Biological Conservation 171 (2014) 107–113

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Short communication

Absence of evidence is not evidence of absence: Discovery of a large, continuous population of *Pan troglodytes schweinfurthii* in the Central Uele region of northern DRC

Thurston C. Hicks [a,b,*], Sandra Tranquilli [b,c], Hjalmar Kuehl [b], Geneviève Campbell [b], Jeroen Swinkels [a], Laura Darby [d], Christophe Boesch [b], John Hart [e], Steph B.J. Menken [a]

[a] *Institute for Biodiversity and Ecosystem Dynamics, The University of Amsterdam, Postbus 94248, 1090 GE Amsterdam, The Netherlands*
[b] *Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany*
[c] *Department of Biological Anthropology, University College London, United Kingdom*
[d] *UNEP/DEPI/GRASP c/o UNON, PO Box 20, Grand Central Station, New York, NY 10163-0020*
[e] *Lukuru Wildlife Research Foundation, 1235 Avenue Poids Lourds, Kinshasa, Democratic Republic of the Congo*

ARTICLE INFO

Article history:
Received 9 July 2013
Received in revised form 20 December 2013
Accepted 2 January 2014

Keywords:
Bili-Uéré Protected Area Complex (BUPAC)
Bushmeat
The Democratic Republic of the Congo (DRC)
Eastern chimpanzee (*Pan troglodytes schweinfurthii*)
Line transect surveys

ABSTRACT

With great ape populations in decline across much of their range, it is crucial to obtain a global picture of their distribution and abundance, in order to guide conservation activities and to provide baseline data against which to monitor their trends. Although great apes are popular, charismatic species, we still do not possess a complete understanding of their distribution and abundance, which hinders their long-term protection. We highlight this problem by providing information on the distribution and abundance of the Eastern chimpanzee (*Pan troglodytes schweinfurthii*) in the northern Democratic Republic of the Congo (DRC), a region which has until now received little attention. We conducted a standing crop nest survey in the Bili area in 2005 and exploratory reconnaissance walks (recces) across the Bas-Uele region between 2004 and 2009. At Bili, the nest encounter rate in the remote forest was 4.84 nests per km (CI = 2.78–8.55) and in the area closer to the road it was 1.92 nests per km (CI = 1.08–3.43). In 2012, we repeated a part of the original transect survey and found that the nest encounter rate had remained stable over that period. On our recce walks across the region, we encountered chimpanzee nests in all forests surveyed, and within 13 km of the largest population centers. Our results suggest that the Central Uele landscape and neighboring regions are home to one of the largest remaining continuous populations of Eastern chimpanzees, that extends across at least 50,000 km^2, likely representing thousands of individuals, but which is falling under increasing pressure from habitat destruction, mining and the bushmeat trade. This population has until now remained hidden from researchers and is not protected. Our results reflect gaps in our current understanding of ape distribution and abundance, and highlight the importance of obtaining more sound and complete data before assessing species status and making recommendations to guide conservation efforts.

1. Introduction

A major conservation crisis faces our closest evolutionary cousins the African great apes. Over the course of the last century, their populations have declined from millions to only a few hundreds of thousands (Butynski, 2001; Walsh et al., 2003). Populations of even the most widespread and abundant great ape species, the chimpanzee (*Pan troglodytes*) are undergoing drastic declines in many areas of their range (Hicks et al., 2010; Plumptre et al., 2010; Hughes et al., 2011; Junker et al., 2012); in some areas, encounter rates for chimpanzee nests have dropped by up to 90% over the past 20 years (Campbell et al., 2008). Across Africa, chimpanzee habitat is being destroyed by expanding shifting agriculture, logging and uncontrolled natural resource extraction (Campbell et al., 2008; Plumptre et al., 2010). Chimpanzees are also being killed for bushmeat (Hicks et al., 2010), and by diseases such as the Ebola virus (Walsh et al., 2003) and respiratory diseases transmitted by humans (Leendertz et al., 2006; Goldberg et al., 2007). An accurate assessment of chimpanzee population status has, however, been hampered by the absence of systematic and recent data on the species; for large areas of Africa there simply is no data, or what survey data exists is old and outdated (Oates, 2006).

* Corresponding author at: Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany. Tel.: +49 341 3550 232.

E-mail addresses: clevehicks@hotmail.com (T.C. Hicks), sandra.tranq@gmail.com (S. Tranquilli), kuehl@eva.mpg.de (H. Kuehl), genevieve_c@hotmail.com (G. Campbell), jlswinkels@yahoo.com (J. Swinkels), laura@primatologist.me (L. Darby), boesch@eva.mpg.de (C. Boesch), johnhartdrc@gmail.com (J. Hart), s.b.j.menken@uva.nl (S.B.J. Menken).

0006-3207/$ - see front matter © 2014 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2014.01.002

In order to monitor chimpanzee population trends and to decide where to best allocate scarce conservation resources, it is crucial that we develop the means to accurately map the species' distribution and make precise estimates of abundance (Kuehl et al., 2007). Nowhere is this more the case than in the Democratic Republic of the Congo (DRC), where large tracts of potential habitat for Eastern chimpanzees (*Pan troglodytes schweinfurthii*) have never been surveyed (Varty, 2005). As this country is probably home to about half of the world's remaining chimpanzees (Butynski, 2001), and because much of the chimpanzee habitat remains intact, achieving a better understanding of the distribution and density of the apes in this region should be a top priority. Given the current infiltration of the commercial bushmeat trade into formerly remote areas of DRC, accompanied by commercial logging and unregulated artisanal mining operations (Hicks et al., 2010), we must act quickly to identify priority populations and ensure their immediate and long-term protection.

Attempts to map chimpanzee distribution in DRC using extrapolations from historical and current presence localities (Butynski, 2001; Varty, 2005), or models of potential occurrence based on covariates associated with occupied range (Plumptre et al., 2010; Junker et al., 2012) have been hampered by a lack of data from relevant regions. Given the rapid human population growth in DRC (Alexandratos, 2005) and expansion of populations into previously un-occupied landscapes in the north, as well as the dynamic political and economic context, even high-quality survey results become rapidly out of date. In West Africa, recent surveys (Brncic et al., 2010; Tweh et al., in press) have revealed the presence of large, viable chimpanzee populations (*Pan troglodytes verus*) in regions formerly thought to be poorly-suited for the species. Likewise, Rainey et al. (2009) revealed that a substantial population of Western lowland gorillas (*Gorilla gorilla gorilla*) survived in northern Republic of Congo, which increased the likely number of individuals by thousands. Surveys can reveal the opposite – steep population declines – as well (Campbell et al., 2008).

In this paper we present data on chimpanzee occurrence in northern DRC between 2° and 5° north latitude and 23° and 26° east longitude, a region where chimpanzee populations have never previously been systematically assessed. Between 2004 and 2009, we surveyed chimpanzee occurrence and their population threats at 22 localities in DRC's Central Uele Basin (Figs. 1 and 2), in a range of habitats across the area, from primary forest to savanna woodland, and including disturbed forest and agricultural land that are in close proximity to major cities. In 2012, we returned to Bili and repeated segments of our 2005 transects to assess the stability of the chimpanzee population in this sub-region.

2. Methodology

2.1. The study region

Our surveys took place within DRC's Bas-Uele district and are geographically separated by the Uele River into northern and southern sectors. The area extends from the Central African Republic (CAR)–DRC border to the north and the Rubi-Tele Domaine de Chasse to the south; from Monga in the west to Bambesa in the east (Figs. 1 and 2). The minimum area that includes all survey locations totals 55,163 km^2, but the majority of our surveys was carried out within a core area of 32,912 km^2. The northern sector of the survey area included portions of the Bili-Uéré Protected Area Complex (BUPAC). The primary eco-type north of the Uele River was forest-savanna mosaic, and to the south primary moist tropical forest [Fig. 2; see Supplementary Materials 1 and Hicks (2010) for more details].

2.2. Surveys

2.2.1. Exploratory reconnaissance walks (recces)

We conducted exploratory reconnaissance walks (recces) looking for chimpanzees and their artifacts along hunting, fishing and elephant trails or, in the Camp Louis and Gangu areas, along paths we had opened. Upon hearing chimpanzee vocalizations, we would leave these trails and move in the direction of the apes. We took GPS points as frequently as possible along our routes, and whenever we encountered evidence of human or wildlife presence. We walked a total of 2276.7 km of recces: 1781.3 km to the north of the Uele River and 495.4 km to its south (Table S1). Because the methodology of our recces differed from that used in other studies (Supplementary Materials 2) and because we were biased in actively looking for chimpanzees as opposed to following 'the path of least resistance', these results should be treated with caution when being compared to other surveys.

2.2.2. Line transect sampling: baseline data

Between March and July 2005, the first author (TH) conducted line transect surveys (Buckland et al., 2001) of chimpanzee nests in the forest and savanna ecotone northwest of the town of Bili (4°09′09″N, 25°10′16″E, Fig. 3). This period corresponded with the end of the dry season and the beginning of the rainy season. We conducted three parallel line transects of approximately 55 km each and separated by 4 km (Fig. 3). The total distance walked summed to 160 km, comprised of 99 km in the Camp Louis region and 61 km in the remote Gangu Forest. To assure the independence of sampling units, we ran two separate analyses, one using every other segment of the 160 km of transects (i.e. skipping one km segment in between) (dataset A) and one using all other skipped segments (dataset B) (80 km for each analysis) (see Supplementary Materials 3 for details of the analysis).

2.2.3. Trend estimate 2005–2012

In order to assess the stability of the Bili-Gangu chimpanzee population over time, we revisited Bili in 2012 during the rainy season (logistical constraints prevented us from returning during the same period as in 2005; see Discussion). Between 22 August and 18 September we repeated 26 km of our northernmost 2005 transect, resurveying every other 2 km segment (10.5 km in the Gangu Forest and 15.5 km in the Camp Louis region) (see Supplementary Materials 4 for methodological details and caveats).

For this analysis, we considered only nest encounter rate, due to the smaller sample size that prevented us from estimating trend in population size. In order to statistically compare tree nest encounter rates between our 2005 and 2012 transect surveys, we ran a generalized linear model in R (version 2.15.0; R Development Core Team, 2012), with year as the factor and an auto-correlation term incorporated to control for non-independence of transect lines (Fürtbauer et al., 2011). The response variable was the total number of tree nests encountered on the transects, including those found when, after we spotted a nest group, we fanned out and controlled alongside the transects.

3. Results

3.1. Chimpanzee distribution across the northern DRC Uele region

3.1.1. Chimpanzee presence at northern DRC Uele sites

Fig. 1 shows localities where chimpanzee presence has been confirmed by our study and also by other observers over the past 10 years. On our recce walks, we found chimpanzee nests in all of the forest sites we surveyed across the region (Fig. 2; Hicks

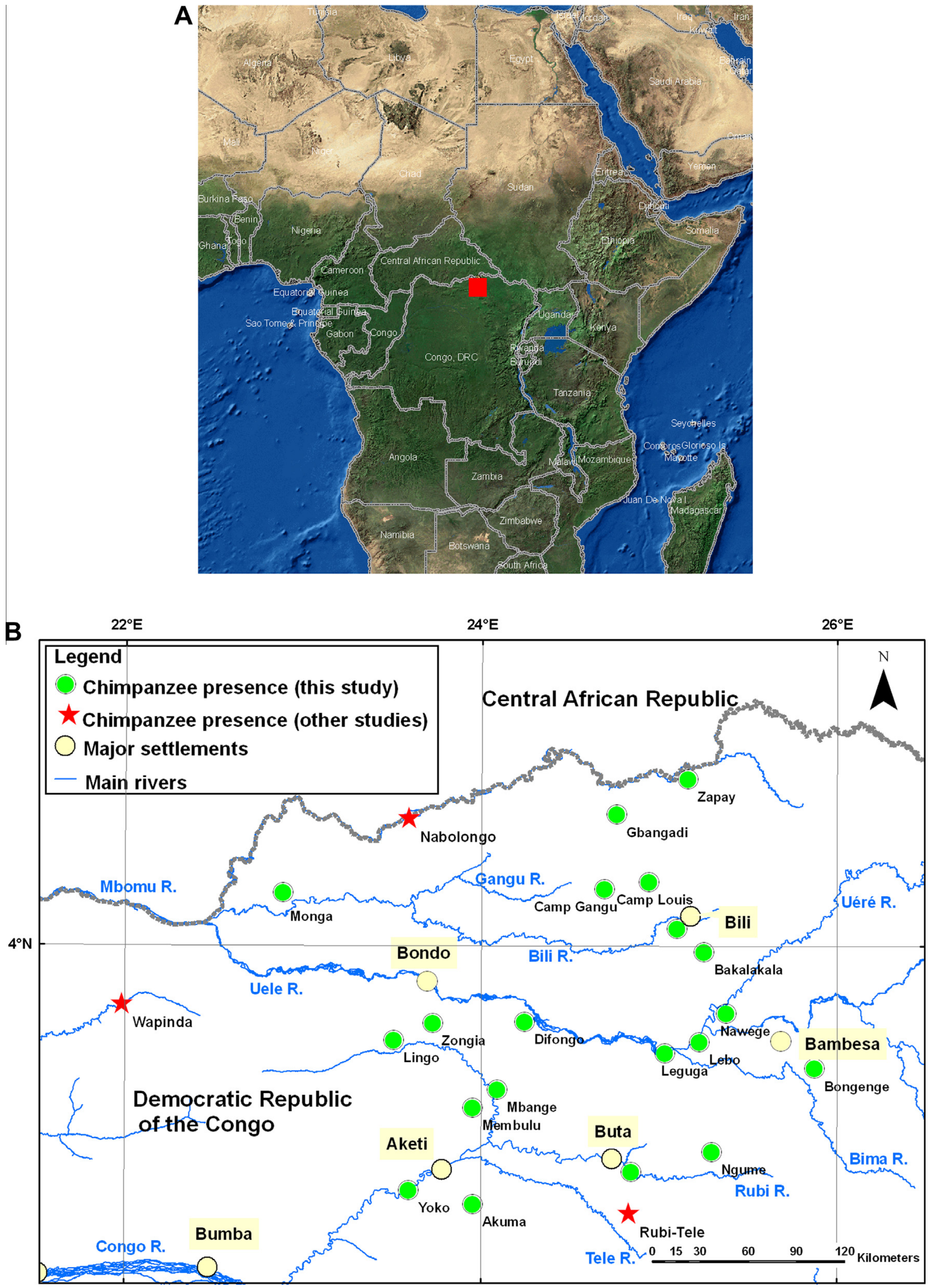

Fig. 1. (A) Northern DRC Central Uele study area inset into a map of Africa. (B) Map showing areas in northern DRC where chimpanzee presence has been confirmed (by sleeping nests or contacts with the apes themselves) within the past 10 years, indicated by green circles. Red stars indicate studies other than the current one: Wapinda: J. Erikkson, pers. comm., cited in Hicks (2010); Nabolongo: D. Greer, pers. comm., cited in Hicks (2010); Rubi-Tele: Hart (2007). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2010). We found chimpanzee nests within 4 km of Bili, within 13 km of Bambesa and Buta and within 20 km of Aketi (see Table S2 for the population sizes of these settlements).

3.1.2. Chimpanzee nest encounter rates on recces

We present recce nest encounter rates in Table S1. Recces conducted in the South Uele forests following the same methodology

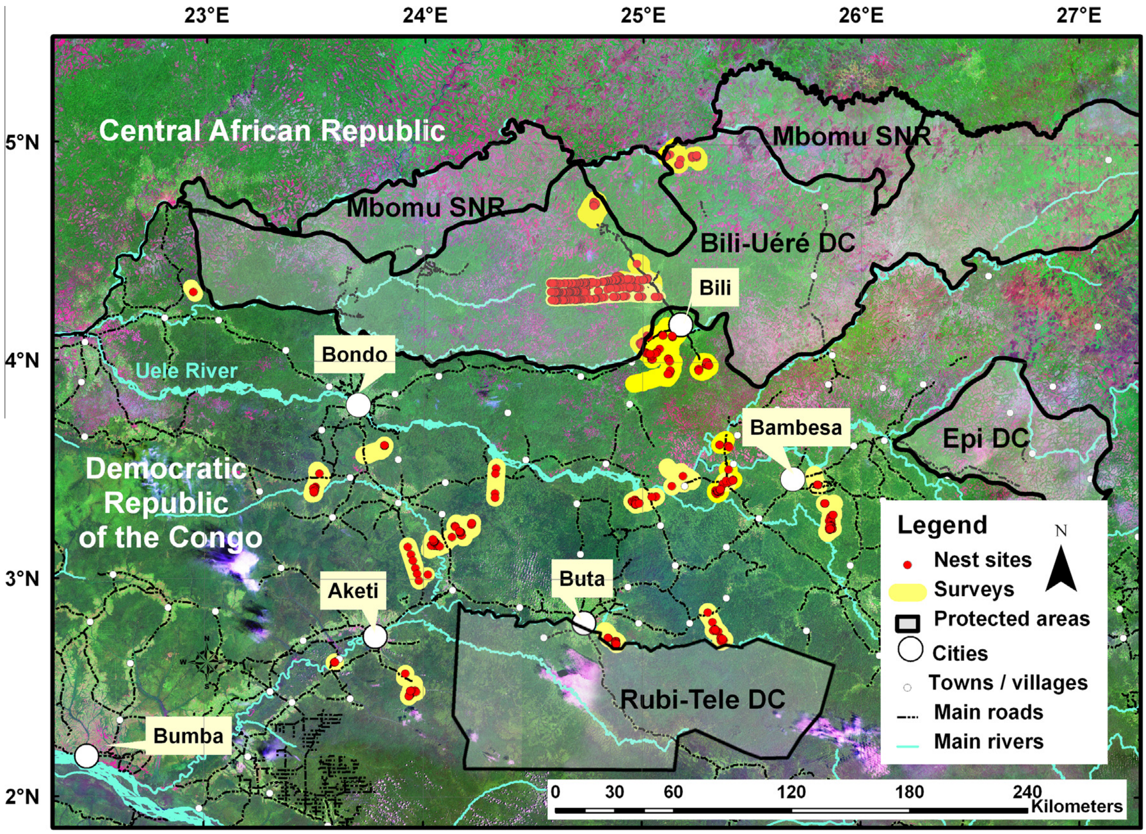

Fig. 2. Map showing all nest sites recorded in the context of our recce and transect routes, along with protected areas, human settlements, major roads, rivers and habitat-types. Dark green = forests, purple = savannas, light green = human-disturbed regions (including plantations, roads, villages and towns). Data for the boundaries of Rubi-Tele are from Hart (2007). (The Landsat ETM + image files date are from 2000 and were downloaded from GLCF (Global Land Cover Facility, http://glcf.umiacs.umd.edu.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

as to the north resulted in tree nest encounter rates 3.4 times higher than to the north, a non-significant difference (South: 1.65 nests/km; North: 0.48 nests/km; Mann–Whitney U test, 2 tails: $W = 39$, $p = 0.49$; North Uele $n = 7$ sites, South Uele $n = 14$ sites). South Uele encounter rates were 5.7 times higher than those in the Camp Louis forest and 3.1 times higher than at Gangu. This suggests that chimpanzees are probably at least as abundant in the South Uele forests as they are in the forest-savanna mosaic to the north. In Table S3 we present our results together with recce encounter rates from other sites in DRC, but due to the different recce methodologies used, comparisons should be treated with caution.

3.2. Chimpanzee density estimation at Bili-Gangu from line-transect survey

3.2.1. Baseline population estimation

Nest density of both datasets (A and B) gave similar results (Table 1; detection curves shown in Fig. S1), and are here presented as an average. The overall nest encounter rate was 3.03 nests per km (CI = 2.01–4.58). The encounter rate in the remote Gangu Forest was 4.84 nests per km (CI = 2.78–8.55) and in the Camp Louis area closer to the road it was 1.92 nests per km (CI = 1.08–3.43). In order to allow us to estimate a range of densities and numbers of weaned chimpanzees, we selected from the literature the lowest available nest decay rates (Budongo: Plumptre and Reynolds, 1996) and the highest [Kibale: Skorupa, J.P. (unpublished) in Plumptre and Reynolds (1996)], and used the nest production rate of 1.1 nests per day from Budongo, Uganda (Plumptre and Reynold, 1997). For Gangu this would give us a density of 1.01–2.95 per km^2 (between 190 and 556 weaned individuals), for Camp Louis, 0.46–1.43 per km^2 (131–408 individuals), and overall 0.66–2.08 per km^2 (313–984 individuals).

3.2.2. Trend estimation

On our transect resurveys, we found no significant difference between tree nest encounter rates in 2005 and 2012 (GLM: $N = 13$ transects; $z = 0.85$, $p = 0.40$; Fig. S2; Tables S4 and S5). As only 26 km were re-walked in 2012, the sample size gathered was not large enough to estimate the size of the chimpanzee population at that time.

3.2.3. Comparisons with transect surveys of other East African sites

We compared the results of our transect data with those recorded for the other available transect surveys of *Pan troglodytes schweinfurthii* across their range. The nest encounter rate and the estimated density of weaned chimpanzees for Bili-Gangu were comparable to the averages for other East African populations (Fig. S3, Table S6).

4. Discussion

The results of our study suggest that a large and widespread population of chimpanzees inhabits the forests and savannas of northern DRC. This population has remained unnoticed to researchers until now and may represent the largest continuous viable population of this subspecies, but it currently lacks any protection. Chimpanzee densities determined from our transect work

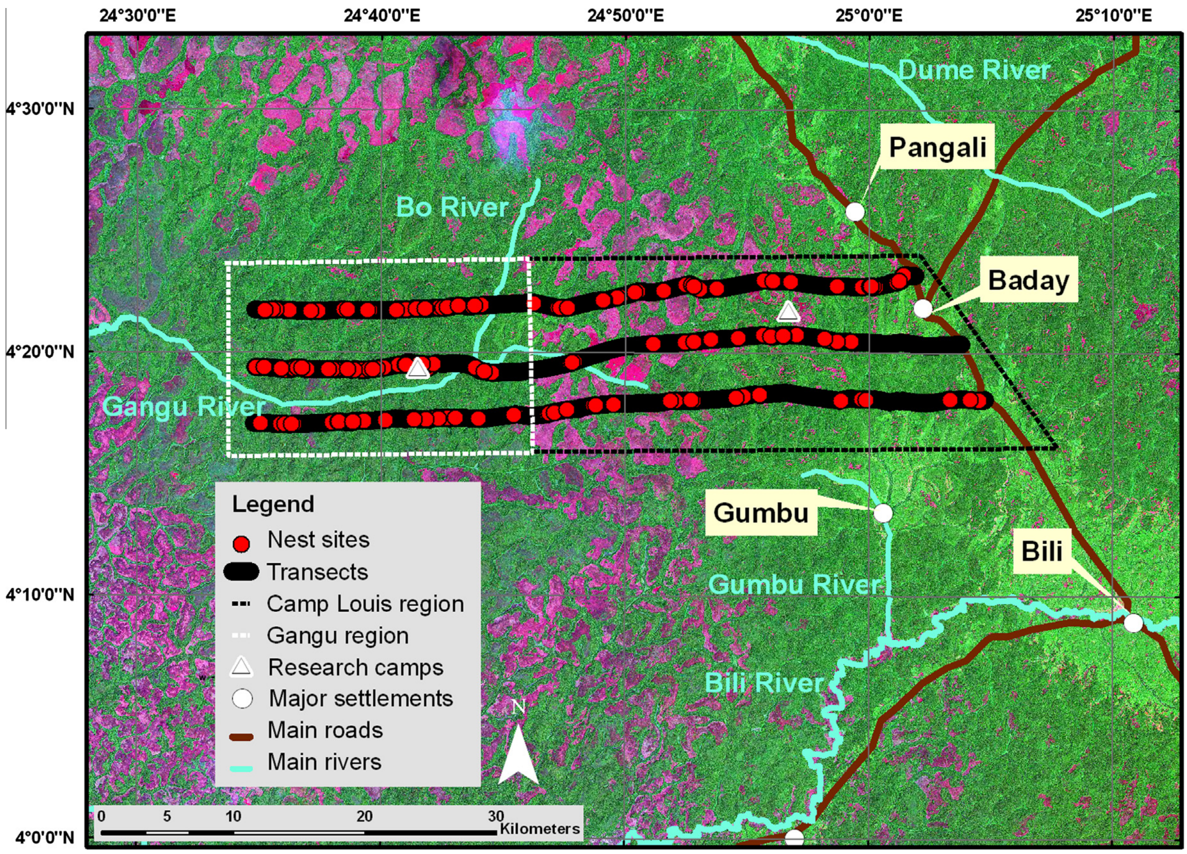

Fig. 3. Map showing the routes of the three transects through the Camp Louis and Gangu regions in relation to roads and settlements, along with nest sites. Dark green = forests, purple = savannas, light green = human-disturbed regions (including plantations, roads, villages and towns). The northernmost transect was the one we re-surveyed in 2012. (The Landsat ETM + image files date are from 2000 and were downloaded from GLCF (Global Land Cover Facility, http://glcf.umiacs.umd.edu). Data for rivers, roads, borders and other geographical features were acquired from Le Référential Géographique Commun (2009) at http://www.rgc.cd.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at Bili-Gangu compared favorably to those at other East African sites. Chimpanzee nests were found in close proximity to even the largest human settlements throughout the survey region. Because we omitted ground nests from the transect analysis, which made up 9.4% of nests in the Camp Louis/Gangu region and accounted for up to 28% of nests in some forest regions (Hicks, 2010), our estimates of chimpanzee densities are conservative.

It is important to point out that when comparing the nest encounter rates on our recce walks to the north and south of the Uele River, which were conducted using the same methodology, those in the more continuously-forested South Uele region were much higher than those to the north, although the difference was not statistically significant. Differences in methodologies between studies prevent a direct comparison of the nest encounter rates on our recces to those in other regions in DRC.

Encouragingly, our 2012 re-walk of 26 km of the previous transects from 2005 showed no decline in nest encounter rate, making it unlikely that there has been any decline in the chimpanzee population over that period. Our conclusions, however, are limited to our core study area, and this may be unrepresentative of the region due to Bili's relative isolation.

Considering that chimpanzees were found in all of the forests we surveyed, even in close proximity to major human population centers, it is likely that the apes form a continuous population extending across the forests of northern DRC to the border with CAR, contradicting the distribution maps of Butynski (2001) and Varty (2005). Given that the recce nest encounter rates in non-transect-surveyed forests were on average much higher than on the recce surveys of Gangu and Camp Louis, we have reason to think that chimpanzee densities there should be at least comparable to and not lower than those in the latter regions. If we make the reasonable assumption that chimpanzee density across the 55,000 km^2 area lies somewhere in the range between the densities of Camp Louis and Gangu (conservatively between 0.41 and 1.1 individuals/km^2 respectively), then the region would be home to thousands of chimpanzees and should be considered a priority site for conservation of the eastern subspecies. Evidence of behavioral continuity both to the north and south of the Uele River and in eastern DRC may be another indication that these chimpanzee populations are interconnected across a large area (Hicks, 2010).

We used data from our surveys and from other sources [Nabolongo Island: D. Greer, pers. comm., 2009; Wapinda: J. Eriksson, pers. comm., 2009; Rubi-Tele: Hart (2007); for further details see Hicks (2010)] to highlight the areas in northern DRC where chimpanzee presence has been confirmed in the past 10 years (Fig. 1). Evidence for a more widespread chimpanzee presence across northern DRC is presented in Supplementary Materials 5.

Considering that in the past this area was shown on distribution maps as probably not harboring chimpanzees, our results underline the danger of making assumptions about the distribution of species based on a lack of evidence. Interestingly, these results also contradict the predictions made by the distribution model used in Junker et al. (2012) which was estimated using our dataset along with those from a number of other sites. The question remains as to why the model classified the Bili-Uéré region as poorly-suited for great apes. Bias may have been introduced into the model by the fact that (1) Junker et al. used presence-only datasets, (2) the majority of presence localities were recorded in forested habitats,

Table 1
Relative abundance and population size estimates of chimpanzees based on arboreal sleeping nests observed during line transect surveys (datasets A and B) through the Bili-Gangu forests, 2005. (1) Truncation at 25 m, ESW (effective strip width) = 17.47 m, CV (coefficient of variation) = 0.18; (2) truncation at 30 m, ESW = 15.18, CV = 0.28; (3) truncation at 35 m, ESW = 17.83, CV = 0.23; (4) truncation at 30 m, ESW = 17.36, CV = 0.25; (5) truncation at 30 m, ESW = 16.95, CV = 0.33; (6) truncation at 35 m, ESW = 19.62, CV = 0.35.

Region	Area (km^2)	Survey effort (km)	No. nest groups [( ) incl. groups with only ground nests)]	Avg. no. tree nests per site [( ) incl. ground nests)	No. tree nests	No. ground nests	Raw encounter rate (tree nests/km)	Tree nest encounter rate/km walked, with truncation – (CI)	Tree nest density (nests/km^2) – (CI)	Estimated density of weaned individuals/km^2 – ((lower)[c]	Estimated density of weaned individuals/km^2 – (upper)[c]	No. weaned individuals – (lower)[c]	No. weaned individuals – (upper)[c]
Data set A													
Overall[1]	473.1	80	116 (126)	2.20 (2.27)	255	31	3.19	3.13[a] (2.21–4.43)	89.63[a] (62.47–128.59)	0.68	2.14	322	1012
Camp Louis[2]	284.7	49.5	56 (62)	1.80 (1.95)	101	20	2.04	1.95[a] (1.15–3.31)	64.12[a] (36.91–111.38)	0.49	1.52	140	433
Gangu[3]	188.4	30.5	60 (64)	2.57 (2.58)	154	11	5.05	4.90[b] (3.14–7.66)	137.51[b] (86.65–218.20)	1.1	3.0	207	565
Data set B													
Overall[4]	473.1	80	105 (115)	2.51 (2.65)	264	41	3.30	2.93[a] (1.82–4.73)	84.48[a] (51.79–137.82)	0.64	2.02	303	956
Camp Louis[5]	284.7	49.5	51 (55)	2.29 (2.35)	117	12	2.36	1.90[a] (1.01–3.55)	55.95[a] (29.22–107.13)	0.43	1.34	122	382
Gangu[6]	188.4	30.5	54 (60)	2.72 (2.93)	147	29	4.82	4.77[b] (2.41–9.43)	121.47[b] (60.34–244.51)	0.92	2.90	173	546

[a] (Key function plus series expansion): Half-normal + Cosine.
[b] (Key function plus series expansion): Half-normal + Simple polynomial.
[c] We used the formula Nest density/proportion of nest builders in population × nest decay rate × nest production rate. We used the proportion of nest builders of 0.83 from Kuehl et al. (2008) and the nest production rate of 1.09 per day used by Plumptre and Reynolds (1997). We used the extreme shortest and longest nest decay rates in the literature: Budongo, Uganda at 45.9 days (Plumptre and Reynolds, 1996) and Kibale, Uganda at 144 days [Skorupa, J. P. (unpublished) in Plumptre and Reynolds (1996)].

therefore biasing suitability predictions towards these and away from savannas, and (3) the coarse spatial resolution of 25 km^2, neglecting fine-scale dynamics (Junker et al., 2012).

Reliance on patchy, incomplete and sometimes randomly-acquired datasets risks conservation priority being assigned to areas of low potential value, whereas areas of high potential value may be ignored for decades. Likewise, modeling, though an important tool in understanding ape distribution, cannot replace field surveys. In the recent past, important field surveys have 'changed the game' in our understanding of great ape distribution and numbers (Western lowland gorillas: Rainey et al., 2009; Western chimpanzees: Brncic et al., 2010; Tweh et al., in press; Campbell et al., 2008). It is our hope that the current study will do the same for Eastern chimpanzees, and at the same time encourage funding for more 'terra incognita' survey projects in the near future (i.e. northern DRC to the west of Bili and the massive forested zone between Bili and Ituri Forest).

5. Outlook

The existence of a large and likely interconnected population of chimpanzees distributed across such a vast area in northern DRC is certainly good news. In particular, the 'naïve' behavior shown towards observers by chimpanzees living in the remote Gangu Forest indicates that these apes have suffered little or no human hunting pressure in the recent past (Hicks et al., 2012). Our 2012 transect re-survey provides strong evidence that, at least in the Gangu Forest – Camp Louis core area, this chimpanzee population has remained stable over the past decade. This knowledge should not, however, make us complacent, considering the rapid expansion of the commercial bushmeat trade throughout the region (Hicks et al., 2010). During our 1.5-year study to the south of the Uele River we encountered 42 chimpanzee orphans and 34 carcasses along roads and in settlements, compared to only two orphans and one carcass encountered over a similar period of time to the north of the Uele. The absence of enforcement of conservation laws, the spread of artisanal mining, the influx into the region of large numbers of immigrants, and the lack of alternative livelihoods to hunting since the collapse of the region's infrastructure are placing heavy pressure on the chimpanzees south of the Uele. Although our results indicate that the chimpanzee population of Bili has remained stable over the past decade, increasing numbers of bushmeat carcasses and orphans seen in Bili and nearby areas (Table S7) may be a worrying sign that things are beginning to change. Without proper management and protection, the chimpanzees of BUPAC may succumb to the same factors that are eliminating populations of the species elsewhere (Hart, 2007; Hicks et al., 2010; Tranquilli et al., 2012) (see Supplementary Materials 6 for details of our conservation and research efforts in the region between 2012 and 2013).

See Supplementary Materials 7 for Glossary of Terms.

Acknowledgements

We thank the Ministère de l'Environnement of DRC for granting us permission to work in the country, and traditional Zande chiefs Etienne Zelesi Yakisi Fils and Jean-Remy Ndolomo for welcoming us at Bili. Adam Singh assisted with the South Uele surveys. David Greer and Jonas Eriksson kindly shared information on their surveys of forests in northern DRC and southern CAR. Vincent Nijmen, Andy Plumptre, Terese Hart, Rene Beyers, Jessi Junker and Andrew Fowler provided invaluable comments on the manuscript. Judy Song helped prepare Fig. S3. Roger Mundry provided advice on the statistics. We thank the following supporters of our project: The US Fish and Wildlife Service, The Wasmoeth Wildlife Foundation, Lucie Burgers Foundation for Comparative Behaviour Research in Arnhem, The Netherlands, The International Primate Protection League, Le Centre de Rehabilitation des Primates de Lwiro, L'Institut Congolais pour la Conservation de la Nature, The African Wildlife Foundation, Karl Ammann, Jo Myers Thompson, Jan Sevink and Jan van Hooff. We also thank our field assistants:

in particular Team Leaders Ligada Faustin, Mbolibie Cyprian, and Kisangola Polycarpe, as well as Olivier Esokeli, Seba Koya, Dido Makeima, Makassi Constant, Likambo, Likongo, Garavura and Kongonyesi. Some earlier analyses based on this data were originally presented as Chapter 4 of Hicks (2010), and were briefly summarized in Hicks et al. (2010).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.01.002.

References

Alexandratos, N., 2005. Countries with rapid population growth and resource constraints: issues of food, agriculture, and development. Popul. Dev. Rev. 31 (2), 237–258.

Brncic, T.M., Amarasekaran, B., McKenna, A., 2010. Final Report of the Sierra Leone National Chimpanzee Census Project. Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone, p. 118.

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

Butynski, T.M., 2001. Africa's great apes. In: Beck, B.B., Stoinski, T.S., Hutchins, M., Maple, T.L., Norton, B., Rowan, A., Stevens, E., Arluke, A. (Eds.), Great Apes and Humans: The Ethics of Coexistence. Smithsonian Institution Press, Washington, DC, pp. 3–56.

Campbell, G., Kuehl, H., Kouamé, P., Boesch, C., 2008. Alarming decline of West African Chimpanzees in Côte d'Ivoire. Curr. Biol. 18, R903–904.

Fürtbauer, I., Mundry, R., Heistermann, M., Schülke, O., Ostner, J., 2011. You mate, I mate: macaque females synchronize sex not cycles. PLoS ONE 6, e26144.

Goldberg, T.L., Gillespie, T.R., Rwegood, I.B., Wheeler, E., Estoff, E.L., Chapman, C.A., 2007. Patterns of gastrointestinal bacterial exchange between chimpanzees and humans involved in research and tourism in western Uganda. Biol. Conserv. 135, 511–517.

Hart, T., 2007. Evaluation de l'Etat de Conservation Domaine de Chasse de Rubi-Télé: Inventaires fauniques, contexte historique et recommandations pour assurer la conservation du site en rapport avec la réhabilitation de la Route National 4. Un rapport soumis à l' AGRECO dans le cadre de la mise en oeuvre de l'Etude d'Impact Environnemental et Social dans la Zone du Projet PROROUTES.

Hicks, T.C., 2010. A Chimpanzee Mega-Culture? Exploring Behavioral Continuity in *Pan troglodytes schweinfurthii* across Northern DR Congo. Ph.D. Thesis. University of Amsterdam, 300 pp.

Hicks, T.C., Darby, L., Hart, J., Swinkels, J., January, N., Menken, S.B.J., 2010. Trade in orphans and bushmeat threatens one of the Democratic Republic of the Congo's most important populations of Eastern Chimpanzees (*Pan troglodytes schweinfurthii*). Afr. Primates 7, 1–18.

Hicks, T.C., Roessing, P., Menken, S.B.J., 2012. Reactions of Bili-Uele chimpanzees to humans in relation to their distance from roads and villages. Am. J. Primatol. Folia Primatol. 84 (3), 135–156.

Hughes, N., Rosen, N., Gretsky, N., Sommer, V., 2011. Will the Nigeria-Cameroon chimpanzee go extinct? Models derived from intake rates of ape sanctuaries. In: Sommer, Volker, Ross, Caroline (Eds.), Primates of Gashaka: Socioecology and Conservation in Nigeria's Biodiversity Hotspot. Springer, New York, pp. 493–523.

Junker, J., Bergl, R., Blake, S., Blanc, J., Boesch, C., Campbell, G., Dunn, A., Du Toit, L., Duvall, C., Ekobo, A., Etoga, G., Galat-Luong, A., Gamys, J., Ganas-Swaray, J., Gatti, S., Ghiurghi, A., Granier, N., Greengrass, E., Hart, J., Head, J., Herbinger, I., Hicks, T.C., Huijbregts, B., Imong, I.S., Kuempel, N., Lahm, S., Lindsell, J., Maisel, F., McLennan, M., Martinez, L., Morgan, B., Morgan, D., Mulindahab, F., Mundry, R., N' Goran, K.P., Normand, E., Ntongho, A., Okon, D.T., Petre, C.-A., Plumptre, A., Rainey, H., Regnaut, S., Sanz, C., Stokes, E., Tondossama, A., Tranquilli, S., Sunderland-Groves, J., Walsh, P., Warren, Y., Williamson, E.A., Kuehl, H.S., 2012. Recent decline in suitable environmental conditions for African great apes. Divers. Distrib. 18, 1077–1091.

Kuehl, H., Williamson, L., Sanz, C., Morgan, D., Boesch, C., 2007. Launch of the A.P.E.S. database. Gorilla J. 34, 20–21.

Kuehl, H., Maisels, F., Ancrenaz, M., Williamson, E.A., 2008. Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations. IUCN SSC Primate Specialist Group, Gland.

Leendertz, F.H., Pauli, G., Maetz-Rensing, K., Boardman, W., Nunn, C.L., Ellerbrok, H., Jensen, S.A., Junglen, S., Boesch, C., 2006. Pathogens as drivers of population declines: the importance of systematic monitoring in great apes and other threatened mammals. Biol. Conserv. 131, 325–337.

Oates, J., 2006. Is the chimpanzee, *Pan troglodytes*, an endangered species? It depends on what "endangered" means. Primates 47, 102–112.

Plumptre, A.J., Reynold, V., 1997. Nesting behavior of chimpanzees: implications for censuses. Int. J. Primatol. 18 (4), 475–485.

Plumptre, A.J., Reynolds, V., 1996. Censusing chimpanzees in the Budongo Forest, Uganda. Int. J. Primatol. 17 (1), 85–99.

Plumptre, A., Rose, R., Nagnendo, G., Williamson, E., Didier, K., Hart, J., Mulindahabi, F., Hicks, C., Griffin, B., Ogawa, H., Nixon, S., Pintea, L., Vosper, A., McLennan, M., Amsini, F., McNeilage, A., Makana, J.R., Kanamori, M., Hernandez, A., Piel, A., Stewart, F., Moore, J., Zamma, K., Nakamura, M., Kamenya, S., Idani, G., Saka, T., Yoshikawa, M., Greer, D., Tranquilli, S., Beyers, R., Bennett, E., 2010. Status Survey and Conservation Action Plan for the Eastern Chimpanzee (*Pan troglodytes schweinfurthii*), 2010–2020. IUCN, Gland, Switzerland, 48 pp.

R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. <http://www.R-project.org/>:.

Rainey, H.J., Iyenguet, F.C., Malanda, G.-A.F., Madzoc, B., Santos, D.D., Stokes, E.J., Maisels, F., Strindberg, S., 2009. Survey of raphia swamp forest, Republic of Congo, indicates high densities of critically endangered western lowland gorillas *Gorilla gorilla gorilla*. Oryx 44, 124–132.

Tranquilli, S., Abedi-Lartey, M., Amsini, F., Arranz, L., Asamoah, A., Babafemi, O., Barakabuye, N., Campbell, G., Chancellor, R., Davenport, T.R., Dunn, A., Dupain, J., Ellis, C., Etoga, G., Furuichi, T., Gatti, S., Ghiurghi, A., Greengrass, E., Hashimoto, C., Hart, J., Herbinger, I., Hicks, T.C., Holbech, L.H., Huijbregts, B., Imong, I., Kumpel, N., Maisels, F., Marshall, P., Nixon, S., Normand, E., Nziguyimpa, L., Nzooh-Dogmo, Z., Tiku Okon, D., Plumptre, A., Rundus, A., Sunderland-Groves, J., Todd, A., Warren, Y., Mundry, R., Boesch, C., Kuehl, H., 2012. Lack of conservation effort rapidly increases African great ape extinction risk. Conserv. Lett. 5, 48–55. http://dx.doi.org/10.1111/j.1755-263X.2011.00211.

Tweh, C., Menladi, L., Kouakou, C., Hillers, A., Kuehl, H., Junker, J., in press. Conservation status of chimpanzees (*Pan troglodytes verus*) and other large mammals across Liberia: results from a nationwide survey, Oryx.

Varty, N., 2005. Democratic Republic of the Congo. In: Caldecott, J., Miles, L. (Eds.), World Atlas of Great Apes and Their Conservation. UNEP World Conservation Monitoring Center, p. 334.

Walsh, P., Abernathy, K., Bermejo, M., Beyers, R., De Wachter, P., Akou, M., Huijbregts, B., Mambounga, D., Toham, A., Kilbourn, A., Lahm, S., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Obaing, S., Effa, E., Starkey, M., Telfer, P., Thibault, M., Tutin, C., White, L., Wilkie, D., 2003. Catastrophic ape decline in western equatorial Africa. Nature 422, 611–614.