Title: Population status of chimpanzees outside of National Parks in the Masito-Ugalla Ecosystem, western Tanzania

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ABSTRACT

More than 75 percent of Tanzania's remaining chimpanzees live at low densities on land outside National Parks. Chimpanzees are one of the key conservation targets in the region and long-term monitoring of these populations is essential for assessing the overall status of ecosystem health and the success of implemented conservation strategies. We aimed to assess change in chimpanzee density within the Masito-Ugalla Ecosystem (MUE) by comparing results of re-walking the same line transects in 2007 and 2014. We further used remote sensing data derived from Landsat satellites to assess landscape change within a 5km buffer of these transects in that same period. Our results indicate that there has not been a significant decline in chimpanzees across the surveyed areas of MUE between 2007 and 2014. Comparisons between 2007 and 2014 results suggest that the MUE chimpanzee population has been stable over this period, and represents approximately 576 individuals. Although the overall mean density of chimpanzees may have declined from 0.09 individuals/km^2 in 2007 to 0.05 individuals/km^2 in 2014, whether this change is significant cannot be detected due to small sample sizes and large error margins. Some areas (Issa Valley, Mkanga, Kamkulu), in fact, showed an increase in chimpanzee density. Seasonality of chimpanzee habitat preference for ranging or nesting may explain variation in density at some of the survey sites between 2007 and 2014. We found a relationship between increasing habitat loss derived from Landsat satellite imagery and decreasing chimpanzee density. Future surveys will need to ensure a larger sample size, broader geographic effort, and random survey design, in order to more precisely determine trends in MUE chimpanzee density and population size over time.

KEY WORDS: Chimpanzee; Density; Survey; Remote sensing, Masito-Ugalla; Tanzania

INTRODUCTION

Chimpanzees (*Pan troglodytes*) have been classified as an endangered species since 1996 (IUCN) and are threatened across their distribution [but see Oates, 2006]. Over the last four decades, researchers and conservationists alike have described the impact of habitat destruction [Lehmann et al., 2010; Junker et al., 2012; Young et al., 2013], human introduced [Leendertz et al., 1993; Köndgen et al., 2008; Ryan & Walsh, 2011] and natural [Keele et al., 2009; Kaiser et al., 2010; Rudicell et al., 2010] disease, and poaching [Sugiyama & Soumah, 1988; Reynolds, 1992; Ohashi & Matsuzawa, 2011; McLennan et al., 2012] on wild chimpanzee populations.

Tanzania, home to the two longest, continuous studies of chimpanzees [Gombe Stream - Pusey et al., 2007; Mahale Mountains - Nishida, 2011], hosts between two and three thousand chimpanzees, all within three regions in the western part of the country [Plumptre et al., 2010]. Almost one third of these chimpanzees live within the boundaries of the two aforementioned national parks. However, the rest are distributed across approximately 30,000km^2 of land outside of National Parks, comprised mostly (>80%) of miombo woodland [Moyer et al., 2006]. These extra-park savanna-woodland chimpanzees naturally occur at extremely low densities and thus offer a significant challenge to those trying to monitor changes in population size and distribution over time [Moyer et al., 2006; Piel et al., 2015].

Monitoring of these apes is critical given the nature of the threats facing much of Tanzania's wildlife. Specifically, numerous recent reports show that whilst the primary threat to chimpanzees is habitat loss due to human settlement expansion and conversion to agriculture, annual burning, logging and poaching are also playing a role [JGI, 2007; Davenport et al., 2010; Plumptre et al., 2010; Piel & Stewart, 2013, 2014; Piel et al., 2013] and conservationists have focused on establishing priority areas based on remaining chimpanzee habitat. In western Tanzania, human incursion into the Masito area is mostly for conversion of chimpanzee habitat into oil palm plantations, but also for slash and burn agriculture [Pintea et al., 2002, 2012]. Given the known impact of oil palm habitat conversion, from the loss in biodiversity to increases in habitat fragmentation and pollution [Fitzherbert et al., 2008] and specifically the impact on apes [Swarna Nantha & Tisdell, 2008], we predicted a similar relationship between habitat loss and Masito chimpanzee population density.

Results from monitoring studies inform on change over time and, when combined with other data (e.g. forest cover changes derived from multi-temporal satellite imagery), conservationists can better understand how human threats in Tanzania affects wildlife abundance, distribution, and behavior [Newmark et al., 1994; Banda et al., 2006; Pintea, 2007]. Subsequent conservation strategies and actions can then be adapted to directly address these threats [Mulder et al., 2007]. Accordingly, we recently conducted a survey of five different previously surveyed areas across the Masito-Ugalla Ecosystem in western Tanzania. Our primary goal was to compare results from a similar survey conducted in 2007 [JGI, 2007]. We predicted that overall chimpanzee population density would have declined over the seven years between surveys in response to increased human pressure. We also predicted that the largest declines in density would be found nearest to the largest human settlements (here, in the Masito region), whereas Ugalla areas would show stable densities.

METHODS

Survey areas

The original survey in 2007 was designed and conducted by JGI in collaboration with the Tanzanian Institute for Resource Assessment (IRA), Tanzania Wildlife Research Institute (TAWIRI), District Wildlife and Forest Officers from Mpanda and Kigoma districts [see JGI, 2007 for further details]. Six survey sites were selected non-randomly based on known chimpanzee presence. Where possible four radial transects of 5km length following cardinal directions from the central campsite were conducted at each site. Such non-randomly selected transects are not ideal for estimating overall population size across MUE, however, these data do allow for comparison over time.

In order to control for regional variation in chimpanzee density we repeated identical surveys of five of the six 2007 sites in 2014 (two in Ugalla and three in Masito). Data from the sixth survey site are not presented here given that there is no longitudinal comparison. We followed 2007 track logs and waypoints taken along transects (Figure 1). Both surveys were conducted during the wet season (October to April), with 2007 surveys conducted during the early rains (October and November), and 2014 surveys during the late rains (January and February).

FIGURE 1 ABOUT HERE

Data collection and nest encounters

To determine chimpanzee density from nest counts, we used standard line transect methods to first estimate densities of chimpanzee nests and then convert these to densities of individuals [Plumptre & Reynolds, 1996]. This method relies on the fact that chimpanzees, like all great apes, construct nightly nests. We decided to use nest counts instead of direct encounters with chimpanzees given the low density of chimpanzees across MUE and overall paucity of actual encounters.

On each transect, in 2007 all data were recorded in hard copy and in 2014 we recorded all data using Google Android Nexus 7 tablets with pre-designed data forms using Open Data Kit (ODK) software. We recorded all direct (sightings) and indirect (print, nest, feces) evidence of large mammals, specifically chimpanzees, noting GPS coordinate, vegetation (miombo woodland, closed forest, open forest, swamp, or grassland), number (of animals for direct encounters only), age classification (of nest or feces traces) and perpendicular distance to the transect. We categorized nest state of decay as ages 1 to 4: (1) leaves green and nest structure intact; (2) some leaves brown, but nest structure intact; (3) nest rotting and structure disintegrating; and (4) only the frame and <5% of leaves remaining. Nests were considered decayed from stage 4, following Plumptre and Reynolds [1996], therefore only nests of age 1 to 3 were used for further analyses.

We measured the perpendicular distance from each item of evidence to the transect line [sensu Buckland et al., 2010] and entered data into DISTANCE 6.0 [Buckland et al., 2001] to calculate the Effective Strip Width (ESW), and from the total area surveyed, obtain a nest density estimate (nests/km^2). Several models can be used for nest density estimation, and we selected the model that yielded the lowest Akaike's Information Criterion (AIC) value as recommended by previous studies (Thomas et al. 2010). We entered data for each area surveyed into DISTANCE, and stratified by vegetation type in order to separately calculate (ESW) for 'Open' (miombo woodland, grassland, swamp) and 'Closed' (evergreen closed & open forest) vegetation types. This analysis therefore yields a nest density estimate for open and closed vegetation, in addition to a global nest density estimate that controls for survey effort in each vegetation type.

We used an available production rate of nests of 1.1 per day [Plumptre & Reynolds, 1996]. Unlike previous studies that used a nest decay rate of 97, we used a nest decay rate specific to each vegetation type, described in Stewart et al. [2011]. We thus calculated the number of individuals per km^2 by correcting for the time for nests to decay to age four, and nest production rate, using the below formula [Plumptre & Reynolds, 1996]:

Density of chimpanzees = Density of nests/(production rate x mean time to decay)

Given that the 2007 results did not consider vegetation-specific decay rates (which vary by two-fold), we obtained the raw data from 2007 and re-analyzed them using DISTANCE, stratified by vegetation type, and also used the most up to date decay rate and thus we analyzed both 2007 and 2014 datasets identically for comparative purposes. Finally, we converted chimpanzee density (number of individuals/km^2) to estimated population size by multiplying this density estimate by the total area of interest (number of km^2).

We first re-analyzed the 2007 raw data using transect lengths measured in an identical way to 2014 transect lengths using high resolution satellite imagery in Google Earth, updated decay rates for dry season nests and using two different vegetation classifications. Transect lengths walked in 2014 differed slightly in a few cases in 2007 (Table 1). We therefore controlled for this difference in effort by incorporating 2007 transect lengths into our re-analysis of 2007 data.

All research complied with protocols approved by the Tanzania Wildlife Research Institute and adhered to the legal requirements of Tanzania and the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

RESULTS

In 2007 and 2014, we walked 16 transects (12 in Masito, 4 in Ugalla), covering a total of 70.30 km in 2007 and 66.07 km in 2014 (Table 1). In both surveys, we documented chimpanzee nests at all survey sites, even when we removed age 4 nests from the dataset. When we partitioned transects into open (woodland) and closed (evergreen forest) vegetation, we found that ~92% of transects were in open vegetation, versus ~8% in closed vegetation in both 2007 and 2014 (Table 1). This is remarkably different than the overall average of these figures across MUE, which is estimated to be 83% woodland, 14% grasslands, wetlands and bare lands, and 2-3% forest [Moyer et al., 2006].

TABLE 1 ABOUT HERE

Using the values that DISTANCE provided for effective strip widths (ESW) for each open and closed vegetation types, we calculated the number of individual chimpanzees per km^2 to be over 15x higher in forests than in woodlands (Table 2). When we incorporated the proportion of available forest across the whole of MUE we calculated an overall population density of 0.09 individuals/km^2 in 2007 and 0.05 individuals/km^2 in 2014 (Table 2). From these figures, we can estimate the population size for chimpanzees living in suitable habitat (2,699 km^2; n= ~243 chimpanzees) and across the entire ecosystem (5,756 km^2; n= ~518 chimpanzees). However, these estimates have large error margins (Table 3).

TABLE 2 ABOUT HERE

To test whether seasonality played a role in the difference between 2007 (early wet season) and 2014 (late wet season) chimpanzee densities, we examined the proportion of all nests observed (per km^2 to control for different ESWs) in closed versus open habitats between 2007 and 2014. A significantly smaller proportion of the total nests/km^2 observed in 2014 were found in closed vegetation and a greater proportion in open vegetation, compared to the proportions of total nests/km^2 found in closed and open vegetation in 2007 & 2014 (Fishers exact test, $p=0.012$).

Overall, we re-calculated the 2007 chimpanzee density on the surveyed transects to be 0.12 individuals/km^2, compared to 0.06 individuals/km^2 in 2014, taking into account only the proportion of vegetation types sampled along the transects (Table 2). To further test whether there was a change in density from 2007 to 2014 we conducted a Wilcoxon's matched pairs test to compare density of each surveyed region and found that there was not a significant decline ($W=6$, $N=5$, $p>0.05$, one-tailed). This result holds if comparisons are made between years for each transect ($W=18.5$, $N=11$, $p>0.05$, one-tailed) rather than regions, as above. The lack of a significant decline overall reflects that changes in density were not consistent across each transect area. Instead, Issa, Kamukulu Hills, and Mkanga river all exhibited an increase in density, whilst Kigoma River and Kalulumpeta Hills exhibited large declines (Figure 2).

FIGURE 2 ABOUT HERE

The overall density between 2007 and 2014 differed only within closed vegetation. Given that the 2007 surveys were conducted in the early wet season, versus the 2014 survey which was conducted in the late wet season, it is possible that seasonal nesting site preferences of chimpanzees could explain the lower mean density in 2014. We therefore compared the individual chimpanzee densities across surveyed areas in closed versus open vegetation (Figure 3). Kalulumpeta Hills and Kigoma River showed declines in chimpanzee density in open vegetation as well as closed, whilst Mkanga and Kamukulu hills show an increase in density in closed vegetation in 2014. A statistical comparison yielded no significant difference in density between closed ($W=3$, $N=6$, $p>0.05$, two-tailed) and open ($W=17$, $N=10$, $p>0.05$, two-tailed) vegetation types between 2007 and 2014.

FIGURE 3 ABOUT HERE

Human threats

To assess whether a loss in forest and woodland habitats may explain some of the variation in chimpanzee density between the survey periods, we analyzed the total amount of forest and woodland lost in each survey area each year between 2000 and 2012 derived from Landsat satellite imagery [Hansen et al., 2014]. We found that areas within five kilometers of the MUE line transects lost a combined 1,134Ha between 2008 and 2012.

We then correlated habitat loss against changes in densities to examine whether there was a relationship between forest loss and chimpanzee densities, and found a trend for increased negative change in chimpanzee density with increasing forest loss (Figure 4; spearman's rank correlation, $r_s=-0.80$, $n=5$, $p<0.10$).

FIGURE 4 ABOUT HERE

DISCUSSION

Overall we found no significant decline in chimpanzee density between 2007 and 2014 across the surveyed areas of the Masito-Ugalla Ecosystem in western Tanzania. Although we found chimpanzee density in 2014 to be almost half of that in 2007, the confidence limits surrounding these means are almost entirely overlapping. Thus, neither global nor local densities were statistically different across years. The differences in density were variably distributed across space, with some areas showing declines, whilst others, an increase. Large confidence intervals in both 2007 and 2014 data sets are due to too few transects (n= ~20), kilometers walked (<100), and nests recorded to assess change across an area estimated at >5,500km^2. A larger number of all of these parameters would provide greater definition for us to more reliably determine changes in chimpanzee density over time. Nonetheless, the difference in mean density suggests that although not detectable in this study, there may be an overall decline so we explore here two possible reasons for this, as well as compare both 2007 and 2014 data with those from another (2011-2012) survey across western Tanzania [Piel & Stewart, 2013] (Table 3).

Seasonality

The savanna woodlands of western Tanzania are characterized by dramatic seasonality. In the heterogeneous MUE habitat, chimpanzees nest more frequently in forest relative to forest availability [Stewart & Pruetz, 2013], in addition to selectively nesting on woodland slopes [Hernandez-Aguilar, 2009]. However, the extent to which chimpanzees select closed or open vegetation for nesting changes seasonally. In the dry season, chimpanzees avoid nesting in woodland and preferentially select forest vegetation, likely due to the seasonal loss of foliage in woodland vegetation [Stewart, 2011; Stewart & Pruetz, 2013].

Whilst the 2014 survey was conducted in January, in the latter part of the wet season, the earlier 2007 survey was conducted in October-November, at the very beginning of the wet season. We would thus expect for most chimpanzee nests to be found in the gallery forests then, as woodland trees lose leaves in the dry season, versus in 2014 when many would be in the woodlands. Given that >92% of the survey effort was conducted in woodland, we expect this difference in seasonality to influence the number of nests observed on our line transects. The overall relative proportion of chimpanzee density in closed versus open vegetation was greater in 2007 than 2014, a difference which approached significance, suggesting that chimpanzees' seasonal use of vegetation for nesting may have influenced differences in global density across years. In examining differences between the surveyed areas however, we see that although closed vegetation density decreased at Kalulumpeta Hills and Kigoma River, open vegetation use also decreased. Additionally, those areas that showed a slight increase, or similar density overall, exhibited a density increase in closed vegetation (e.g. Kamukulu Hills and Mkanga River; Figure 3). These findings suggest that geographic-specific changes in density are not related to seasonal use of vegetation.

Habitat loss

If seasonal differences do not explain variation in chimpanzee density across time, recent habitat loss may. We found a strong correlation between the amount of deforestation since 2007 and a decline in chimpanzee density. This relationship is part of a widespread pattern seen across great ape distribution [see Junker et al., 2012], and Tanzania is no exception. Human settlement and agriculture expansion along with other threats such as illegal timber harvesting and fires continues to threaten Tanzania's chimpanzee habitat [Mwampamba, 2007; Fisher et al., 2011] and specifically evergreen forests [Pintea, 2007; Pfeifer et al., 2012]. In an arid landscape like western Tanzania, gallery forests and woodland slopes are important refugees for chimpanzees, providing key food and nesting sources at various times of year [Hernandez-Aguilar et al., 2013; unpublished data], and a reduction in forest abundance clearly threatens chimpanzee viability across Tanzania [Plumptre et al., 2010; Lasch et al., 2011; Piel & Stewart, 2013; Stewart & Piel, 2013].

Our results quantify this relationship, and show that for each 1000ha of forest loss, the MUE landscape loses a corresponding density of 0.1 individuals/km^2 of wild chimpanzees (Figure 4). If the current rate of forest loss each year continues at its current rate of ~1.4% [JGI, 2014] forest lost/year and is not mitigated soon, we can expect all of Tanzania's remaining extra-park chimpanzees in MUE to be habitat-less in approximately 70 years. To more robustly test this prediction, more data on the rate of habitat loss and chimpanzee density are required across not only for the MUE but also adjacent ecosystems.

COMPARISON TO PREVIOUS REPORTS

Given the large error margins that we have calculated for 2007 chimpanzee density estimates, it is impossible to say with confidence whether chimpanzees have declined over the last seven years. However, a recent survey across the MUE in 2012 that combined genetic censusing techniques with traditional transect methods produced results with far lower error margins [Piel & Stewart, 2013] and so is worthy of inclusion here. Across 160 kilometers of line transects, Piel and Stewart [2013] recorded 169 nests and collected 131 chimpanzee fecal samples. By using capture-recapture analyses using CAPWIRE [Miller et al., 2005; Pennell et al., 2013], they described a density across the MUE of 0.10 individuals/km^2 (Lower CL: 0.09; Upper CL 0.13). This estimate is similar to that of the 2007 data reported here, and yet was conducted only two years earlier than the lower 2014 estimate.

These 2007 and 2012 estimates are also consistent with historical reports of chimpanzee density in the region. Except for one of the earliest studies in the mid 1950s in one high density chimpanzee area of Kasakati in Masito, which estimated densities at 0.46-0.71 [Suzuki, 1969], all previous (transect) survey work across Tanzania has reported values repeatedly and consistently between ~ 0.01 - 0.14 individuals/km^2 [reviewed in Moyer et al., 2006; see also Table 3].

TABLE 3 ABOUT HERE

RECOMMENDATIONS FOR FUTURE SURVEYS AND CONSERVATION ACTIONS

In assessing change over time of chimpanzee presence, historical data can be useful. However, given the differences we identified above in survey design and effort, neither the 2007 or 2014 data are reliably informative for investigating chimpanzee density across MUE. For that, we recommend more extensive spatial and temporal coverage, e.g. more and longer transects that reduce error margins [Kühl et al., 2008; see detailed recommendations in: Buckland et al., 2010; Thomas et al., 2010]. Future surveys should also include a greater proportion of gallery forest than the current ones. In a heterogeneous landscape like MUE, Moyer et al. [2006] discuss zig-zagging forests, for example.

We further recommend that (1) new transects be added, (2) at random locations, rather than areas of known chimpanzee presence, across MUE, (3) using parallel or random transect lines designed using DISTANCE to determine the most appropriate sampling method for this heterogeneous habitat, rather than transects radiating from central locations which results in over-sampling, and finally (4) transects be walked semi-annually at the same time each survey year to control for seasonal differences in chimpanzee nesting behaviour.

One advantage of the above-described transects is that they (temporally) frame the 2012 UPP/JGI surveys recently described [Piel & Stewart, 2013], and thus provide an opportunity for longitudinal changes over time. Thus, whilst results from 2007/2014 are not directly comparable to those from 2012 because of methodological differences, these data from various areas together could be used to assess temporal patterns of chimpanzee presence/activity across various snapshots of MUE. Finally, we need to bear in mind that in all of the studies (2007, 2012, & 2014), the surveyed areas were specifically targeted because of known chimpanzee presence, and represent only a fraction of the larger ecosystem, so any extrapolations to overall population sizes and broader temporal patterns across the ecosystem need to be interpreted with caution.

There are already various strategies employed to address the threats to MUE [JGI, 2009; Lasch et al., 2011]. For example, JGI has recently facilitated village land use plans developed by the local communities and worked together with District governments, (Tanzania National Parks (TANAPA), local communities and other non-government organisations to establish Local Area Forest Reserves that cover all the general land in the MUE. Additionally, it is now well established that researcher presence deters illegal human activity [Pusey et al., 2007; Campbell et al., 2011; Laurance, 2013; Piel et al., 2015] and so even long-term research projects may help mitigate these threats. Therefore there is a need to use the results and recommendations from this study to design a comprehensive survey approach that would allow continuously evaluation of the success of ongoing conservation efforts in the region.

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REFERENCES

Banda T, Schwartz MW, Caro T. 2006. Woody vegetation structure and composition along a protection gradient in a miombo ecosystem of western Tanzania. Forest Ecology and Management 230:179–185.

Buckland ST, Anderson DR, Burnham KP, et al. 2001. Introduction to Distance Sampling. Oxford: Oxford University Press.

Buckland ST, Plumptre AJ, Thomas L, Rexstad E a. 2010. Design and Analysis of Line Transect Surveys for Primates. International Journal of Primatology 31:833–847.

Campbell G, Kuehl H, Diarrassouba A, N'Goran PK, Boesch C. 2011. Long-term research sites as refugia for threatened and over-harvested species. Biology letters 7:723–6.

Davenport TRB, Mpunga NE, Phillipps GP, et al. 2010. The Conservation Status of the Chimpanzee Pan troglodytes schweinfurthii in " Southern Tanganyika " 2005 - 2009.

Fisher B, Lewis SL, Burgess ND, et al. 2011. Implementation and opportunity costs of reducing deforestation and forest degradation in Tanzania. Nature Climate Change 1:161–164.

Fitzherbert EB, Struebig MJ, Morel A, et al. 2008. How will oil palm expansion affect biodiversity? Trends in Ecology & Evolution 23:538–45.

Hansen MC, Potapov PV, Moore R, et al. 2014. High-Resolution Global Maps of. Science 850:850–853.

Hernandez-Aguilar R. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. Journal of Human Evolution 57:350–64.

Hernandez-Aguilar RA, Moore J, Stanford CB. 2013. Chimpanzee nesting patterns in savanna habitat: environmental influences and preferences. American Journal of Primatology 75:979–94.

JGI. 2007. Biological surveys in the Masito-Ugalla Ecosystem.

JGI. 2009. Masito-Ugalla Ecosystem Conservation Action Plan.

JGI. 2014. Masito-Ugalla Ecosystem REDD+ Pilot Project.

Junker J, Blake S, Boesch C, et al. 2012. Recent decline in suitable environmental conditions for African great apes. Biodiversity Research:1–15.

Kaiser M, Löwa A, Ulrich M, et al. 2010. Wild chimpanzees infected with 5 Plasmodium species. Emerging infectious diseases 16:1956–9.

Keele BF, Jones JH, Terio K a, et al. 2009. Increased mortality and AIDS-like immunopathology in wild chimpanzees infected with SIVcpz. Nature 460:515–9.

Köndgen S, Kühl H, N'Goran PK, et al. 2008. Pandemic human viruses cause decline of endangered great apes. Current Biology 18:260–4.

Kühl H, Maisels F, Ancrenaz M, Williamson EA. 2008. Best practice guidelines for surveys and monitoring of great ape populations. IUCN.

Lasch C, Pintea L, Traylor-Holzer K, Kamenya S. 2011. Tanzania Chimpanzee Conservation Action Planning Workshop Report.

Laurance WF. 2013. Does research help to safeguard protected areas? Trends in Ecology & Evolution 28:261–6.

Leendertz FH, Ellerbrok H, Boesch C, et al. 1993. Anthrax kills wild chimpanzees in a tropical rainforest. 290:451–452.

Lehmann J, Korstjens AH, Dunbar RIM. 2010. Apes in a changing world - the effects of global warming on the behaviour and distribution of African apes. Journal of Biogeography 37:2217–2231.

McLennan MR, Hyeroba D, Asiimwe C, Reynolds V, Wallis J. 2012. Chimpanzees in mantraps: lethal crop protection and conservation in Uganda. Oryx 46:598–603.

Miller CR, Joyce P, Waits L. 2005. A new method for estimating the size of small populations from genetic mark-recapture data. Molecular Ecology 14:1991–2005.

Moyer D, Plumptre AJ, Pintea L, et al. 2006. Surveys of Chimpanzees and other Biodiversity in Western Tanzania. Report submitted to USF&W, Great Apes Fund.

Mulder MB, Caro T, Msago OA. 2007. The role of research in evaluating conservation strategies in Tanzania: the case of the Katavi-Rukwa ecosystem. Conservation Biology 21:647–58.

Mwampamba TH. 2007. Has the woodfuel crisis returned? Urban charcoal consumption in Tanzania and its implications to present and future forest availability. Energy Policy 35:4221–4234.

Newmark WD, Manyanza DN, Gamassa DM, Sariko HI. 1994. The Conflict between Wildlife and Local People Living Adjacent to Protected Areas in Tanzania : Human as a Predictor Density. Conservation Biology 8:249–255.

Nishida T. 2011. Chimpanzees of the lakeshore: natural history and culture at Mahale. Cambridge, UK: Cambridge University Press.

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

Ohashi G, Matsuzawa T. 2011. Deactivation of snares by wild chimpanzees. Primates 52:1–5.

Pennell MW, Stansbury CR, Waits LP, Miller CP. 2013. Capwire: a R package for estimating population census size from non-invasive genetic sampling. Molecular Ecology Resources 13:154–157.

Pfeifer M, Burgess ND, Swetnam RD, et al. 2012. Protected areas: mixed success in conserving East Africa's evergreen forests. PloS one 7:e39337.

Piel AK, Lenoel A, Johnson C, Stewart FA. 2015. Deterring poaching in western Tanzania: The presence of wildlife researchers. Global Ecology and Conservation.

Piel AK, Lenoel A, Stewart FA. 2013. Mammals and menaces on general land in the Issa Valley, Katavi Region. In: Proceedings of the 9th Annual TAWIRI Scientific Conference. Arusha.

Piel AK, Stewart FA. 2013. Identifying Critical Habitats for Savanna Chimpanzee Conservation in Western Tanzania Using New Landscape-Scale Censusing Techniques. Report submitted to the Jane Goodall Institute, USA.

Piel AK, Stewart FA. 2014. Census and conservation status of chimpanzees (Pan troglodytes schweinfurthii) across the Greater Mahale Ecosystem. Report submitted to the The Nature Conservancy, USA.

Pintea L, Pusey AE, Wilson ML, et al. 2012. Long-term ecological changes affecting the chimpanzees of Gombe National Park, Tanzania. In: Long Term Changes in Africa's Rift Valley: impacts on biodiversity. New York, NY: Nova Science Publishers. p 194–210.

Pintea L. 2007. Applying satellite imagery and GIS for chimpanzee habitat change detection and conservation.

Pintea LP, Bauer ME, Bolstad PV, Pusey A. 2002. Matching multiscale remote sensing data to interdisciplinary conservation needs: the case of chimpanzees in western Tanzania. In: Pecora 15/Land Satellite Information IV/ISPRS Commission I/FIEOS.

Plumptre AJ, Reynolds V. 1996. Censusing Chimpanzees in the Budongo. International Journal of Primatology 17:85–99.

Plumptre AJ, Rose R, Nangendo G, et al. 2010. Eastern Chimpanzee (Pan troglodytes schweinfurthii): Status Survey and Conservation Action Plan. IUCN.

Pusey AE, Pintea L, Wilson ML, Kamenya S, Goodall J. 2007. The Contribution of Long-Term Research at Gombe National Park to Chimpanzee Conservation. Conservation Biology 21:623–634.

Reynolds V. 1992. Chimpanzees in the Budongo Forest, 1962-1992. Journal of Zoology 228:695–699.

Rudicell RS, Jones JH, Wroblewski EE, et al. 2010. Impact of Simian Immunodeficiency Virus Infection on Chimpanzee Population Dynamics. PLoS Pathogens 6:e1001116.

Ryan SJ, Walsh PD. 2011. Consequences of non-intervention for infectious disease in African great apes. PloS one 6:e29030.

Stewart F, Pruetz JD. 2013. Do chimpanzee nests serve an anti-predatory function? American Journal of Primatology 75:593–604.

Stewart FA, Piel AK, McGrew WC. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. Journal of Human Evolution 61:388–95.

Stewart FA, Piel AK. 2013. Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania. Primates 55:35–40.

Stewart FA. 2011. The evolution of shelter: ecology and ethology of chimpanzee nest building. :236.

Sugiyama Y, Soumah AG. 1988. Preliminary survey of the distribution and population of chimpanzees in the Republic of Guinea. Primates 29:569–574.

Suzuki A. 1969. An ecological study of chimpanzees in a savanna woodland. Primates 148:103–148.

Swarna Nantha H, Tisdell C. 2008. The orangutan–oil palm conflict: economic constraints and opportunities for conservation. Biodiversity and Conservation 18:487–502.

Thomas L, Buckland ST, Rexstad E a, et al. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of Applied Ecology 47:5–14.

Young H, Griffin RH, Wood CL, Nunn CL. 2013. Does habitat disturbance increase infectious disease risk for primates? Ecology letters 16:656–63.

FIGURE LEGENDS

Figure 1 – Map of western Tanzania and the transect locations. Shaded green areas represent predicted chimpanzee habitat.

Figure 2 - Chimpanzee density within each area surveyed in 2007 & 2014.

Figure 3 - Chimpanzee density within each vegetation type (open and closed) and compared across years in each area surveyed in 2007 and 2014.

Figure 4 – Comparing loss in forest with difference in chimpanzee density between 2007 and 2014.

TABLE LEGENDS

Table 1 - Transect lengths and habitat proportions for each transect walked in 2007 and 2014

Table 2 – Density estimates compared across vegetation types and globally for our re-analysis of 2007 data reported in JGI (2007) using updated nest decay rates and re-walked transects in 2014.

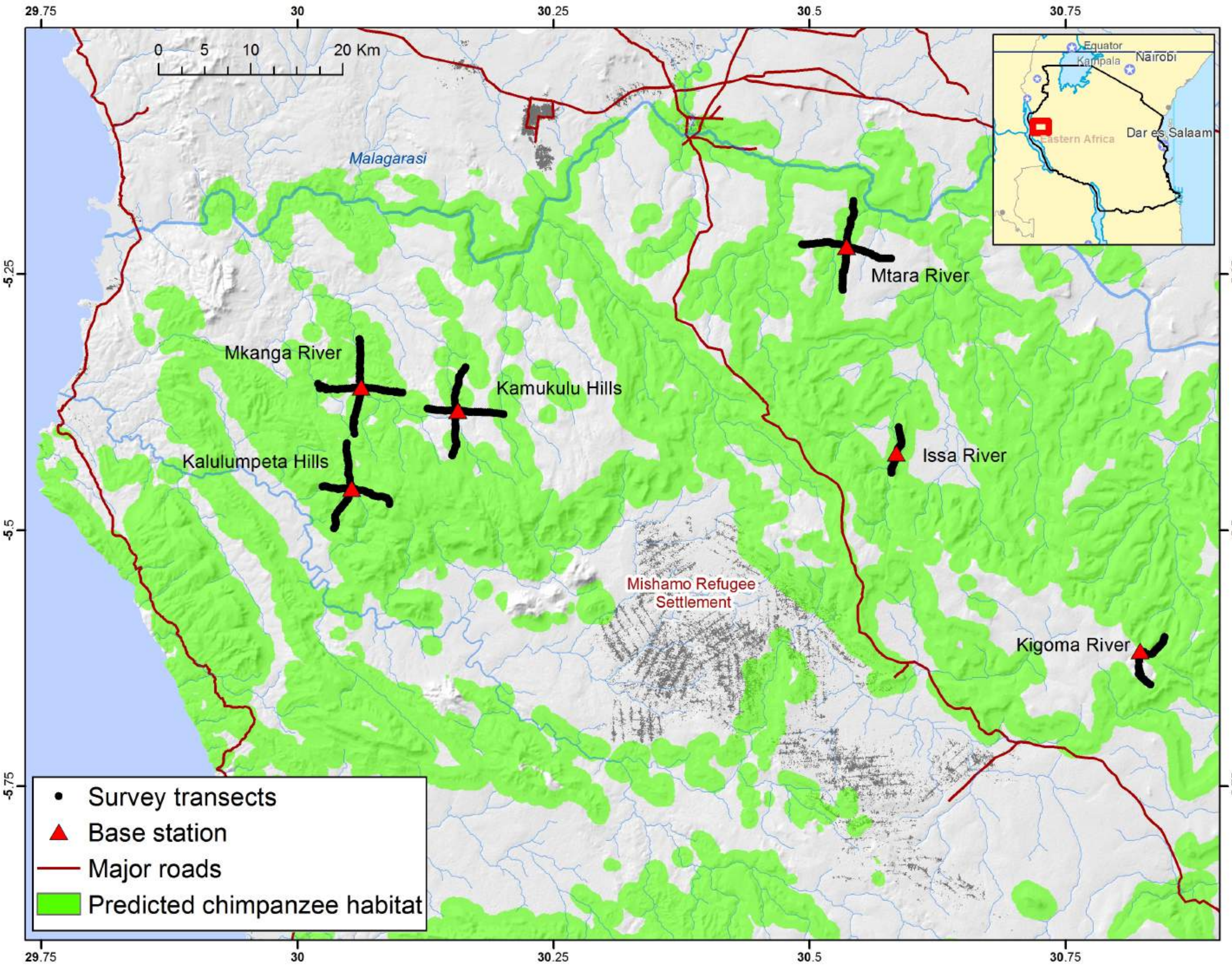
Table 3 - A comparison of MUE chimpanzee population sizes from various studies: (1) our recalculations of 2007 (JGI) survey data, (2) the current, 2014 re-walking of the 2007 survey, (3) an independent survey of other MUE areas in 2012, and (4) compiled estimates using historical data.

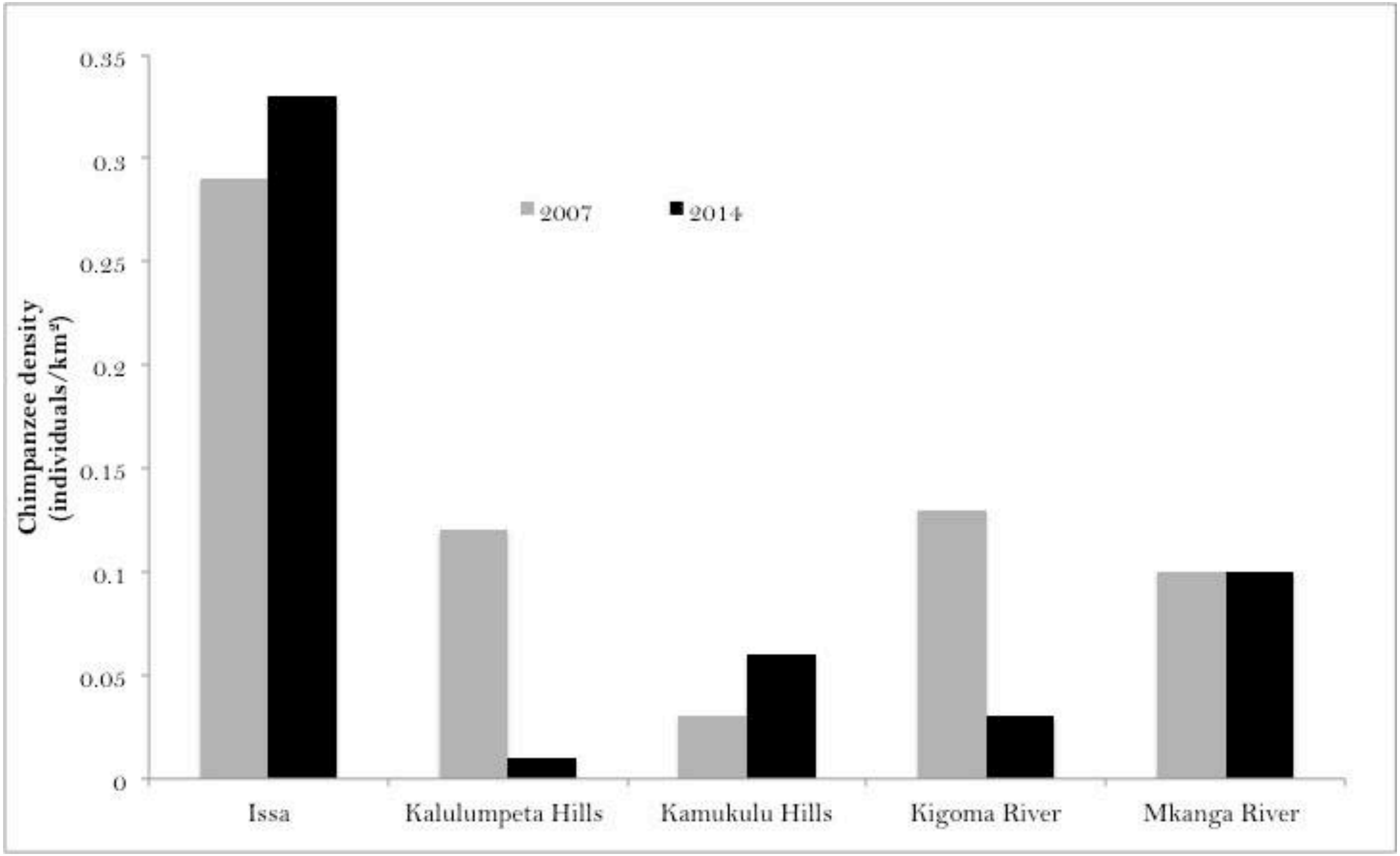
Table 1

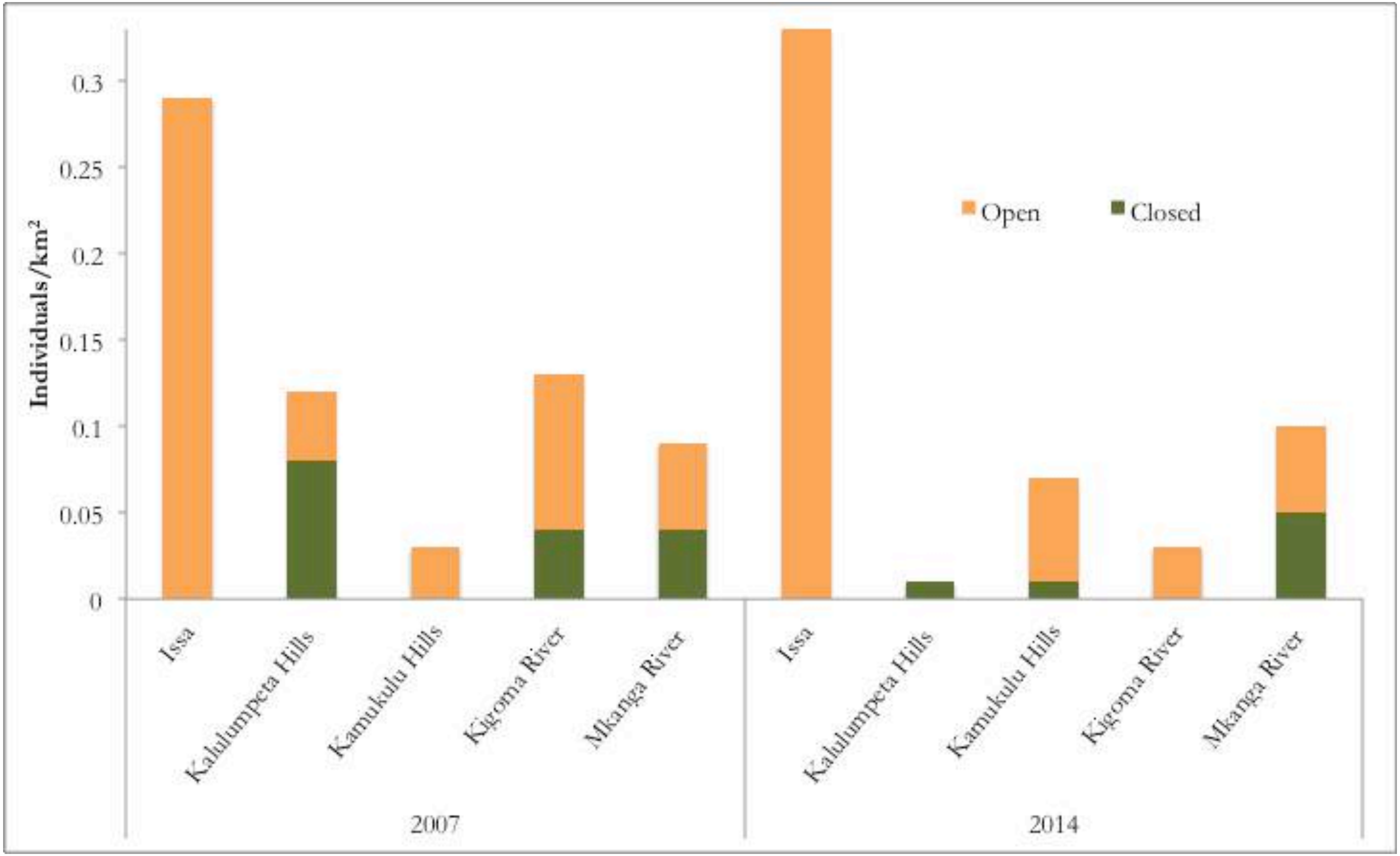
		2007 Transects				2014 Transects			
	Survey area	Lengths (km)			#	Lengths (km)			#
Region	(abbreviated)	Open	Closed	Total	Nests	Open	Closed	Total	Nests
Ugalla	Kigoma	9.50	0.47	9.97	25	8.18	0.47	8.64	3
	Issa	4.97	0.00	4.97	33	4.97	0.00	4.97	11
Masito	Mkanga	17.97	1.86	19.83	37	15.61	1.76	17.37	8
	Kamkulu	16.33	1.48	17.81	13	16.33	1.48	17.81	2
	Kalululempeta	16.22	1.50	17.72	28	15.77	1.50	17.27	2
	TOTAL	**64.99**	**5.31**	**70.30**	**136**	**60.86**	**5.21**	**66.07**	**26**

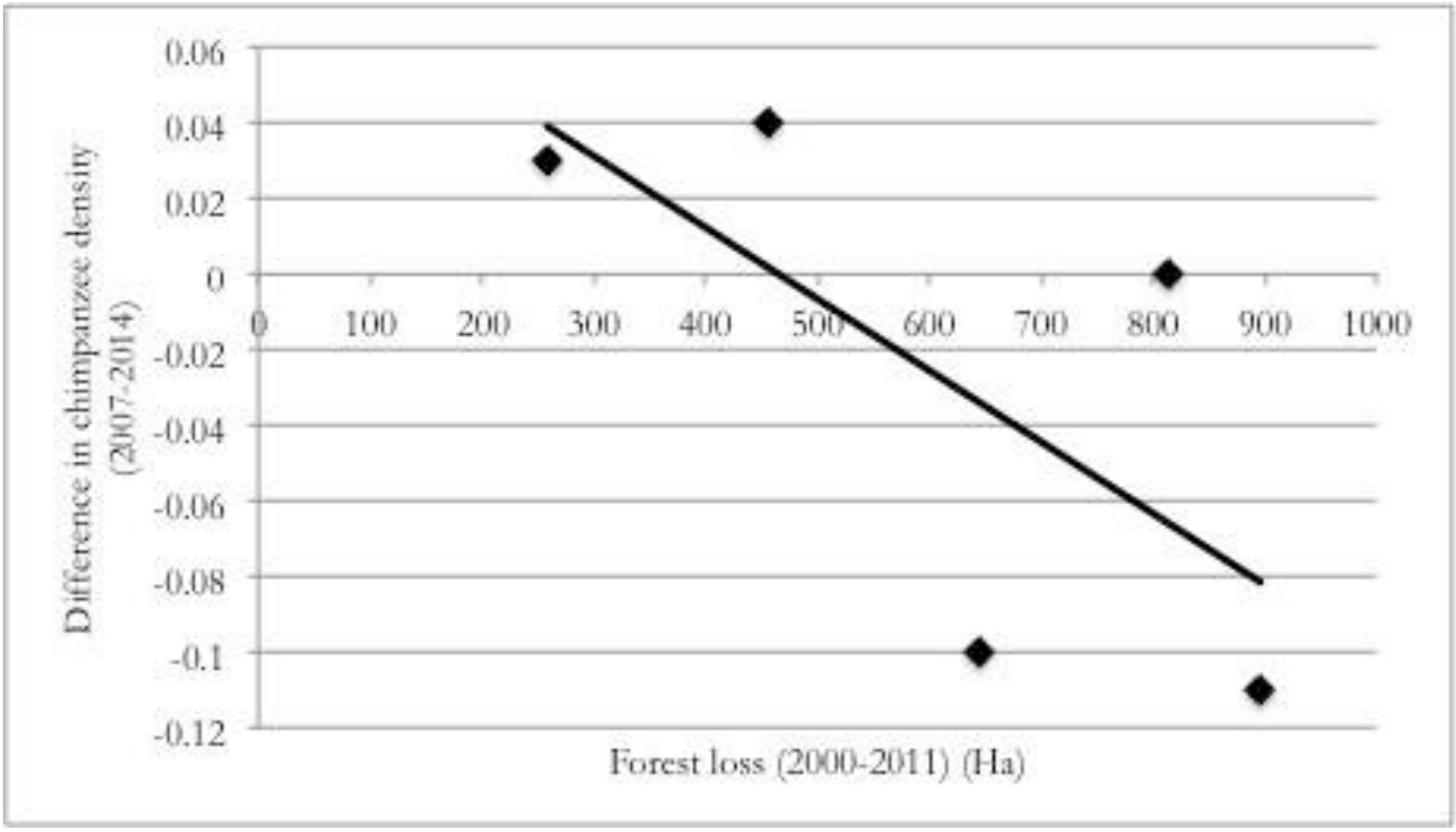
Table 2

	Chimpanzee density (individuals/km^2)					
	2007			2014		
Vegetation	Mean	LCL	UCL	Mean	LCL	UCL
Open	0.05	0.02	0.12	0.04	0.01	0.27
Closed	1.34	0.47	3.83	0.29	0.12	0.70
Overall (controlling for 7.9% forest on transects)	0.12	0.06	0.23	0.06	0.02	0.23
Overall (controlling for 3% forest across MUE)	**0.09**	**0.03**	**0.23**	**0.05**	**0.01**	**0.30**


29.75
30
30.25
30.5
30.75
-5.25
-5.5
-5.75
0
5
10
20 Km
Malagarasi
Equator
Kampala
Nairobi
Eastern Africa
Dar es Salaam
Mtara River
Mkanga River
Kamukulu Hills
Issa River
Kalulumpeta Hills
Mishamo Refugee Settlement
Kigoma River
Survey transects
Base station
Major roads
Predicted chimpanzee habitat


Chimpanzee density (individuals/km²)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
2007
2014
Issa
Kalulumpeta Hills
Kamukulu Hills
Kigoma River
Mkanga River


Individuals/km²
0.3
0.25
0.2
0.15
0.1
0.05
0
Open
Closed
Issa
Kalulumpeta Hills
Kamukulu Hills
Kigoma River
Mkanga River
2007
Issa
Kalulumpeta Hills
Kamukulu Hills
Kigoma River
Mkanga River
2014



0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
0
100
200
300
400
500
600
700
800
900
1000
Difference in chimpanzee density (2007-2014)
Forest loss (2000-2011) (Ha)