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Piel, AK, Cohen, N, Kamenya, S, Ndimuligo, SA, Pintea, L and Stewart, FA (2015) Population status of chimpanzees in the Masito-Ugalla Ecosystem, Tanzania. American Journal of Primatology, 77 (10). pp. 1027-1035. ISSN 1098-2345

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1 2 2	Title : Population status of chimpanzees outside of National Parks in the Masito-Ugalla Ecosystem, western Tanzania
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7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26	 ³QG, United Kingdom ² Ugalla Primate Project, Tanzania ³ The Jane Goodall Institute, Kigoma, Tanzania ⁴ Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, Universit of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway ⁵ The Jane Goodall Institute, 1595 Spring Hill Road, Suite 550 Vienna, Virginia 22182, USA Corresponding author: Alex Piel, Division of Biological Anthropology, Pembroke Street,

28 ABSTRACT

29

More than 75 percent of Tanzania's remaining chimpanzees live at low densities on land 30 outside National Parks. Chimpanzees are one of the key conservation targets in the region 31 32 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 33 assess change in chimpanzee density within the Masito-Ugalla Ecosystem (MUE) by 34 35 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 36 5km buffer of these transects in that same period. Our results indicate that there has not 37 been a significant decline in chimpanzees across the surveyed areas of MUE between 38 2007 and 2014. Comparisons between 2007 and 2014 results suggest that the MUE 39 chimpanzee population has been stable over this period, and represents approximately 576 40 individuals. Although the overall mean density of chimpanzees may have declined from 41 0.09 individuals/km² in 2007 to 0.05 individuals/km² in 2014, whether this change is 42 significant cannot be detected due to small sample sizes and large error margins. Some 43 areas (Issa Valley, Mkanga, Kamkulu), in fact, showed an increase in chimpanzee density. 44 Seasonality of chimpanzee habitat preference for ranging or nesting may explain variation 45 in density at some of the survey sites between 2007 and 2014. We found a relationship 46 between increasing habitat loss derived from Landsat satellite imagery and decreasing 47 chimpanzee density. Future surveys will need to ensure a larger sample size, broader 48 geographic effort, and random survey design, in order to more precisely determine trends in 49 MUE chimpanzee density and population size over time. 50 51 KEY WORDS: Chimpanzee; Density; Survey; Remote sensing, Masito-Ugalla; Tanzania 52 53

55 **INTRODUCTION**

56

Chimpanzees (Pan troglodytes) have been classified as an endangered species 57 58 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 59 habitat destruction [Lehmann et al., 2010; Junker et al., 2012; Young et al., 2013], human 60 introduced [Leendertz et al., 1993; Köndgen et al., 2008; Ryan & Walsh, 2011] and natural 61 [Keele et al., 2009; Kaiser et al., 2010; Rudicell et al., 2010] disease, and poaching 62 63 [Sugiyama & Soumah, 1988; Reynolds, 1992; Ohashi & Matsuzawa, 2011; McLennan et al., 2012] on wild chimpanzee populations. 64

65 Tanzania, home to the two longest, continuous studies of chimpanzees [Gombe Stream - Pusey et al., 2007; Mahale Mountains - Nishida, 2011], hosts between two and 66 three thousand chimpanzees, all within three regions in the western part of the country 67 [Plumptre et al., 2010]. Almost one third of these chimpanzees live within the boundaries of 68 69 the two aforementioned national parks. However, the rest are distributed across approximately 30,000km² of land outside of National Parks, comprised mostly (>80%) of 70 71 miombo woodland [Moyer et al., 2006]. These extra-park savanna-woodland chimpanzees 72 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; 73 Piel et al., 2015]. 74

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]

80 and conservationists have focused on establishing priority areas based on remaining chimpanzee habitat. In western Tanzania, human incursion into the Masito area is mostly 81 for conversion of chimpanzee habitat into oil palm plantations, but also for slash and burn 82 83 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 84 85 [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 86 population density. 87

88 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), 89 90 conservationists can better understand how human threats in Tanzania affects wildlife 91 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 92 93 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 94 95 Tanzania. Our primary goal was to compare results from a similar survey conducted in 96 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. 97 We also predicted that the largest declines in density would be found nearest to the largest 98 99 human settlements (here, in the Masito region), whereas Ugalla areas would show stable densities. 100

101 **METHODS**

102 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,

110 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).

118 FIGURE 1 ABOUT HERE

119 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.

126 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 127 Open Data Kit (ODK) software. We recorded all direct (sightings) and indirect (print, nest, 128 129 feces) evidence of large mammals, specifically chimpanzees, noting GPS coordinate, vegetation (miombo woodland, closed forest, open forest, swamp, or grassland), number 130 (of animals for direct encounters only), age classification (of nest or feces traces) and 131 132 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; 133 134 (3) nest rotting and structure disintegrating; and (4) only the frame and <5% of leaves 135 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. 136

137 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., 138 2001] to calculate the Effective Strip Width (ESW), and from the total area surveyed, obtain 139 a nest density estimate (nests/km²). Several models can be used for nest density 140 141 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 142 143 for each area surveyed into DISTANCE, and stratified by vegetation type in order to 144 separately calculate (ESW) for 'Open' (miombo woodland, grassland, swamp) and 'Closed' (evergreen closed & open forest) vegetation types. This analysis therefore yields a nest 145

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, 149 1996]. Unlike previous studies that used a nest decay rate of 97, we used a nest decay rate 150 specific to each vegetation type, described in Stewart et al. [2011]. We thus calculated the 151 number of individuals per km² by correcting for the time for nests to decay to age four, and 152 nest production rate, using the below formula [Plumptre & Reynolds, 1996]:

153

154 Density of chimpanzees = Density of nests/(production rate x mean time to decay) 155

Given that the 2007 results did not consider vegetation-specific decay rates (which vary by 156 two-fold), we obtained the raw data from 2007 and re-analyzed them using DISTANCE, 157 stratified by vegetation type, and also used the most up to date decay rate and thus we 158 159 analyzed both 2007 and 2014 datasets identically for comparative purposes. Finally, we converted chimpanzee density (number of individuals/km²) to estimated population size by 160 multiplying this density estimate by the total area of interest (number of km^2). 161 162 We first re-analyzed the 2007 raw data using transect lengths measured in an 163 identical way to 2014 transect lengths using high resolution satellite imagery in Google

164 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

166 (Table 1). We therefore controlled for this difference in effort by incorporating 2007 transect

167 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.

171

172 **RESULTS**

In 2007 and 2014, we walked 16 transects (12 in Masito, 4 in Ugalla), covering a 173 total of 70.30 km in 2007 and 66.07 km in 2014 (Table 1). In both surveys, we documented 174 chimpanzee nests at all survey sites, even when we removed age 4 nests from the dataset. 175 When we partitioned transects into open (woodland) and closed (evergreen forest) 176 vegetation, we found that ~92% of transects were in open vegetation, versus ~8% in closed 177 178vegetation 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% 179 grasslands, wetlands and bare lands, and 2-3% forest [Moyer et al., 2006]. 180

181

182 TABLE 1 ABOUT HERE

183

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 km² 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/km² in 2007 and 0.05 individuals/km² in 2014 (Table 2). From these figures, we can estimate the population size for chimpanzees living in suitable habitat (2,699 km²; n= ~243 chimpanzees) and across the entire ecosystem (5,756 km²; n= ~518

191 chimpanzees). However, these estimates have large error margins (Table 3).

192

193 TABLE 2 ABOUT HERE

194

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 km² to control for different ESWs) in closed versus open habitats between 2007 and 2014. A significantly smaller proportion of the total nests/km² observed in 2014 were found in closed vegetation and a greater proportion in open vegetation, compared to the proportions of total nests/km² 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 202 be 0.12 individuals/km², compared to 0.06 individuals/km² in 2014, taking into account only 203 204 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 205 206 matched pairs test to compare density of each surveyed region and found that there was 207 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 208 regions, as above. The lack of a significant decline overall reflects that changes in density 209 were not consistent across each transect area. Instead, Issa, Kamukulu Hills, and Mkanga 210 211 river all exhibited an increase in density, whilst Kigoma River and Kalulumpeta Hills exhibited large declines (Figure 2). 212

213

214 FIGURE 2 ABOUT HERE

215 The overall density between 2007 and 2014 differed only within closed vegetation. 216 Given that the 2007 surveys were conducted in the early wet season, versus the 2014 217 survey which was conducted in the late wet season, it is possible that seasonal nesting site 218 preferences of chimpanzees could explain the lower mean density in 2014. We therefore 219 compared the individual chimpanzee densities across surveyed areas in closed versus 220 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 221 222 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) 223 224 and open (W=17, N=10, p>0.05, two-tailed) vegetation types between 2007 and 2014.

225

FIGURE 3 ABOUT HERE

227

Human threats

To assess whether a loss in forest and woodland habitats may explain some of the 229 230 variation in chimpanzee density between the survey periods, we analyzed the total amount 231 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 232 233 kilometers of the MUE line transects lost a combined 1,134Ha between 2008 and 2012. 234 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 235 for increased negative change in chimpanzee density with increasing forest loss (Figure 4; 236 spearman's rank correlation, r_s =-0.80, n=5, p<0.10). 237

238

239 FIGURE 4 ABOUT HERE

240 **DISCUSSION**

Overall we found no significant decline in chimpanzee density between 2007 and 241 242 2014 across the surveyed areas of the Masito-Ugalla Ecosystem in western Tanzania. 243 Although we found chimpanzee density in 2014 to be almost half of that in 2007, the 244 confidence limits surrounding these means are almost entirely overlapping. Thus, neither 245 global nor local densities were statistically different across years. The differences in density 246 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 247 transects (n= ~20), kilometers walked (<100), and nests recorded to assess change across 248 an area estimated at >5,500km². A larger number of all of these parameters would provide 249 greater definition for us to more reliably determine changes in chimpanzee density over 250 time. Nonetheless, the difference in mean density suggests that although not detectable in 251 252 this study, there may be an overall decline so we explore here two possible reasons for this, 253 as well as compare both 2007 and 2014 data with those from another (2011-2012) survey 254 across western Tanzania [Piel & Stewart, 2013] (Table 3).

255

256 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].

265 Whilst the 2014 survey was conducted in January, in the latter part of the wet 266 season, the earlier 2007 survey was conducted in October-November, at the very beginning 267 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 268 269 many would be in the woodlands. Given that >92% of the survey effort was conducted in 270 woodland, we expect this difference in seasonality to influence the number of nests 271 observed on our line transects. The overall relative proportion of chimpanzee density in 272 closed versus open vegetation was greater in 2007 than 2014, a difference which 273 approached significance, suggesting that chimpanzees' seasonal use of vegetation for 274 nesting may have influenced differences in global density across years. In examining 275 differences between the surveyed areas however, we see that although closed vegetation density decreased at Kalulumpeta Hills and Kigoma River, open vegetation use also 276 277 decreased. Additionally, those areas that showed a slight increase, or similar density 278 overall, exhibited a density increase in closed vegetation (e.g. Kamukulu Hills and Mkanga 279 River; Figure 3). These findings suggest that geographic-specific changes in density are not 280 related to seasonal use of vegetation.

281

282 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

286 pattern seen across great ape distribution [see Junker et al., 2012], and Tanzania is no 287 exception. Human settlement and agriculture expansion along with other threats such as illegal timber harvesting and fires continues to threaten Tanzania's chimpanzee habitat 288 289 [Mwampamba, 2007; Fisher et al., 2011] and specifically evergreen forests [Pintea, 2007; 290 Pfeifer et al., 2012]. In an arid landscape like western Tanzania, gallery forests and 291 woodland slopes are important refugees for chimpanzees, providing key food and nesting 292 sources at various times of year [Hernandez-Aguilar et al., 2013; unpublished data], and a 293 reduction in forest abundance clearly threatens chimpanzee viability across Tanzania [Plumptre et al., 2010; Lasch et al., 2011; Piel & Stewart, 2013; Stewart & Piel, 2013]. 294 295 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/km² of wild chimpanzees 296 (Figure 4). If the current rate of forest loss each year continues at its current rate of ~1.4% 297 [JGI, 2014] forest lost/year and is not mitigated soon, we can expect all of Tanzania's 298 299 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 300

301 density are required across not only for the MUE but also adjacent ecosystems.

302 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/km² (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/km² [reviewed in Moyer et al., 2006; see also Table 3].

320

321 TABLE 3 ABOUT HERE

322 **RECOMMENDATIONS FOR FUTURE SURVEYS AND CONSERVATION ACTIONS**

323 In assessing change over time of chimpanzee presence, historical data can be 324 useful. However, given the differences we identified above in survey design and effort, 325 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. 326 327 more and longer transects that reduce error margins [Kühl et al., 2008; see detailed 328 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 329 330 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, 331

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 338 2012 UPP/JGI surveys recently described [Piel & Stewart, 2013], and thus provide an 339 opportunity for longitudinal changes over time. Thus, whilst results from 2007/2014 are not 340 directly comparable to those from 2012 because of methodological differences, these data 341 342 from various areas together could be used to assess temporal patterns of chimpanzee 343 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 344 345 because of known chimpanzee presence, and represent only a fraction of the larger 346 ecosystem, so any extrapolations to overall population sizes and broader temporal patterns 347 across the ecosystem need to be interpreted with caution.

348 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 349 developed by the local communities and worked together with District governments. 350 351 (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 352 353 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 354 even long-term research projects may help mitigate these threats. Therefore there is a need 355

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.

359

360 **ACKNOWLEDGMENETS**

We are grateful to TAWIRI, COSTECH, and the Mpanda and Kigoma Districts for 361 permission to conduct research in western Tanzania. The Jane Goodall Institute (Tanzania) 362 provided critical logistical support and facilitation, especially in villages in Masito. Many 363 thanks to Mashaka Alimas, Busoti Juma, Parag Kadam, Shedrack Lucas, Jovin Lwehabura, 364 Tanu Msekenyi, Msigwa Rashid, and Amos Thomas for field assistance. Funding for this 365 366 work was provided by the Jane Goodall Institute, Tanzania and long-term research for the Ugalla Primate Project comes from the UCSD/Salk Institute Center for Academic Research 367 and Training in Anthropogeny (CARTA). Many thanks to Alice Macharia for comments on a 368 369 previous version of this manusript.

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495 FIGURE LEGENDS

- Figure 1 Map of western Tanzania and the transect locations. Shaded green areas
 represent predicted chimpanzee habitat.
- 498 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.
- 501 Figure 4 Comparing loss in forest with difference in chimpanzee density between 2007 502 and 2014.
- 503
- 504 TABLE LEGENDS
- Table 1 Transect lengths and habitat proportions for each transect walked in 2007 and2014
- 507 Table 2 Density estimates compared across vegetation types and globally for our re-
- 508 analysis of 2007 data reported in JGI (2007) using updated nest decay rates and re-walked 509 transects in 2014.
- 510 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
- 512 survey, (3) an independent survey of other MUE areas in 2012, and (4) compiled estimates
- 513 using historical data.

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20	66.07	5.21	60.86	136	70.30	5.31	64.99	TOTAL	
2	17.27	1.50	15.77	28	17.72	1.50	16.22	Kalululempeta	
N	17.81	1.48	16.33	13	17.81	1.48	16.33	Kamkulu	
œ	17.37	1.76	15.61	37	19.83	1.86	17.97	Mkanga	Masito
11	4.97	0.00	4.97	သ	4.97	0.00	4.97	lssa	
ω	8.64	0.47	8.18	25	9.97	0.47	9.50	Kigoma	Ugalla
Nests	Total	Closed	Open	Nests	Total	Closed	Open	(abbreviated)	Region
#	n)	.engths (km	Le	#	1)	.engths (km	Le	Survey area	
	Insects	2014 Transects			Transects	2007 Trai			

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







