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Article

1 **Ecological correlates of chimpanzee (*Pan troglodytes schweinfurthii*)**

2 **density in Mahale Mountains National Park, Tanzania**

3 **Short title: Ecological correlates of chimpanzee (*Pan troglodytes schweinfurthii*) density**

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Abstract

Understanding the ecological factors that drive animal density patterns in time and space is key to devising effective conservation strategies. In Tanzania, most chimpanzees (~75%) live outside national parks where human activities threaten their habitat's integrity and connectivity. Mahale Mountains National Park (MMNP), therefore, is a critical area for chimpanzees (*Pan troglodytes schweinfurthii*) in the region due to its location and protective status. Yet, despite its importance and long history of chimpanzee research (>50 years), a park-wide census of the species has never been conducted. The park is categorized as a savanna-woodland mosaic, interspersed with riparian forest, wooded grassland, and bamboo thicket. This heterogeneous landscape offers an excellent opportunity to assess the ecological characteristics associated with chimpanzee density, a topic still disputed, which could improve conservation plans that protect crucial chimpanzee habitat outside the park. We examined the influence of fine-scale vegetative characteristics and topographical features on chimpanzee nest density, modeling nest counts using hierarchical distance sampling. We counted 335 nests in forest and woodland habitats across 102 transects in 13 survey sites. Nests were disproportionately found more in or near evergreen forests, on steep slopes, and in feeding tree species. We calculated chimpanzee density in MMNP to be 0.23 ind/km^2, although density varied substantially among sites (0.09 - 3.43 ind/km^2). Density was associated with factors related to the availability of food and nesting trees, with topographic heterogeneity and the total basal area of feeding tree species identified as significant positive predictors. Species-rich habitats and floristic diversity likely play a principal role in shaping chimpanzee density within a predominately open landscape with low food abundance. Our results provide valuable baseline data for future monitoring efforts in MMNP and enhance our understanding of this endangered species' density and distribution across Tanzania.

36

Introduction

Wildlife populations are experiencing a global decline in what has become a sixth mass extinction, a phenomenon primarily driven by human-mediated activities such as habitat destruction, overexploitation, and a rapidly changing global climate [1,2]. Obtaining baseline data and monitoring populations over space and time are essential for guiding and evaluating the effectiveness of conservation strategies [3]. Population density and abundance estimates are useful indicators of population status [4] and capacity for long-term survival [5]. Identifying ecological factors associated with species' density can inform conservation and management bodies by helping guide the prioritization of conservation areas and enhancing our understanding of the potential consequences of environmental change.

Chimpanzees (*Pan troglodytes*) are threatened across their distribution [6], with habitat destruction and degradation, hunting, and disease as some of the leading threats to their survival [7,8]. In Tanzania, 90% of the country's chimpanzees occur in the Greater Mahale Ecosystem (GME) where suitable habitat is being lost and fragmented by expanding human settlements, agriculture, logging, and cattle herding [8–10]. Research shows that chimpanzee density ranges from $0.1 - 3.7$ ind/km^2 across sites in the GME [11,12] and that the potential decrease in chimpanzee density between 2007 and 2014 is correlated with habitat loss [10], demonstrating the value of baseline data and repeated surveys to track population trends. Chimpanzees in savanna-woodland mosaics like the GME already live at relatively low densities (Table 1), accentuating the need to identify and protect areas critical towards chimpanzee conservation in the region.

58

3

59 **Table 1. Comparison of chimpanzee density estimates reported from surveys using nest**

60 **count methodologies.**

Location	Vegetation type	Elevation (m)	Average rainfall (mm)	Density estimate (ind/km²)	Source
Forest dominated landscapes					
Budongo (Uganda)	Semi-deciduous forest	1000 - 1600	1,620	1.8 - 1.9	[13]
Gombe (Tanzania)	Tropical forest mosaic	766 - 1623	1,495	2.5	[14]
Kahuzi Biega (Dem. Rep. Congo)	Montane rainforest	2030 - 2350	1,586	0.1	[15]
Kalinzu (Uganda)	Moist evergreen forest	1000 - 1500	1,150 - 1,400	2.8 - 4.7	[16]
Kibale (Uganda)	Semi-deciduous forest	1100 - 1600	1,395	2.4	[17]
Kibira (Burundi)	Montane rainforest	1600 - 2600	> 2,000	0.5	[18]
Nouabale-Ndoki (Republic of Congo)	Semi-evergreen forest	330 - 600	1,728	1.8	[19]
Nyungwe (Rwanda)	Montane rainforest	1600 - 2900	1,744	0.4	[20]
Odzala (Republic of Congo)	Semi-evergreen forest	300 - 600	1,957	0.3 - 0.4	[19]
Tai (Ivory Coast)	Lowland rainforest	100 - 400	1,800	0.8 - 1.8	[21]
Open vegetation dominated landscapes					
Fongoli (Senegal)	Savanna woodland mosaic	-	< 1,000	0.4	[22]
Haut-Niger (Republic of Guinea)	Savanna woodland mosaic	-	1,300	0.9	[23]
Issa Valley (Tanzania)	Savanna woodland mosaic	900 - 1800	1,200	0.3	[24]
Mbam-Djerem (Cameroon)	Forest - woodland - savanna mosaic	650 - 930	1,900	0.3	[25]
Mt. Assirik (Senegal)	Savanna woodland mosaic	100 - 300	954	0.1	[26]

61

62   Mahale Mountains National Park (MMNP) is the largest national park where chimpanzees

63 in Tanzania reside and is a refugee that offers protection from common threats to them (e.g.,

64 poaching) and their habitat (e.g., settlement expansion) within the GME. While one community

65 in the park (M group) has been the focus of long term study for decades [27], a comprehensive

66 survey of MMNP has never been conducted, resulting in a lack of baseline data on chimpanzees

67 distribution and density in the park . These data are crucial given the present threat of isolation and

68 increased human disturbance the park faces from road development and growing human

69 settlements along its periphery, which could impact animal movement and increase human

70 encroachment [28]. Furthermore, an investigation into the drivers of chimpanzee density and

71 abundance in the region is lacking. Previous short and geographically restricted surveys in the park

72 have revealed variation in chimpanzee density between some areas. However, they did not

73 consider the effect of ecological factors [29], such as dominant vegetation type or species diversity

74 – known to be important drivers in other populations [5,30]. MMNP is an ideal landscape to

75 address this topic as variation in density may arise from its immense topographic and vegetative

76 heterogeneity. Moreover, while numerous studies have contributed on the subject of chimpanzee

77 distribution and density patterns [7,19,23,25], few have quantitatively assessed density correlates

78 for those living in savanna-mosaics [30,31], a habitat type often deemed marginal for the species

79 with distinct ecological challenges (e.g., thermoregulatory stress, hydration, low fruit abundance)

80 [31,32].

81   Animal species naturally exhibit variability in their densities in response to differences in

82 ecological variability (e.g. vegetation, topography, predation) [33,34]. Food availability, generally

83 influenced by vegetation structure and composition, is one of the most fundamental influences on

84 species density, distribution, and ranging (rodents [35]; primates [36]; birds [33]; reptiles [37]),

85 and chimpanzees are no exception [38]. As a highly frugivorous species, chimpanzees depend on

86 the presence and distribution of fruiting trees for feeding [39,40], as well as suitable trees for

87   constructing nightly nests [41–43]; thus, resource abundance, especially that of fruit-bearing trees,

88   can be used to predict chimpanzee density [44]. In particular, the abundance of fruit trees from

89   species that provide food during periods of fruit scarcity can be one of the most critical factors

90   influencing and limiting chimpanzee density [38] as it helps reduce the intensity of seasonal shifts

91   in fruit availability [45,46]. Similarly, floristic diversity can have a strong effect on chimpanzee

92   density [5,38,47] when it helps chimpanzees sustain their dietary requirements throughout the year

93   [38,48]. For chimpanzees living in marginal habitats that often have lower overall fruit abundance

94   and diversity and likely face more frequent or pronounced periods of resource scarcity [5],

95   chimpanzee density may be more closely related to diversity than to overall food abundance

96   [32,49]. Yet, the influence of floristic diversity on chimpanzee density varies across sites, even

97   between different savanna-mosaics [30,49], and highlights the need for more data on this topic.

98   Aside from the abundance and diversity of fruit trees, increased food patch size (e.g., tree size)

99   may also help alleviate constraints from food scarcity in resource-poor areas [50], although this

100   topic remains unexplored. The incorporation of fine-scale vegetation data into density models can

101   assess the potential mechanisms driving variation in chimpanzee density [5,31,38,51].

102   Chimpanzees do not uniformly utilize the landscape in time or space [52,53]; thus, the

103   inclusion of ecological factors related to land cover and topography, often obtained from remote-

104   sensing data, is valuable for modeling species density and distribution [51,54]. In open, dry

105   landscapes, chimpanzees disproportionately rely on riparian forests for food [40,55], nesting

106   [26,56], and shade [53]. Previous research in the GME suggests an association between forest

107   cover and chimpanzee density[57]. Elevation and slope can also be important predictors of

108   chimpanzee distribution and habitat suitability [7,51,58,59] because they can influence

109   chimpanzee nest site selection [56,60]. However, other potentially useful and readily available

6

110 topographical variables [61] remain understudied. For example, topographic heterogeneity could

111 be valuable for predicting chimpanzee density and distribution because of the positive relationship

112 between topographic heterogeneity and species richness [62,63], as well as other factors like slope

113 [61]. While chimpanzees likely respond to the availability of essential resources (e.g., food, water,

114 nesting materials) in space and time rather than biophysical variables like percent forest cover or

115 topographic heterogeneity, these variables can serve as insightful proxies. By incorporating both

116 fine and broad-scale biotic and abiotic metrics within density models, we can better understand the

117 ecological factors associated with chimpanzee density, as well as the value of remotely sensed data

118 necessary for large-scale predictive models.

119   This study examines the relationship between chimpanzee density and specific vegetative

120 characteristics and topographical features across the MMNP landscape. To evaluate possible

121 associations, we employed a hierarchical distance sampling (HDS) approach [64] that allows for

122 explicit consideration of covariate influence on both the density and detection processes to more

123 precisely model chimpanzee density patterns [65]. We predicted chimpanzee density to be higher

124 in areas with 1) greater fruit abundance and diversity, 2) high topographic heterogeneity, and 3)

125 more evergreen forested vegetation (includes all available forested vegetation types, i.e., riparian,

126 lowland, and montane forests). We aim to provide baseline data on chimpanzees and their habitat

127 (e.g., an evaluation of resource availability) in MMNP and fixed sites widely distributed across

128 the park that can help future efforts to monitor, identify, and evaluate potential changes. MMNP

129 is arguably the most critical area for chimpanzee conservation in Tanzania because of its size,

130 location, and protective status; therefore, it is imperative that an assessment of this endangered

131 species in the park (spatially) extends well-beyond the long-term research of a single community.

132 Additionally, as a protected area, data from MMNP can serve as a point of comparison and provide

133   insight for what to expect in the absence of human activity in the GME. For extra-park

134   chimpanzees that face a more perilous future than those living inside park boundaries, we hope

135   these data will allow for greater understanding of population shifts that may arise from future

136   environmental change and better inform conservation bodies in their determination of valuable

137   chimpanzee habitat outside of national parks.

138

Methods

Study area

141   MMNP covers 1,517 km^2 of rugged terrain along Lake Tanganyika in western Tanzania (Fig 1).

142   Part of the Albertine Rift, MMNP is home to numerous endemic and threatened plant and animal

143   species [66]. The park also hosts the Mahale Mountains Chimpanzee Research Project, which

144   along with the Gombe Stream Research Center based in Gombe NP 180km north, is one of the

145   longest-running chimpanzee research projects in Africa, now in its 7th decade [14,27].

146   MMNP is a mosaic of closed (i.e., forest) and open (e.g., woodland, grassland) vegetation

147   types [67]. Although the northwestern region contains large blocks of continuous evergreen forest,

148   the park is otherwise dominated by miombo and bamboo woodlands and intersected by strips of

149   riparian forest. Elevation in the park ranges from 780 – 2,460 m above sea level, and the park

150   exhibits two distinct seasons: a rainy season from October to mid-May, and a dry season, from

151   mid-May to September.

152

153   **Fig 1. Map of MMNP and its position within the GME and Tanzania. The 13 survey sites**

154   **visited during the current study are indicated with their letter name. Land cover**

155 **classification courtesy of Holly E. Copeland (University of Wyoming) who sourced the data**

156 **from USGS/NASA Landsat imagery.**

157

158 Study design

159 We collected data in MMNP from March 2018 – January 2019 along 102 transects at 13 survey

160 sites (sequentially labeled sites A – M). Considering feasibility and the average community home

161 range sizes previously reported in MMNP [12], we determined a survey site size of 25 km^2. To

162 facilitate the random site selection, we superimposed a 5 x 5 km grid over our study area, MMNP,

163 and randomly selected grid cells (sites) using QGIS software [68]. Within each site, line transects,

164 each 1 km long, were positioned according to a random start point and spaced $\geq$1 km apart.

165 Transects were orientated in a north to south direction, perpendicular to the drainage system.

166   We obtained all necessary permits from the Tanzania Wildlife Research Institute, Tanzania

167 Commission for Science and Technology, and Tanzania National Parks and complied with all

168 relevant regulations while conducting research within a national park and on a protected species.

169

170 Distance sampling

171 Chimpanzees build nests daily for rest and sleep, allowing researchers to indirectly estimate

172 chimpanzee density using a standing nest crop count method [13]. Walking at a pace of 1 km/hour,

173 survey teams recorded all chimpanzee nests observed along transects. To help us evaluate habitat

174 conditions and the level of human encroachment in the park, we also recorded observations of

175 human presence and activity (e.g., cut trees, snares). Following the standardized distance sampling

176 protocol [69], we recorded the perpendicular distance between the center of each observation (e.g.,

177 nest) and the transect line using a Nikon Laser Rangefinder 550AS or measuring tape (for distances

178   <25m). For each observation, we recorded the GPS position, vegetation type, canopy cover (%),

179   understory cover (%), and slope (flat, mild, moderate, steep). Vegetation types included: montane

180   and lowland forests (forests not restricted to riparian zones), riparian forest (forests formed along

181   watercourses), miombo woodland (discontinuous canopy of deciduous trees dominated by

182   *Brachystegia* sp., *Julbernardia* sp., and *Isoberlinia* with grass understory), bamboo woodland

183   (woodland with bamboo dominated understory), bamboo thicket (dense bamboo stands with scarce

184   to no trees), wooded grassland (dominated by grasses with isolated shrubs and trees), grassland

185   (scarce to no woody plants), and swamp. Forests were distinguished as closed or open canopy,

186   with closed-canopy forests showing >50% canopy cover. We also recorded the tree species and

187   age class of each nest. Nest age class was determined according to the state of nest decay based on

188   leaf decomposition [70]: (1) leaves green and nest solid; (2) leaves wilted but nest solid; (3) some

189   leaves lost and nest structure disintegrating; and (4) only the nest frame and <5% of leaves

190   remaining.

191

Vegetation survey

193   In conjunction with our chimpanzee census, we conducted a vegetation survey at each survey

194   site with a trained botanist familiar with the plants of western Tanzania. The vegetation survey

195   followed a belt transect design that utilized the same transects as our chimpanzee survey. We

196   sampled five 100m x 5m plots, spaced 100m apart, along each transect. We measured and

197   identified all trees and lianas ≥10cm diameter at breast height. We also identified and recorded

198   vegetation type, canopy cover, and understory cover transitions continuously along transects to

199   assess the proportion of different vegetation characteristics along each transect.

200

Statistical analysis

Predictor variables

We determined predictor variable values at the transect level to correspond with our chimpanzee nest counts. Predictor variables derived from our vegetation survey included: forest cover (i.e., the proportion of forested habitat encountered along each transect) and several proxies of chimpanzee food availability: total basal area, mean basal area, and diversity of feeding tree species. We identified the feeding tree species that contributed to our predictors from published literature from three long-term field sites in Tanzania: Gombe [51,71], MMNP [39], and the Issa Valley [40]. While total basal area represents overall potential food abundance, mean basal area addresses the possible influence of tree size as a food patch [31,72]. These variables also correspond to nesting resources as chimpanzees in the GME prefer nesting in feeding species [41,43] and large trees [60]. We calculated tree species diversity using the Shannon diversity index that accounts for the richness, relative abundance, and evenness of species [73]. We also included topographical predictors using Shuttle Radar Topography Mission satellite imagery (30 m resolution; http://earthexplorer.usgs.gov): elevation; steep slopes (proportion of slopes along each transect ≥20 degrees) [59]; topographic heterogeneity. We used terrain ruggedness to determine the degree of topographic heterogeneity, reflecting the amount of local elevation change according to the mean difference in elevation between neighboring raster cells [61]. We also included survey site as a nominal covariate to account for potential variation in nest detectability or density among sites that cannot be explained by the other variables included in our models [74].

We z-transformed all quantitative covariates to ease model convergence and achieve estimate comparability [75]. We examined the collinearity of predictor variables at the outset of our analysis using Pearson product- moment correlation coefficient and Spearman rank

11

224   correlation coefficient. We considered variables highly collinear and potentially problematic when

225   coding our models if test statistics were ≥ 0.7 or ≤ -0.7 [76]. We subsequently prevented highly

226   collinear covariates from occurring in the same model [75]. We then constructed a global model

227   of the final covariates, from which all future models were based (Table 2).

228   Additionally, we evaluated the overall variability of ecological factors across sites by

229   conducting a series of Kruskal-Wallis non-parametric analysis of variance (ANOVA) tests.

230   Moreover, we assessed the relationship between topographic heterogeneity and other ecological

231   characteristics, such as overall species richness and slope, using p-values obtained from the

232   Pearson correlation coefficient test in order to confirm whether the trends generally associated

233   with topographic heterogeneity also exist in MMNP (e.g., positive correlation between

234   topographic heterogeneity and slope). We set the alpha level to identify p-value significance at

235   ≤ 0.05 for all tests.

236

237   **Table 2. The hypothesized relationship between chimpanzee density and the covariates used**

238   **to model the detection and density processes within our HDS models. Covariate influence on**

239   **the detection and density of chimpanzees were examined during model building and are**

240   **reported as positive or negative (+/-) or not available (n/a).**

Habitat variables	Variable effect	Hypothesized relationship with the detection and abundance processes
Detection covariates		
Survey site	n/a	Control for disparities that may arise from differences in the seasonal conditions experienced among sites.
Forest cover	-	Greater tree density and foliage can reduce detectability because of reduced light or obstructing/camouflaging nests.
Steep slopes	+	Steep terrain increases detectability as it leads to naturally-broken canopy [77].

Survey site	n/a	Representative of the variability in biotic and abiotic factors between sites given that each location is a discrete area sampled.
Elevation	n/a	Possible proxy for weather conditions [78] and vegetation [67] that influence habitat use.
Forest cover	+	Forests are disproportionately used in dry landscapes, offering food [40] and nesting [56] resources.
Total basal area	+	Higher values indicate a greater abundance of food sources related to both the quantity and size of feeding tree species.
Mean basal area	+	Larger trees are generally associated with greater fruit production.
Diversity	+	Higher feeding tree species diversity can reduce the incidence of fruit seasonality and potentially offer greater resource availability in time and space [79].
Steep slopes	+	Associated with suitable chimpanzee habitat [58,59] and nesting sites [60].
Topographic heterogeneity	+	Correlated with slope [61] and associated with topographical features that can influence vegetation [63] and may impact food and nesting resources.

241

Hierarchical distance sampling

243 We performed all analyses using R version 3.4.2 statistical software (R Core Team, 2017). We

244 included only nests aged 1-3 in our analysis as age four nests were considered decayed [13]. We

245 modeled observations of nests as a multinomial hierarchical coupled logistic regression [65],

246 whereby the regression modeling the state (i.e., nest density) process is conditional on the

247 regression modeling the detection (i.e., how animals are detected) process, accounting for

248 imperfect detection. We applied this framework using the function 'gdistsamp' in the R package

249 'unmarked' [80]. Following Buckland et al. [69], we defined a truncation distance of 52 m by

250 assessing the plotted distance frequency distribution and removing outliers from the dataset, which

251 provide little information towards estimating the detection probability. Continuous distances were

252 grouped into four-meter intervals to smooth heaping but retain detail. To describe nest abundance

253 at the transect level, we used a negative binomial distribution commonly used to describe count

254 variation in the presence of over-dispersion [65]. To verify the regression assumption of

255 independence, we tested for spatial autocorrelation using Moran's I test [76].

256   We first tested and compared the performance of different detection functions (half-norm,

257 hazard-rate) on our null model, retaining the detection function with the lowest Akaike Information

258 Criterion (AIC) [81]. Transect-specific covariates were then incorporated into the detection and

259 density sub-models using a log-link function. We selected our 'best' detection model via AIC

260 comparison and held this sub-model constant while we incorporated and compared density models.

261 Using a combination of stepwise regression and theoretical knowledge, we tested density models

262 and ranked them using corrected AIC (AICc) [81]. We evaluated the goodness of fit of the top-

263 ranked model using parametric bootstrapping, simulating 1000 datasets from the fitted model, and

264 defining a function that returned three fit-statistic (chi-square, Freeman-Tukey, sum of squares

265 errors). For parameter estimates, we employed a multimodel based inference approach where we

266 quantified the uncertainty that each model is the best model through the computation of model

267 weights. We report averaged-model predictions based on models with an AICcΔ<4 as these

268 models have greater empirical support [81]. We also calculated predictor weight on a scale of 0-

269 1 to estimate each covariate's relative importance by summing the AICc weights for each model

270 in which that variable appears [82] and report the significance of predictors for the top-ranked

271 model [82].

272

Conversion of nest density to chimpanzee density

273

274 We used correction factors to convert estimates of nest density to chimpanzee density (ind/km^2)

275 by incorporating nest production and decay rates (*Chimpanzee density = nest density / (nest*

276 *production rate * mean nest decay rate*) [83]. We used a nest production rate of 1.1 nests/day from

277 previous research [13], calculated according to the number of nests built per day, the proportion

278 of nest builders, and re-use. For decay rate, we utilized all available decay rates from the GME

279 [84–86], computed following Plumptre et al. [70]. As factors such as weather and topography

280 affect nest decay [87], we determined the decay rate of each survey site according to location

281 (lakeshore vs. inland), sampling season (e.g., dry vs. wet), and the proportion of open vs. closed

282 vegetation types. As climate conditions change as one travels inland from the lake, we applied

283 decay rates based on lake proximity. All sites within 6 km of the shoreline were considered to be

284 within the lakeshore zone as this area encompasses lakeshore decay rate study locations [84,85].

285 Lakeshore decay rates estimate 49 (dry season) and 76 days (wet season) for nests in closed

286 vegetation and 126 days for nests in open vegetation (wet season) [84,85]. Unfortunately, no

287 lakeshore decay rate is available for open vegetation during the dry season, so, we calculated a rate

288 of 167.9 days by applying the proportional difference in decay rate observed between seasons in

289 inland open vegetation (33% increase) to the lakeshore wet season rate. For inland sites, we applied

290 decay rates estimated by Stewart et al. [86] from the Issa Valley: 83.3 (dry) and 118.9 days (wet)

291 for closed vegetation; 185.5 (dry) and 139.2 (wet) for open vegetation.

292

Results

294 Transects passed through a mixture of vegetation types and consisted of 20% forested (closed-

295 canopy 5%, open-canopy 15%) and 80% open (miombo woodland 30%, lowland bamboo

woodland 30%, grassland/swamp 14%, bamboo thicket 7%) vegetation (Fig 2). Closed-canopy

forests showed the greatest diversity, density, and basal area of trees ≥10cm DBH, although, for

feeding tree species, miombo woodlands displayed greater species richness and diversity (Table

3). We observed minimal human presence and activity throughout the park (0.10 observations/km

vs. 14.5 observations/km for wildlife), with observations recorded along only 6% of transects and

at five sites. Most observations revealed only human presence (e.g., campsites, trails) and did not

indicate a specific activity, although there was some direct evidence of wildlife poaching (0.01

snares/km).

Fig 2. Graph showing vegetation type percentages observed at each site. We distinguish

forests according to canopy cover (open forest <50% coverage; closed-canopy ≥ 50%).

"Other" includes non-wooded vegetation types (e.g., grassland, swamp).

Table 3. Overview of important vegetation types found in MMNP and utilized by

chimpanzees for nesting.

	Open-canopy forest	Closed-canopy forest	Miombo woodland	Bamboo woodland
All species				
No. of species	95	95	149	19
Diversity (Shannon Index)	3.5	4.7	3.8	2.4
Tree density/ha	76	237	190	5
Basal area/ha	4.9	14.5	3.8	2.4
Feeding species				
No. of species	40	52	56	10

Diversity (Shannon Index)	3.0	3.6	5.3	1.3
Tree density/ha	38	122	118	3
Basal area/ha	2.7	6.6	5.6	0.1

311

312   We recorded 335 nests, but following truncation and the removal of age four nests, which

313   were considered decayed according to our definition, only 263 nests were included in our analysis

314   [70]. Of these nests, 34% were found in forests (closed-canopy 8%, open-canopy 26%) and 66%

315   in open vegetation (miombo 46%, bamboo 19%, wooded grassland 1%). Nests were

316   disproportionately observed on steep slopes ($\geq$20 degrees), with 56% of nest locations found on

317   steep slopes even though steep slopes accounted for only 14% of transect terrain. We found nests

318   in >33 tree species, but we observed the majority (51%) in only four species: *Julbernardia*

319   *globiflora*, *Brachystegia spiciformis*, *B. bussei*, and *Xylopia parvaiflora*. Feeding tree species

320   accounted for 78% of the nesting species utilized by chimpanzees in MMNP and 94% of all

321   nesting trees we recorded. We identified at least 259 different species of trees during and

322   vegetation survey, of which 83 species are used for feeding by chimpanzees [39,40,51,71] (S1

323   Table).

324   We found that steep slopes and topographic heterogeneity were highly correlated (r_p < -

325   0.93, df = 100, P < 0.001) and coded models accordingly. We also found a significant positive

326   correlation between topographic heterogeneity and overall tree species richness (r_p = 0.20, df =

327   100, P = 0.05), but not feeding tree species (r_p < 0.001, df = 100, P = 0.98). Non-parametric

328   ANOVA tests revealed significant differences among sites for all ecological characteristics

329   considered in our models (*elevation*: $F_{2,\,12}$ = 80.6, P < 0.001; *forest cover*: $F_{2,\,12}$ = 59.8, P < 0.001;

330   *total basal area:* $F_{2,\,12}$ = 72.5, P < 0.001; *mean basal area*: $F_{2,\,12}$ = 46.1, P < 0.001; *diversity*: $F_{2,}$

17

331 $_{12}$ = 53.0, P < 0.001; *steep slopes:* F$_{2, 12}$ = 30.1, P = 0.003); *topographic heterogeneity:* F$_{2, 12}$ =

332 41.0, P < 0.001) (Table 4). Moran's I test confirmed the independence of our samples, showing

333 no spatial autocorrelation between nest counts (Moran's I = 0.04, p = 0.02).

334

335 **Table 4. Chimpanzee density estimates with 95% confidence interval (CI) and mean**

336 **covariate values for each sample site.**

Site	Topographic heterogeneity	Forest cover	Total basal area (m²/ha)	Mean basal area (m²/ha)	Shannon diversity index	Chimpanzee density (ind/km²)	Chimpanzee density (ind/ km²) 95% CI
A	9.13	57%	10.60	0.05	2.00	3.43	1.36 - 8.67
B	7.23	86%	11.91	0.07	2.13	3.24	1.23 - 8.74
C	4.62	42%	7.22	0.04	2.34	0.54	0.30 - 0.97
D	3.93	2%	6.89	0.05	1.22	0.10	0.06 - 0.20
E	3.09	2%	4.51	0.04	1.75	0.08	0.04 - 0.14
F	5.46	4%	6.52	0.07	1.56	0.20	0.12 - 0.32
G	5.51	11%	1.42	0.06	0.97	0.11	0.06 - 0.21
H	4.44	13%	1.10	0.04	1.33	0.09	0.05 - 0.16
I	3.57	15%	3.27	0.04	1.63	0.09	0.05 - 0.16
J	5.55	5%	0.48	0.01	1.35	0.11	0.06 - 0.20
K	7.12	23%	2.98	0.04	1.39	0.39	0.23 - 0.65
L	5.79	10%	5.31	0.06	1.89	0.34	0.22 - 0.53
M	4.04	4%	7.47	0.07	1.95	0.21	0.12 - 0.36

337

Covariate influence on density and detection

The hierarchical modeling approach that we applied allowed us to derive a model that performed better than null models that did not consider covariate effects on detection or density. The results of our bootstrapped goodness of fit test confirmed that our top-ranked model exhibited good fit with our data (Chi-square: $x^2 = 0.26$; Freeman-Tukey: q = 0.23; sum of squares: SSE = 0.27). Of the models we tested, only eight models contributed towards the cumulative AICc weight (Table 5), and predictor weights differed considerably in their relative importance and contribution towards density estimates: topographic heterogeneity (0.98), total basal area (0.63), diversity (0.55), forest cover (0.53), mean basal area (0.16), steep slopes (0.03), elevation (0), site (0). Covariates included in the top-ranked model exhibited a significant effect on chimpanzee density (topographic heterogeneity: $p < 0.001$; *total basal area*: $p < 0.001$) (Fig 3). Our results estimate chimpanzee density at 0.23 ind/km^2 (0.16 – 0.35 95% CI) across all MMNP, but estimates varied significantly among sites ($F_{2, 12} = 58.23$, $P < 0.001$), ranging from 0.09 – 3.43 ind/km^2.

Table 5. The weight and AICc value of each model contributing to our chimpanzee density predictions. All models include our best detection sub-model (p) but vary by density sub-model (λ).

Model	AICc	Model weight	Cumulative weight
λ(heterogeneity[a] + TBA[b]) p(site)	751.44	0.21	0.21
λ(heterogeneity + forest cover + diversity[c]) p(site)	751.89	0.17	0.38
λ(heterogeneity + forest cover + TBA) p(site)	752.00	0.16	0.53
λ(heterogeneity + TBA + diversity) p(site)	752.37	0.13	0.66

λ(heterogeneity+ MBA[d] + diversity) p(site)	752.52	0.12	0.79
λ(heterogeneity + forest cover + TBA + diversity) p(site)	753.33	0.08	0.87
λ(heterogeneity + forest cover) p(site)	753.95	0.06	0.93
λ(heterogeneity + forest cover + TBA + MBA + diversity) p(site)	754.6	0.04	0.97

355   [a] Topographic heterogeneity

356   [b] Total basal area

357   [c] Shannon diversity index

358   [d] Mean basal area

359

360   **Fig 3. Predictor variable plots from the top-ranked model of nest density**

361   (a) Plot of coefficient estimates (circles) presented with 95% CI (vertical lines), confirming their

362   significance (because CI does not cross zero); (b) response curves of predicted nest density against

363   topographic heterogeneity and (c) total basal area.

364

Discussion

366   MMNP is home to one of the longest-running research studies of any single chimpanzee

367   community (Nakamura et al. 2015). Yet, in>50 years of research and 35 years since the park's

368   creation, there was no park-wide census of one of its most charismatic speciesuntil the current

369   study. Given the park's protective status, limited human encroachment, and that it's located within

370   the GME where the greatest number of Tanzania's chimpanzees occur, MMNP is a key area for

371   chimpanzee conservation. Chimpanzees were present throughout the ecologically diverse park

372   and we found that characteristics related to food and nesting resources are strongly associated with

373   chimpanzee density, resulting in significantly variable densities that ranged from 0.09 – 3.43

374   ind/km^2 among 13 sites.

375

Vegetation type

377   Our results are consistent with those from other chimpanzee surveys (see Table 1), showing

378   that across the savanna-woodland mosaic of MMNP, chimpanzees exist at a relatively low density

379   of 0.23 ind/km^2. Like other sites dominated by open vegetation [23,25,30], forests are an important

380   vegetation type in MMNP. Our results show that chimpanzees disproportionately use forests for

381   nesting and that there is a positive association between forest cover and chimpanzee density. Sites

382   located in the park's northwestern region exhibit the most forest cover and the highest chimpanzee

383   densities (e.g., site B = 3.24 ind/km^2), with densities 6 – 38 times greater than woodland dominated

384   sites that characterize the remainder of the park. These findings support observations from

385   previous researchers that this region of MMNP hosts a high density of chimpanzees [29], which

386   they largely attributed to high food availability [88]. Our study provides empirical support for this

387   assertion by demonstrating that the northwest region hosts the greatest basal area of feeding

388   species. Furthermore, Site B coincided substantially with the home range of M-group. Based on

389   the direct identification of community members, M-group density has varied over the years,

390   ranging from 2.6 – 3.7 ind/km^2 from 1996 – 2012 [12] and 3.5 ind/km^2 during the study period.

391   Similarities between these independent metrics of density validate our methodology and analysis

392   for estimating chimpanzee density.

393   In a primarily open landscape, non-forested vegetation types inevitably provide crucial

394   resources for chimpanzees (Fig 4). Regionally, chimpanzees derive much of their food [40,55] and

395   nesting species [41,43] from miombo woodlands, and several results from our study indicate the

396   value of this vegetation type in MMNP. For example, chimpanzee density seems to fluctuate with

397   the availability of miombo woodland when survey sites have the same amount of forest cover, e.g.,

398   site G (10% forest, 0% miombo, 0.11 ind/km^2) vs. site L (11% forest cover, 34% miombo, 0.34

399   ind/km^2). Additionally, chimpanzee density was positively associated with the basal area and

400   diversity of feeding tree species, reflecting the importance of species-rich habitats like miombo

401   woodlands that display a comparatively high diversity and abundance of feeding tree species. This

402   contrasts findings from the savanna-forest mosaic of Lagoas de Cufada Natural Park (Guinea-

403   Bissau), where chimpanzee nest abundance was negatively correlated with the basal area of food

404   plant species that is indicative of dense forests. The relatively greater importance of basal area than

405   forest cover showcases the necessity of resources across the landscape. These results are likely

406   driven by the highly seasonal nature of the GME [27,40,89] that results in the variable use of

407   different vegetation types over the year. Previous research describes chimpanzee reliance on

408   woodlands during the dry season when forest fruits are less abundant [40]. Moreover, the density

409   of feeding tree species in MMNP (5.3 m^2/ha, SD = 3.5) is low in comparison to other chimpanzee

410   sites where similar data are available, e.g., Kibale National Park (Uganda) (7.6 – 9.9 m^2/ha for top

411   10 fruit species only) [5], and likely compels chimpanzees to seek resources wherever available.

412   Therefore, areas with a diversity of vegetation types (Fig 4) capable of supplying a greater

413   abundance and diversity of resources are likely advantageous for chimpanzees in MMNP.

414

415   **Fig 4. Selection of vegetation types observed in MMNP, illustrating its mosaic landscape.**

416   (a) lowland closed canopy forest; (b) miombo woodland; (c) grassland; (d) lowland bamboo

417   woodland (Photos courtesy of A.C.).

418

Fruit availability

Our results support similar findings from other locations [19,38,90] that floristic differences between sites play a pivotal role in density variability. In addition to the significant, positive effect of total basal area, the mean basal area of feeding trees had a positive, albeit relatively weak, effect on chimpanzee density in our models and demonstrates the value of large food trees, with presumably greater amounts of food, for chimpanzees living in a primarily open landscape. However, this finding may also be influenced by chimpanzee preference for nesting in large trees, as shown by previous research conducted in the GME [43,60]. Our analysis also confirmed the importance of floristic diversity for this species in MMNP, with our models demonstrating a positive correlation between chimpanzee density and feeding tree species diversity. In addition, our results showed that topographic heterogeneity, the most important predictor in our models, adheres to the positive trend generally shown between heterogeneity and species richness [62]. This suggests the importance of species-rich areas for chimpanzees, which may also provide diverse resources from food items not analyzed during this study (e.g., herbaceous growth, insects). The importance of diversity for chimpanzees in MMNP, compared to other chimpanzee sites, may be the result of both necessity and functionality. Resource diversity may be more valuable for chimpanzees living in low fruit abundance areas like MMNP, where an ability to diversify their diet allows individuals to compensate for low food density and maintain their nutritional needs. Potts et al. (2011) examined two adjacent communities in Kibale and found that Kanyawara chimpanzees (who live at a lower density than their Ngogo neighbors) demonstrate greater dietary diversity than Ngogo chimpanzees that live in an area with a significantly greater abundance important food species. For frugivorous animals, floristic diversity is advantageous when it reduces the fluctuation of fruit availability across seasons [90]. Thus, a diversity of plants

23

442   that all produce fruit simultaneously is not functionally equivalent to species diversity that helps

443   diminish fruit scarcity, e.g., via asynchronous fruiting [38]. That MNNP has comparatively low

444   food availability likely explains the importance of feeding tree species abundance, size, and

445   diversity towards chimpanzee density. Future research that includes an investigation into the

446   phenology of chimpanzee food resources is necessary to evaluate if and how chimpanzee density

447   shifts with the availability of different resource functional classes (e.g., fallback food).

448

Nesting trees

450   The ecological characteristics of sleeping sites inherently drive our assessment of chimpanzee

451   density patterns in MMNP due to our use of chimpanzee nests for our analysis. The significant

452   correlation between total basal area and chimpanzee density is, therefore, likely related to nesting

453   resources and not only food. In the savanna-woodland mosaic of MMNP, where tree density is

454   low compared to forest-dominated sites, chimpanzees may strategically utilize feeding species.

455   Nesting in feeding trees may help individuals reduce travel costs and energy expenditure [91] and

456   defend key resources from frugivorous competitors [42]. Likewise, as topographic heterogeneity

457   is positively correlated with slope, the significance of this variable in our models is likely partially

458   driven by our finding that chimpanzees in MMNP prefer to nest on steep slopes. Chimpanzee

459   preference for nesting on steep slopes is unlikely to be the byproduct of where preferred nesting

460   trees are located since most trees from nesting species (69%) were not found on steep slopes.

461   Instead, a preference for nesting on steep slopes may reflect an alternative motivation, such as

462   vocal communication [92], or predator defense as steep slopes may provide a better view of the

463   surrounding habitat and taller trees [56,60]. Large carnivores, such as leopards (*Panthera pardus*)

464   and lions (*P. leo*), are found across MMNP (Chitayat, unpublished data) and the GME [93], and

465   are a well-documented threat to chimpanzees [94,95]. Yet, steepness was a relatively unimportant

466   predictor in our models (predictor weight = 0.03), especially in comparison to topographic

467   heterogeneity, whose association with density extends beyond chimpanzee preference for nesting

468   on steep slopes. Research regarding the impact of predation pressure on chimpanzee density and

469   distribution is needed for greater clarification. Future models could benefit from the incorporation

470   of additional ecological predictors like predator density and other factors that may impact sleeping

471   site selection, such as proximity to water sources [56] and microclimate [86]. Moreover, because

472   our research was limited to one visit per survey site, we could not assess the seasonal effects often

473   reported to influence chimpanzee nesting patterns, habitat use, and ranging within the GME

474   [12,40,43,56]. Future research would benefit from collecting data during both the wet and dry

475   seasons to determine if the patterns we observed in this study are consistent across the annual

476   cycle.

477

478   # Conclusions

479   Our study offers the first comprehensive density data on chimpanzees within a key conservation

480   area in Tanzania. Our results show that survey site estimates are highly variable and dependent on

481   the to ecological conditions of the site, with topographic heterogeneity, forest cover, and food

482   availability demonstrating positive associations with chimpanzee density across the MMNP

483   landscape. With this information, conservation and management bodies are better equipped to

484   identify and prioritize suitable chimpanzee habitat within the GME. For instance, based on our

485   finding that site-wide food availability is more important than forest cover availability, we

486   recommend that conservation practitioners take a landscape approach that considers the

487   importance of species-rich habitats and overall habitat diversity, particularly the availability of

488   miombo woodlands. Moreover, our data do not assess the full extent of these chimpanzees' range

489   but instead, where they sleep, which can be up to nine km from where they range during the day,

490   as observed at Issa Valley (personal communication). Thus, we recommend that conservation

491   practitioners consider other chimpanzee habitat use indicators, e.g., travel paths [96], habitat

492   connectivity [59], to encapsulate the habitats necessary for their continued survival fully.

493   Outside the park, the destruction and degradation of habitat from human activities threaten

494   chimpanzee viability across western Tanzania by altering habitat composition and availability and,

495   consequently, chimpanzee resources and connectivity [54,59,97]. This threat is compounded by

496   land conversion for agriculture that often occurs close to rivers where riparian forests are found.

497   Additionally, while we are encouraged by the limited anthropogenic activity we observed in

498   MMNP, present threats just outside the park (e.g., road development, urban expansion, and

499   growing human population size) that place even protected areas at risk [9], threatening them with

500   human encroachment and eventual isolation. Additionally, the SARS-CoV-2 pandemic may

501   exacerbate conservation threats if it results in reduced funding for protected areas and an increase

502   in poverty that places greater pressure on the park [98]. The pandemic's associated illness

503   (COVID-19) also brings into sharper focus the risk of disease transmission our closest living

504   relatives face when living in close proximity to humans. To track potential changes in chimpanzee

505   density and their habitat, we recommend re-visiting MMNP survey sites, and extra-park locations,

506   at regular intervals (at least every five years) in accordance with Tanzania's national chimpanzee

507   conservation action plan [99]. We hope our results from MMNP can serve not only as a baseline

508   for MMNP but a point of comparison for the region to help researchers identify the impacts of

509   human activities more precisely outside of the national park. Chimpanzees are a resilient species

510   and can persist successfully in human-modified landscapes [26,52,57] when they are not directly

511   exploited through hunting and appropriate conservation actions are taken to promote their

512   longevity [100]. Through continued monitoring efforts and the development of well-informed

513   management strategies that do not only *react* to population declines but adequately anticipate

514   population vulnerability, we can hopefully ensure the long-term persistence of chimpanzees in the

515   GME and Tanzania.

516

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792

Supporting information

S1 Table. Feeding species recorded in MMNP during our vegetation survey and identified

from previous literature from Tanzania: M = Mahale [39]**; G = Gombe** [51,71]**; I = Issa**

Valley [40]**.**

Legend:
- Greater Mahale Ecosystem
- Mahale Mountains National Park
- Survey sites
- Settlements
- Roads
- Woodland
- Forest
- Tanzania
- Gombe National Park
- Lake Tanganyika