collected data on >50 wildlife species from various taxa) and so teams had less time to focus on nests in the trees above them than the teams during the 2009 survey and this study. 3. Since the evacuation in 2010, the number of illegal miners in the park increased rapidly again in the years to follow, especially at the peak of the Ebola crisis in 2014 when park activities were brought to a halt. In July 2017, during a Sapo National Park stakeholders' conference, a deadline of 31 August 2017 was agreed for the illegal miners to vacate the park. Some miners, therefore, may have already started moving out of the park before our survey commenced. If miners frequently used permanent transects as passageways, then chimpanzees may have avoided them in 2014 simply because of the higher 'human traffic' on permanent transects than in 2016/2017.

The estimated percentages of high canopy and middle canopy cover were found to be similar in the parks and the buffer zone, but this was not so for the lower canopy and sapling cover. The similarity may be explained by the physical and chemical soil properties influencing habitat structure, as both the park and buffer zone share potential natural factors such as streams and fruiting trees. This was also shown in the vegetation studies done by Zhang *et al*. (2017). The differences of percent cover observed in the lower canopy and sapling cover may also be attributed to two factors: 1) higher competition for space and sunlight in the various forest strata; 2) the adverse critical factor of cutting the understory trees along the permanent transects to keep them clear.

Although we have found that chimpanzee population in Sapo National Park is one of the few in West Africa that appears not to have declined over the past decade, our results stress the need for increased law-enforcement to more effectively control poaching in the park, which requires, besides, the removal of the remaining illegal miners. Our study showed that 80% of the empty cartridges, found only on or near the permanent transects in the park but not on temporary transects in the buffer zone, were new or recent (Table S2). This suggests that poachers still use the permanent transects to hunt. Even though they do not seem to target chimpanzees, their presence may disturb the chimpanzees and influence their ranging patterns. The number of illegal miners in the park is uncertain, but ranger patrols have suggested that it probably still ranges in the thousands (Forestry Development Authority (FDA) unpubl. data). It is also evident that the current sampling strategy for the long-term monitoring program for chimpanzees and other species needs to be adapted. Temporary instead of permanent transects, camera traps, genetic surveys, or a combination of these will yield more reliable abundance and trend estimates. If temporary transects were to be used in the future, these could be permanently marked to ensure that they are accurately relocated during consecutive surveys, for example by driving pegs or metal stakes with brightly colored flagging tape attached to them into the ground at the beginning and the end of each transect line (Buckland *et al*. 2001). Future surveys should continue to sample the buffer zone and possibly beyond, because it is important to identify any disturbance (for example, human encroachment) and take necessary measures before it extends to the park, and because it is advisable to have a survey design that allows for detecting spatial population- or community expansion into the buffer zone or farther. We also stress the need to officially demarcate the buffer zone around the park, as this area appears to provide important habitat for chimpanzees and probably other species, underpinning its role as a buffer against poaching, habitat destruction and disease.

Conclusion

With more than 1,000 chimpanzees, Sapo National Park is a stronghold for chimpanzees and one of the few viable chimpanzee populations in West Africa. Chimpanzee numbers been relatively stable over the past eight years. The survival of this and other populations in Liberia is, however, threatened by bushmeat hunting and the rapidly growing mining, forestry and agricultural sectors (Tweh *et al.* 2014; Junker *et al.* 2015a). Our study demonstrates the importance of carefully-planned and robust monitoring programs to yield reliable biomonitoring data for guiding conservation strategies. There are numerous implications of using inaccurate population status and trend estimates for conservation decision-making. For example, funders may discontinue financing conservation programs if a population is found to be declining despite the conservation measures taken. Investors may prioritize populations that are viable in the long term over those that are declining. Furthermore, with economic development in Africa being on the rise (Edwards *et al.* 2014; Wich *et al.* 2014), inaccurate (underestimated) representation of population status or trends can play into the hands of resource extraction firms that may have an economic interest in the area. As this study has shown, establishing permanent, clear-cut transect lines in a protected area may facilitate access to illegal miners and poachers, which is counterproductive from a conservation point of view. Continuing to put a better mechanism into place to improve the quality of monitoring methods is crucial if conservationists are to most effectively use limited resources and offer chimpanzees in West Africa the best chance of long-term survival.

Acknowledgments

We thank the University of Nairobi for allowing the lead author access to their research and educational facilities. This study was supported by FFI Liberia through funding and logistics from the Arcus Foundation and the U.S. Fish and Wildlife Service. Many thanks to the ArcelorMittal Mining Company, Liberia, and to the ArcelorMittal Liberia Biodiversity and Conservation Program, Yekepa, Nimba County, for providing advanced academic scholarship and financial assistance. We would also like to thank the Department of Conservation at the Forestry Development Authority, Liberia, for giving us permission to conduct this study in Sapo National Park. We thank the Wild Chimpanzee Foundation for their collaboration, and Eric Rexstad and Steve Buckland for their advice on data analysis in Distance. Thanks also to Mimi Arandjelovic who provided extremely helpful comments on the first draft of this manuscript. Lastly, we would like to thank our survey team members Webster Ziegler, Morris Jah, Tolbert Play, Emmanuel Dweh, Garison Kieh, Jerome Farley, and Garity Kieh for their hard work and enthusiasm.

Literature Cited

Akaike, H. 1973. Information Theory and the Maximum Likelihood Principle. In: *2nd International Symposium on Information Theory*, B. N. Petrov and F. Csäki (eds.), pp. 267–281. Akademiai Kiàdo, Budapest.

A.P.E.S Portal. 2017. Ape, Populations, Environments, Surveys (A.P.E.S.) URL: <http://apeportal.eva.mpg.de>. Accessed August 2017.

Brncic, T. M., B. Amarasekaran and A. McKenna. 2010. Final report of the Sierra Leone National Chimpanzee Census Project. Unpublished report. Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone.

Buckland, S. T., D. A. Anderson, K. P. Burnham and J. L. Laake. 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations.* Oxford University Press, Oxford, UK.

Campbell, G., H. Kühl, K. P. N'Goran and C. Boesch. 2008. Alarming decline of West African chimpanzees in Côte d'Ivoire. *Curr. Biol*. 18: 903–904.

Campbell, G., H. Makaga, J. Junker and K. A. I. Nekaris. 2016. Primate abundance and distribution: background concepts and methods. In: *Introduction to Primate Conservation*, S. Wich and A. J. Marshall (eds), pp.79–110. Oxford University Press, Oxford, UK.

Edwards, D. P. S., L. Weng, P. Dirks, J. Sayer and W. F. Laurance. 2014. Mining and the African environment. *Conserv. Lett.* 7: 302–311.

FDA. 2006. *An Act Adopting the National Forestry Reform Law of 2006 (Amending the National Forestry Law of 2000, as amended; and Amending an Act Creating the Forestry Development Authority, as Amended). Approved September, 2006.* Forestry Development Authority (FDA), Monrovia, Liberia.

Freeman, B. G. B. 2014. Habitat Relationships and Anthropogenic Threats in and around Sapo National Park, Liberia. MSc Thesis. University of Jos, Jos, Nigeria.

Galat, G., A. Galat-Luong, I. Ndiaye and Y. Keita. 2000. Geographical distribution of chimpanzees and baboons in Senegal. *Folia Primatol*. 71: 249–267.

GRASS Development Team. 2017. Geographic Resources Analysis Support System (GRASS) Software, Version 7.0.4 Open Source Geospatial Foundation. Electronic document: <http://grass.osgeo.org>

Glennie, R., S. T. Buckland and L. Thomas. 2015. The effect of animal movement on line transect estimates of abundance. *PLoS One* 10: e0121333.

Greengrass, E. 2009. Chimpanzees are close to extinction in southwest Nigeria. *Primate Conserv.* (24): 77–83.

Greengrass, E. 2011. Exploring the Dynamic of Bushmeat Hunting and Trade in Sapo National Park. Report. Fauna & Flora International, Cambridge, UK.

Greengrass, E. 2015. Commercial hunting to supply urban markets threatens mammalian biodiversity in Sapo National Park. *Oryx* 50: 1–8.

Griffiths, M. G. and C. P. van Schaik. 1993. Camera trapping: a new tool for the study of elusive rain forest animals. *Trop. Biodiv.* 1: 131–135.

Hockings, K. J., M. R. McLennan, S. Carvalho, M. Ancrenaz, R. Bobe, R. W. Byrne, R. I. M. Dunbar, T. Matsuzawa, W. C. McGrew, E. A. Williamson, M. L. Wilson, B. Wood, R. W. Wrangham and C. M. Hill. 2015. Apes in the Anthropocene: flexibility and survival. *Trends Ecol. Evol.* 30: 215–222.

Humle, T., C. Boesch, G. Campbell, J. Junker, K. Koops, H. S. Kuehl and T. Sop. 2016. *Pan troglodytes* ssp. *verus* (errata version published in 2016). The IUCN Red List of Threatened Species 2016: e.T15935A102327574. Accessed August 2017.

Junker, J., C. Boesch, T. Freeman, R. Mundry, C. Stephens and H. S. Kühl. 2015a. Integrating wildlife conservation with conflicting economic land-use goals in a West African biodiversity hotspot. *Basic Appl. Ecol.* 16: 690–702.

Junker, J., C. Boesch, R. Mundry, C. Stephens, M. Lormie, C. Tweh and H. S. Kühl. 2015b. Education and access to fish but not economic development predict chimpanzee and mammal occurrence in West Africa. *Biol. Conserv*. 182: 27–35.

Kayjay, G. S. T. 2010. Assessment Tour at the Sapo National Park from January 13th to 22nd 2010. Report. Forestry Development Authority (FDA), Monrovia, Liberia.

Kouakou, C. Y., C. Boesch and H. Kühl. 2009. Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. *Am. J. Primatol.* 71: 447–457.

Kühl, H., F. Maisels, M. Ancrenaz and E. A. Williamson. 2008. *Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations*. IUCN SSC Primate Specialist Group, Gland, Switzerland. 28pp. URL: <http://www.primate-sg.org/BP.surveys.pdf>.

Kühl, H. S., T. Sop, E. A. Williamson, R. Mundry, D. Brugière, G. Campbell, H. Cohen, E. Danquah, L. Ginn, I. Herbinger, S. Jones, J. Junker, R. Kormos, C. Y. Kouakou, P. K. N'Goran, E. Normand, K. Shutt-Phillips, A. Tickle, E. Vandras, A. Welsh, E. G. Wessling and C. Boesch. 2017. The critically endangered western chimpanzee declines by 80%. *Am. J. Primatol*. 79(9): e22681. DOI:10.1002/ajp.22681.

Laing, S. E., S. T. Buckland, R. W. Burn, D. Lambie and A. Amphlett. 2003. Dung and nest surveys: estimating decay rates. *J. Appl. Ecol.* 40: 1102–1111.

Laurance, W. F., M. Goosem and S. W. G. Laurance. 2009. Impacts of roads and linear clearings of tropical forests. *Trends Ecol. Evol.* 24: 659–669.

Manu, S. and W. R. L. Cresswell. 2007. Addressing sampling bias in counting forest birds: a West African case study. *Ostrich* 78: 281–86.

McCarthy, M. S., D. J. Lester, J. H. Eric, M. Arandjelovic, B. C. Stanford and L. Vigilant. 2015. Genetic censuring identifies an unexpectedly sizeable population of an endangered large mammal in a fragmented forest landscape. *BMS Ecol.* 21: 15.

McLennan, M. R. 2008. Beleaguered chimpanzees in the agricultural district of Hoima, western Uganda. *Primate Conserv.* (23): 45−54.

MFA. 2016. *An Act for the Establishment of the Gola Forest National Park. Approved: December 27, 2016.* Ministry of Foreign Affairs (MFA), Monrovia, Liberia.

MFA. 2017. *An Act Establishing the Grebo National Forest as Grebo-Krahn, National Park. Approved: October 9, 2017.* Ministry of Foreign Affairs (MFA), Monrovia, Liberia.

Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. da Fonseca and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conserv. Biol.* 12: 516–520.

Mittermeier, R. A., P. Robles-Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux and G. A. B. da Fonseca. 2004. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecosystems.* CEMEX, Mexico.

N'Goran, K. P., A. F. Yapi, I. Herbinger, A. Tondossama and Boesch, C. 2009. État du Parc National de Taï: rapport de résultats de biomonitoring phase v (Septembre–Mars 2010). Report. Wild Chimpanzee Foundation and L'Office Ivoirien des Parcs et Réserves de Côte d'Ivoire, Abidjan, Côte d'Ivoire.

N'Goran, K. P., C. Y. Kouakou and I. Herbinger. 2010. Report on the Population Survey and Monitoring of Chimpanzee in Sapo National Park, Liberia (June–December 2009). Report. Wild Chimpanzee Foundation, Abidjan, Côte d'Ivoire.

Ordaz-Németh, I., M. Arandjelovic, L. Boesch, T. Gatiso, T. Grimes, H. S. Kühl, M. Lormie, C. Stephens, C. Tweh and J. Junker. 2017. The socio-economic drivers of bushmeat consumption during the West African Ebola crisis. *PLoS Negl. Trop. Dis.* 11: e0005450.

Plumptre, A. J. and D. Cox. 2006. Counting primates for conservation: primate surveys in Uganda. *Primates* 47: 65–73.

Quantum GIS Development Team 2017. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. URL: <http://qgis.osgeo.org>.

Regnaut, S. and C. Boesch. 2012. Offset strategy for the Guinea Alumina Project. Report. Wild Chimpanzee Foundation, Conakry, Guinea.

Sakamoto, Y., M. Ishiguro and G. Kitawaga. 1986. *Akaike Information Criterion Statistics.* KTK Scientific Publishers, Tokyo, Japan.

Sokal, R. R. and F. J. Rohlf. 2012. *Biometry: The Principle and Practice of Statistics in Biological Research.* 4th Edition. W. H. Freeman and Company, New York.

Tagg, H. and J. Willie J. 2013. The influence of transect use by local people and reuse of transects for repeated surveys on nesting in western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) in southeast Cameroon. *Int. J. Primatol.* 34: 445–646.

Thomas L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hadley, J. R. B. Bishop, T. A. Marques and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47: 5–14.

Tweh, C. G., M. M. Lormie, A. Hiller, C. Y. Kouakou, H. S. Kühl and J. Junker. 2014. Conservation status of chimpanzees (*Pan troglodytes verus*) and other large mammals in Liberia: a nationwide survey. *Oryx* 49: 1–9.

Varman, K. S. and Sukumar, R. 1995: The line transect method for estimating densities of large mammals in a tropical deciduous forest: an evaluation of models and field experiments. *J. Biosci.* 20: 273−287.

Vogt, M. 2012. Biomonitoring and Research Program, Sapo National Park: Updated Plan for Research Opportunities and Priorities in and around Sapo National Park. Report. Fauna & Flora International, Monrovia, Liberia.

Walsh, P. D., K. A. Abernethy, M. Bermejo, R. Beyers, P. de Wachter, M. E. Akou, B. Huijbregts, D. I. Mambounga, A. K. Toham, A. M. Kilbourn, S. A. Lahm, S. Latour, F. Maisels, C. Mbina, Y. Mihindou, S. N. Obiang, E. N. Effa, M. P. Starkey, P. Teffer, M. Thibault, C. E. G. Tutin, L. J. T. White and D. S. Wilkie. 2003. Catastrophic ape decline in western equatorial Africa. *Nature* 422: 611–614.

Watkins, C. 2006. Local ecological perceptions on chimpanzees and forest resources. In: *Primates of Western Uganda*, N. E. Newton-Fisher, H. Notman, J. D. Peterson and V. Reynolds (eds.) pp.423–437. Springer, New York.

Wich, S., A. J. Garcia-Ulloa, H. S. Kühl, T. Humle, J. S. Lee and L. P. Koh. 2014. Will oil palm's homecoming spell doom for Africa's great apes? *Curr. Biol.* 24: 1659–1663.

Zhang, B., Xiaozhen Lu, Jiang Jiang, D. L. DeAngelis, Zhiyuan Fu and Jinchi Zhang. 2017. Similarity of plant functional traits and aggregation pattern in a subtropical forest. *Ecol. Evol.* 7: 4086– 4098.

Authors' addresses:
Clement G. Tweh, Wild Chimpanzee Foundation, Oldest Congo Town, Monrovia, Liberia, and School of Biological Sciences, University of Nairobi, Kenya; **Célestin Y. Kouakou**, Unités de Formation et de Recherche (UFR), Université Jean Lorougnon Guédé, Daloa, Côte d'Ivoire, and Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, Abidjan, Côte d'Ivoire; **Robert Chira**, School of Biological Sciences, University of Nairobi, Kenya; **Benedictus Freeman**, Fauna & Flora International, Oldest Congo Town, 1000 Monrovia 10, Liberia; **John M. Githaiga**, School of Biological Sciences, University of Nairobi, Kenya; **Shadrach Kerwillain**, **Mary Molokwu-Odozi**, **Matthew Varney**, Fauna & Flora International, Oldest Congo Town, 1000 Monrovia 10, Liberia; and **Jessica Junker**, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
Corresponding author: Clement G. Tweh <clementweh2g10@gmail.com>.

Received for publication: 23 November 2017
Revised: 31 October 2018

Supplementary Materials

Table S1. Summary of the model with the best fit in Distance

Model	No. of parameters	Effective Strip Width (ESW)	Probability of nest detection (P)	AIC	No. of observations
Half-normal, simple polynomial adjustments	2	15.66	0.78	357.62	95

Table S2. Number of chimpanzee signs and hunting activities detected in Sapo National Park (management zones 1 and 2) and in the buffer zone surrounding them.

Area	Category transect	Survey effort (km)	Number of hunting signs	No. of other signs of human presence	No. of chimpanzee nests	No. of other signs of chimpanzee presence
Zone 1	Permanent transects	16	20	5	41	3
Zone 2	Permanent transects	16	33	5	29	14
Buffer zone	Temporary transects	6.38	10	10	25	2

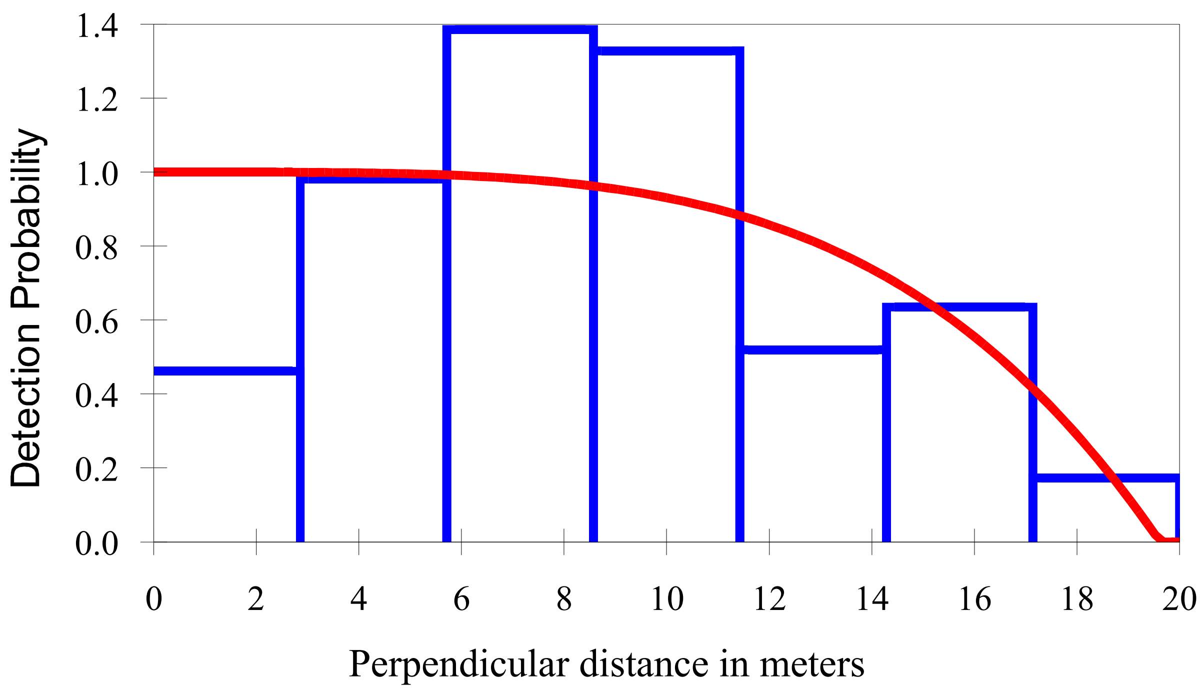

Figure S1. Detection function fitted to the frequency distribution of detected nests.