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7   **Sleeping site selection by savanna chimpanzees in Ugalla, Tanzania**
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29   **Abstract** We examined sleeping site selection by chimpanzees (*Pan troglodytes*) in the

30   Ugalla savanna woodland area, western Tanzania, from 1994 to 2012. We established

31   488 km of line transects and recorded 379 chimpanzee beds within 30 m perpendicular

32   to the transects. Comparisons between 60 × 60-m quadrats containing new and recent

33   beds and the remaining quadrats without beds along the transects indicated that

34   evergreen forests comprised disproportionately more area in quadrats with beds than in

35   those without beds during the dry and rainy seasons, respectively. In Ugalla,

36   chimpanzees coexist with lions (*Panthera leo*) and leopards (*Panthera pardus*). They

37   may sleep in forests to reduce predation risk by these carnivores, as trees are dense and

38   the canopy is high and closed. The angle of slope was steeper in quadrats containing

39   beds than in those without beds during the dry season, whereas the angle was less steep

40   in quadrats with beds than in those without beds during the rainy season. Additionally,

41   fewer beds were found further from forests. The distance between beds and forests

42   during the dry season was shorter than that during the rainy season. Chimpanzees may

43   sleep in or near forests and on slopes because water pools in the valley forests along the

44   slopes during the dry season. Quadrats with beds were at a slightly higher altitude than

45   those without beds during the rainy season; however, the difference was not significant

46   during the dry season. The number of beds found in or close to feeding trees was not

47   related to the fruiting period. Sleeping site selection by chimpanzees may be affected by

48   predation pressure and water availability in the savanna woodland area.

49

50   **Keywords** chimpanzee, sleeping site, savanna woodland, predation pressure, slope

51   angle

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2

Introduction

Whereas many mammals use nests and return to them daily (Hansell 2005), most diurnal primates do not construct nests and instead choose a new sleeping site each day, often sleeping in trees or on rocks along a cliff (Anderson 1998; Kappeler 1998). In addition to the distribution of trees and cliffs available for sleeping, sleeping site selection can also be affected by predation pressure, feeding efficiency, water availability, and physical comfort at the site as well as by other factors such as territorial defense and communication with group members (Anderson 1998). Primates frequently sleep in locations that are not easily accessible by predators and where they can readily see and escape from predators (Reichard 1998; Von Hippel 1998). Primates also often sleep in or near their feeding trees to increase feeding efficiency (Chapman et al. 1989; Day and Elwood 1999; Furuichi and Hashimoto 2004; Hamilton 1982). Primates in dry habitats frequently sleep at sites close to sources of drinking water (Sharman 1982). They can also often be found sleeping at comfortable sites, e.g., warm shelters that are protected from strong winds and rain (Goodall 1962; MacKinnon 1974; Wada et al. 2007). Primates also choose sleeping sites to facilitate the defense of feeding sites and territory (Basabose and Yamagiwa 2002; Smith et al. 2007). Some primates change their sleeping sites to avoid endo-parasite infection (Hausfater and Meade 1982), whereas others reuse their sleeping site repeatedly (Ogawa and Takahashi 2003).

Chimpanzees (*Pan troglodytes*) usually construct a bed in a tree by bending branches (Goodall 1962). Unlike other animals, however, chimpanzees construct a new bed every night (Goodall 1962), although they sometimes reuse the bed site, bed tree, and specific location within the tree after a certain interval of time (Hernandez-Aguilar

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77   2006; Stewart et al. 2011).

78   Studies of chimpanzees in marginal and dry habitats are useful for understanding the

79   variety and flexibility of chimpanzee adaptation and for illuminating models of early

80   hominin behavioral ecology, as savanna woodland areas are considered to be similar to

81   the habitats of early hominins (Itani 1979; Moore 1992). Habitat use and sleeping site

82   selection by chimpanzees in dry habitats were studied in Senegal and Tanzania

83   (Baldwin et al. 1981; Pruetz et al. 2008; Hernandez-Aguilar 2006, 2009; Hernandez-

84   Aguilar et al. 2013; Ogawa et al. 2007; Stewart et al. 2011; Stewart and Pruetz 2013).

85   Because the Ugalla area in western Tanzania is the most eastern and one of the driest

86   and most open habitats of chimpanzees, many researchers have studied chimpanzees in

87   this area (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013; Ogawa et al.

88   2007; Piel and Moore 2007; Stewart et al. 2011; Stewart and Pruetz 2013). Previous

89   studies have revealed that chimpanzees in Ugalla frequently sleep in evergreen forests

90   (Ogawa et al. 2007; Stewart and Pruetz 2013), although they extensively use woodlands

91   as well (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013). However,

92   chimpanzees in Ugalla also frequently sleep on slopes and/or in hilly areas (Hernandez-

93   Aguilar 2006, 2009; Ogawa et al. 2007), similar to chimpanzees in other open habitats

94   in Tanzania (Kano 1972; Suzuki 1969) and at Assirik in Senegal (Baldwin et al. 1981).

95   However, it is not clear whether chimpanzees prefer hilly areas because they harbor

96   valuable habitats such as valleys and ridges between the valleys, or because they simply

97   prefer slopes. Furthermore, it is not known whether chimpanzees sleep along slopes

98   because more evergreen forests exist there, or whether they prefer slopes. Chimpanzees

99   may prefer slopes because predation risk might be lower if there is a paucity of grasses

100   that could deter hunting by terrestrial carnivores (Hernandez-Aguilar 2009). Moreover,

101 chimpanzees may choose slopes to facilitate vocal communication with chimpanzees in

102 other sub-groups, as sounds carry far in hilly areas (Piel and Moore 2007).

103   To investigate the factors affecting sleeping site selection by savanna chimpanzees,

104 we posed five non-mutually exclusive hypotheses.

105   First, we hypothesized that the distribution of sleeping sites would be affected by the

106 availability of sleeping trees. Unlike tropical rain forests, the savanna woodland habitat

107 contains evergreen forests, deciduous woodlands, and grasslands. Few trees are found in

108 grasslands, and fewer sleeping trees are available in deciduous woodlands than in

109 evergreen forests during the dry season, when some deciduous trees lose their leaves.

110 This first hypothesis predicts that chimpanzees frequently sleep in evergreen forests,

111 and that this tendency is conspicuous during the dry season.

112   Second, we hypothesized that chimpanzees would select sleeping sites that would

113 maximize predator avoidance (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al.

114 2013; Ogawa et al. 2007; Pruetz et al. 2008; Stewart and Pruetz 2013). Because

115 chimpanzees are larger bodied than most other primates, few studies have examined

116 predation pressure on chimpanzees (Baldwin et al. 1981; Pruetz et al. 2008;

117 Zuberbühler and Jenny 2002). Although few direct observations have been recorded,

118 however, Tsukahara (1993) documented that chimpanzees have been eaten by lion(s)

119 (*Panthera leo*) in Mahale, Tanzania, whereas others have been killed by leopards

120 (*Panthera pardus*) in Mahale, Tanzania (Nakazawa et al. 2013), in Tai, Côte d'Ivoire

121 (Boesch 1991; Zuberbühler and Jenny 2002), and in Lope, Gabon (Hanschell et al.

122 2005). Chimpanzees in the Ugalla savanna woodland area of western Tanzania coexist

123 with lions, leopards, and other potential predators such as hyenas (*Crocuta crocuta*) and

124 African wild dogs (*Lycaon pictus*) (Hernandez-Aguilar 2009; Ogawa et al. 2007). In the

125   Ugalla woodlands, trees are scattered, the canopy is open (Hernandez-Aguilar 2006,

126   2009), and tree height is no more than 25 m (Ogawa unpublished data); thus,

127   chimpanzees may have difficulty escaping into tall trees when they encounter predators

128   in this area. If the carnivore can climb trees, chimpanzees may have difficulty passing

129   through the branches. Thus, this vegetation can be dangerous for chimpanzees both in

130   the daytime and at night. In contrast to woodlands, forests may provide chimpanzees

131   with better sites for sleeping in terms of predator avoidance (Hernandez-Aguilar 2006,

132   2009; Ogawa et al. 2007; Stewart and Pruetz 2013) for reasons similar to those

133   pertaining to the grassland-forest mosaic area in Fongoli and Assirik, Senegal (Pruetz et

134   al. 2008). A comparison between trees with beds and trees without beds at Issa in Ugalla

135   showed that chimpanzees made their beds in taller trees with a larger diameter and

136   crown height and a higher first branch (Hernandez-Aguilar 2006, 2009; Hernandez-

137   Aguilar et al. 2013). Moreover, they chose trees with more leaves and thicker horizontal

138   branches (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013). A

139   comparison between Issa and Fongoli, where predator pressure is low, showed that

140   chimpanzees at Issa made higher beds at more peripheral places along horizontal

141   branches in the tree (Stewart and Pruetz 2013). These observations indicate that

142   chimpanzees chose safer trees and safer places within the trees. However, chimpanzees

143   may also choose a sleeping site in their home range, depending on the ranging pattern

144   for a particular day. Our second hypothesis also predicted that chimpanzees frequently

145   sleep in forests. However, fewer trees are available in woodlands because tree density is

146   low and some trees in woodlands are deciduous. Therefore, the question of which

147   vegetations chimpanzees select as their sleeping sites when controlling for the

148   availability of sleeping trees remains unanswered. Unlike the first hypothesis, our

149   second hypothesis predicts that chimpanzees would sleep in forests more frequently

150   than expected according to the number of available sleeping trees.

151   Third, we hypothesized that chimpanzees would choose their sleeping sites to

152   increase their feeding efficiency (Furuichi and Hashimoto 2004; Stanford and O'Malley

153   2008). Because one of the best choices to maximize the feeding efficiency is sleeping in

154   their feeding trees, chimpanzees may frequently make their beds in the tree of which

155   they eat fruits and other parts during the period, as observed in *Pan paniscus* in Lomako,

156   Zaïre (Democratic Republic of the Congo) (Badrian et al. 1981). When they do not

157   choose the feeding trees, they may sleep close to the trees. This hypothesis leads to the

158   expectation that chimpanzees sleep in or close to their feeding trees more frequently

159   than expected.

160   Fourth, chimpanzees are expected to select sleeping sites located close to water. This

161   hypothesis predicts that chimpanzees sleep in or near evergreen forests and on slopes,

162   because water is more likely to accumulate at the valley evergreen forests along the

163   slopes. The tendency to choose this environment should be more conspicuous during the

164   dry season in Ugalla, when most drinking water is restricted to the valley forests. The

165   second and the fourth hypotheses predicted that many beds are found in forests. Unlike

166   the second hypothesis, however, the fourth hypothesis predicts that, even when

167   chimpanzees sleep in woodlands, they sleep close to forests, especially during the dry

168   season.

169   Finally, we hypothesized that chimpanzees would choose comfortable sites for

170   sleeping (Koops et al. 2012), just as primates in temperate forests choose warm sites to

171   facilitate thermoregulation (Wada et al. 2007). In contrast to tropical rainforests in the

172   low flatlands of central Africa, savanna woodland areas are distributed in highlands and

173 hilly areas in eastern Africa. Because low altitude sites generally provide warmer

174 temperatures (Salomons 2001), although this remains to be tested in Ugalla, our final

175 hypothesis predicts that chimpanzees sleep at low altitude for thermoregulation.

176   To examine these five hypotheses, we conducted field surveys in the Ugalla area and

177 performed geographic information system (GIS) analyses. The main objectives of this

178 study were to examine habitat use by chimpanzees in terms of sleeping sites in the

179 Ugalla area, to examine factors affecting sleeping site selection, and to discuss the

180 adaptive strategies of savanna chimpanzees.

181

182 **Methods**

183

184 Study Area

185

186 *Location* Eastern chimpanzees (*Pan troglodytes schweinfurthii*) are distributed in the

187 DRC, Uganda, Rwanda, Burundi, and Tanzania (Inskipp 2005). In Tanzania, they are

188 distributed in western regions along the eastern shore of Lake Tanganyika (Kano 1972).

189 We studied wild chimpanzees in the Ugalla area, Tanzania (5°09'–5°57'S, 30°23'–

190 31°01'E). This area is 3352 km^2 with an elevation of 980–1712 m and is surrounded by

191 the Ugalla River to the east, the Malagarasi River to the north, Uvinza-Mpanda Road to

192 the west, and the Niamansi Basin to the south (Kano 1972; Hernandez-Aguilar 2006,

193 2009; Ogawa et al. 2007; Stewart et al. 2011; Fig. 1).

194

195 *Climate* Mean annual rainfall was 980 mm (750–1350 mm) from 1973 to 2005, as

196 recorded by the Tanzanian Directorate of Meteorology at Uvinza (5°06'S, 30°23'E), at

197   the northwest edge of the Ugalla area (Ogawa et al. 2007). No rain fell between June

198   and August during 16 of the 31 years recorded. Average monthly rainfall between May

199   and October was 21 mm, and that between November and April was 148 mm. Because

200   of this extended dry season and the local geographical and geological features (Sutton

201   and Roberts 1968), most streams in Ugalla dry up during the dry season. In the present

202   study, we divide the year into four equal periods, May–July, August–October,

203   November–January, and February–April, for phenology surveys, and we consider the

204   May–October and November–April periods to be the dry and the rainy seasons,

205   respectively. Hernandez-Aguilar (2006, 2009) recorded daily maximum and minimum

206   temperatures at the Issa site (05°25'S, 30°35'E) in the central Ugalla area from August

207   2002 to June 2003. These data showed that average daily maximum temperature was

208   highest in August (34°C) and lowest in November (28°C), whereas the average daily

209   minimum temperature was highest in January (17°C) and lowest in August (14°C).

210

211   *Geography and Vegetation* The Ugalla area consists two plains, plateaus in southwest

212   Ugalla and basins in northeast Ugalla, intersected by slopes with steep scarps and

213   valleys (Fig. 1). In Ugalla, there are three types of evergreen forests: small patchy

214   forests at springs under cliffs and escarpments in slopes; valley forests along flowing

215   water in slopes; and flat riverine forests in flatlands. While flat riverine forests are

216   narrow and not necessarily continuous along streams, as most streams in flatlands dry

217   up during the dry season, some of wide valley forests along slopes and patchy forests

218   under escarpments keep water until the end of the dry season (Itani 1979; Kano 1972;

219   Moore 1992, 1994; Ogawa et al. 1999, 2007). While the evergreen forests comprise

220   only 2% and grasslands comprise 12 % of the area (Ogawa et al. 2007), most of the

9

221   Ugalla area is composed of savanna woodlands locally called "miombo" woodlands

222   (Hernandez-Aguilar 2006, 2009; Itani 1979; Kano 1972; Moore 1992, 1994; Ogawa et

223   al. 2007). Unlike evergreen forests, the ground of savanna woodlands is covered by C4

224   grasses. The woodlands in Ugalla are dominated by deciduous trees of *Brachystegia* and

225   *Julbernardia*. Some trees in the woodlands lose their leaves during the dry season;

226   however, leaf loss and flushing patterns vary so that some trees have leaves throughout

227   the year.

228

229   Study Subjects

230

231   Chimpanzees live in a fission–fusion society of a multi-male and multi-female unit

232   group (community) and form temporal sub-groups (parties) (Nishida 1968). Previous

233   bed surveys have estimated that a total of 200–300 chimpanzees inhabit Ugalla, with a

234   density of 0.07–0.09 individuals/km^2 (Ogawa et al. 2007; Yoshikawa et al. 2008).

235   Genetic identification techniques have revealed that the size of a unit group at Issa was

236   a minimum of 67 individuals (Rudicell et al. 2011). At Nguye, the largest sub-groups

237   were composed of 14 individuals (determined by direct observation) and 23 individuals

238   (determined by bed count) (Ogawa et al. 2007). At Issa, the largest sub-group was 26

239   individuals (determined by bed count; Stewart and Pruetz 2013), suggesting that

240   chimpanzees in Ugalla formed small temporal sub-groups. Previous observations and

241   bed counts have estimated that chimpanzees at Nguye and Bhukalai in Ugalla form

242   temporal sub-groups of 2.0 individuals in the daytime and sub-groups of 5.0 individuals

243   at night during the dry season (Ogawa et al. 2007).

244

245 Data Collection

246

247 ***Study Periods*** Ogawa, Yoshikawa, and/or Idani stayed in the Ugalla area for a total of

248 480 days from 1994 to 2012: 324 days during the dry season in 1994–1997, 1999, 2001,

249 2003, 2007, 2008, and 2010–2012, and 156 days during the rainy season in 1995, 2007,

250 2008, 2010, and 2011. We conducted line transect bed surveys, and line transect and

251 quadrat vegetation surveys during certain portions of the study periods (Table 1).

252

253 ***Bed Survey*** We made line transects for bed surveys at the Mfuwazi, Nguye, Mufombosi,

254 Bhukalai (Mogogwesi), Mtongesi, Bukombe, Shangwa, Issa Basin, Nkondwe, and

255 Niamansi sites in the Ugalla area (Fig. 1, Table 1). Before each daily walk, we planned

256 the transect for that day. We usually made a round trip from our riverside base camp to a

257 plateau or a ridge between valleys. Using a 1/50,000 (1 cm to 0.5 km) map, a compass,

258 and a global positioning system (GPS), we walked on not only traditional paths but also

259 paths made by wild animals and off-paths along the nearly straight-line transects. When

260 we found chimpanzee beds along the line transects, we recorded 1) species of the bed

261 tree and 2) age class of the bed, categorized as new (all leaves were green), recent (some

262 leaves were green), old (all leaves were not green), and disintegrating (no leaves). We

263 also recorded 3) the perpendicular distance between the bed and the transect. We

264 measured this distance using the footsteps of local guides, and after 2007, using a laser

265 range finder (Nikon Laser 550AS).

266 We found chimpanzee beds when we were conducting surveys other than line

267 transects. For example, when we were following or looking for chimpanzees, we found

268 some beds along the non-transect walking routes. When we found beds along the line

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269   transect and went there, we sometimes found additional beds. In these cases, we

270   recorded the same information, with the exception of 3) the perpendicular distance

271   between the bed and the transect.

272   Because several chimpanzees typically sleep together, we defined a bed cluster as

273   ≥1 bed(s) located within 20m of the closest bed that appeared to have been made on the

274   same day. When we found beds, we stood at the center of the bed cluster, at the mid-

275   point between the edge of the beds, and recorded vegetation and location using GPS.

276   Prior to 2003, we did not record the locations of some bed clusters by GPS but instead

277   marked them on a 1/50,000 map.

278   We and our local assistants monitored two 5-km line transects at Nguye every 2

279   weeks for 1 year and recorded the presence of chimpanzee beds (Table 1). These two

280   transects were also used as line transects for phenology surveys (see the next section).

281

282   ***Vegetation Survey*** We conducted vegetation surveys within 50 × 50-m or 100 × 100-m

283   quadrats (2500 m^2 or 10,000 m^2) in a woodland and in a flat riverine evergreen forest at

284   Nguye and in a evergreen forest dominated by *Monopetalanthus richardsiae* at Bhukalai

285   (Ogawa et al. 2007; Table 1). Furthermore, we conducted vegetation surveys along

286   straight 2-, 4-, or 5-km line transects (4-m wide) at Mfuwazi, Nguye, Bhukalai,

287   Shangwa, Issa basin, Nkondwe, and Niamansi (Table 1). We established perpendicular

288   transects across the river. We recorded species name, DBH, and the height of all trees

289   that were ≥5 cm in DBH in the quadrats and transect areas. We used the line transects

290   for vegetation and bed surveys.

291

292   ***Phenology survey*** Because all chimpanzee beds in Ugalla were made in trees with

293   mature unwithered leaves, and 99.8% of the beds were in trees of ≥5-cm DBH (Ogawa

294   et al. 2007), we regarded these trees as available trees for sleeping. We and our local

295   assistants estimated the number of available trees by recording the leaves of each tree of

296   ≥5-cm DBH every 2 weeks for 1 year along two 5-km line transects at Nguye (Table 1).

297   We recorded the proportion of mature unwithered leaves: 0 (<5%), 25%, 50%, 75%, and

298   100%. Based on these data, we calculated the relative amount of leaves that were

299   available for sleeping using the following formula: (amount available leaves in forests) :

300   (amount available leaves in woodlands) = (area [m^2] × tree density [trees/m^2] × average

301   proportion of mature unwithered leaves in each tree [%] in forests) : (area [m^2] × tree

302   density [trees/m^2] × average proportion of mature non-withered leaves in each tree [%]

303   in woodlands).

304

305   Data Analysis

306

307   ***GIS Analysis by Vegetation and Topological Map*** We performed geographic

308   information system (GIS) analyses using satellite images and 1/50,000 topological maps.

309   We classified vegetation into four types: savanna woodland, evergreen forest, grassland,

310   and other (which included areas such as cultivated fields and human settlements). When

311   at a location where the vegetation appeared typical of the area, we recorded the

312   vegetation and its location (longitude and latitude) using GPS to generate a vegetation

313   map during the survey from 1999 to 2008. We recorded 349 points in savanna

314   woodlands, 122 points in evergreen forests, 80 points in grasslands, 30 points in

315   cultivated fields and human settlements. We generated a vegetation map of chimpanzee

316   habitats in Tanzania using ERDAS Imagine (LGGM) based on satellite images (ETM+)

317   recorded on 1 November 2001 and 22 May 2002. Using a 90-m SRTM digital elevation

318   model, we measured the angle (slope) of the ground. We also calculated the distance

319   between each bed cluster and the edge of the nearest forest whose area was $\geq$10,000 m^2,

320   using ArcGIS (ArcView 9.3.1) (ESRI).

321

322   ***Factor Analysis*** We used generalized linear mixed models (GLMM) and two-tailed,

323   non-parametric statistical tests at a significance level of $p = 0.05$. We used R software

324   2.13.10 (R Development Core Team, 2011) and SPSS Statistics 19. Data are shown as

325   means $\pm$ standard deviations (*SD*s) (minimum–maximum).

326   We analyzed conditions in the areas that contained one or more chimpanzee beds.

327   Along the line transects drawn on a map, we drew a 30 + 30-m wide belt transects. This

328   size was used because the detection rate of a chimpanzee bed was constant within 30 m

329   from the line transect. We further divided the belts into 60 m from the start to the end of

330   the transect for each day and drew 60 × 60-m quadrats (3600 m^2). We omitted the

331   fraction of the area at the end of the transect for each day as well as the overlapping

332   areas where the transects crossed. Some of the transects were excluded from the GIS

333   analysis because, prior to 2003, a GPS was not always taken on the walks, and the exact

334   transects could not be determined. We then calculated a) the proportion of the area

335   covered by forests, b) the average slope of the ground, and c) the average altitude in

336   each 60×60-m quadrat. For factor analyses, we conducted GLMM, for which we chose

337   a), b), and c) as predictor variables, the number of beds as a response variable, and a

338   Poisson distribution as the family of distribution. We also compared indices a), b), and

339   c) in quadrats that contained $\geq$1 bed and in quadrats without beds.

340   Along the two 5-km bed and vegetation line transects at Nguye, we established a 30

341   + 30-m wide belt, upon which we overlaid 166 60 × 60-m quadrats. We compared the

342   number of chimpanzee feeding trees within the transects (4-m wide) in quadrats with

343   beds with those in quadrats without beds during each period.

344

345   **Results**

346

347   Bed Distribution and Bed Site Condition

348

349   We recorded a total of 1512 beds in 491 bed clusters, including 379 beds in 172

350   clusters within the quadrats (<30 m from the line transects) and the remaining 1133 beds

351   in 319 bed clusters outside of the quadrats and along non-transect walking routes. All

352   beds were located in trees, and no beds were found on the ground.

353   Along the line transects, we drew 8126 quadrats, for a total analysis of 487.6 km of

354   belts in 29.3 km^2. Because the quadrats were individually hand drawn on the map, the

355   area of each quadrat was not exactly 3600 m^2 but rather 3564.7 ± 508.1 m^2. In each

356   quadrat, deciduous woodland occupied 90.3 ± 21.9% (0–100%), evergreen forest

357   occupied 5.6 ± 17.4% (0–100%), and grassland occupied 4.1 ± 15.0% (0–100%) of the

358   area. The slope of the ground was 5.7 ± 5.1° (0.01–33.5°), and the altitude was 1209 ±

359   21.9 m (1041–1621 m).

360   Within the belts, we found 379 beds in 172 bed clusters across 93 quadrats, whereas

361   8033 quadrats contained no beds. GLMM indicated that the proportion of evergreen

362   forest had the strongest effect on the number of beds within quadrats, followed by slope

363   of the ground and altitude. The model including the proportion of evergreen forests and

364   slopes was selected as the best model (AIC = 3500.5, likelihood ratio χ^2 index = 462.9, p

365   < 0.05; Table 2), indicating that both variables affected bed distribution, although the

366   slope angle was slightly correlated with the proportion of evergreen forest (Kendall rank

367   correlation test, $n = 8126$, $\tau = 0.05$, $z = 7.3$, $p < 0.05$).

368   During the dry season, 52 beds in 17 bed clusters were new and recently made in 11

369   of 5844 quadrats. We analyzed each effect of the proportion of forest, slope of the

370   ground, and altitude, because the interaction among them in GLMM was not significant.

371   Comparisons of the conditions in quadrats with beds and without beds revealed that

372   evergreen forest comprised more area in quadrats with beds (41.8 ± 49.4% [0–100%])

373   than in those without beds (3.7 ± 14.3% [0–100%]) (Mann-Whitney U test with

374   Bonferroni adjustment, $n1 = 11$, $n2 = 5833$, $z = 4.0$, $p < 0.05/3 = 0.017$; Fig. 2a). The

375   angle of the ground was steeper in quadrats with beds (9.8 ± 4.7° [2.5–17.6°]) than in

376   those without beds (4.8 ± 4.6° [0.0–32.5°]) (Mann-Whitney U test with Bonferroni

377   adjustment, $n1 = 11$, $n2 = 5833$, $z = 3.6$, $p < 0.017$; Fig. 2b). Altitude did not

378   significantly differ between quadrats with beds (1205 ± 92.7 m [1096–1392 m]) and

379   those without beds (1200 ± 120.0 m [1041–1549 m]) (Mann-Whitney U test with

380   Bonferroni adjustment, $n1 = 11$, $n2 = 5833$, $z = 0.6$, n.s.; Fig. 2c).

381   During the rainy season, 109 beds in 56 bed clusters were new and recently made in

382   38 of 2282 quadrats. We analyzed each effect of the proportion of forest, slope of the

383   ground, and altitude, because the interaction among them in GLMM was not significant.

384   Similar to the dry season, evergreen forests comprised more of the area in quadrats with

385   beds (29.8 ± 33.3% [0–100%]) than in quadrats without beds (4.5 ± 115.3% [0–100%])

386   (Mann-Whitney U test with Bonferroni adjustment, $n1 = 38$, $n2 = 2,244$, $z=9.4$, $p <$

387   0.017; Fig. 2a). In contrast to the dry season, the angle of the ground was less steep in

388   quadrats with beds (5.7 ± 6.3° [0.6–25.4°]) than in those without beds (8.0 ± 5.5° [0.4–

389   33.5°]) (Mann-Whitney U test with Bonferroni adjustment, $n1 = 38$, $n2 = 2,244$, $z = -3.7$,

390    $p < 0.017$; Fig. 2b). Altitude was higher in quadrats with beds (1246 ± 61.6 m [1150–

391   1435 m]) than in those without beds (1236 ± 97.0 m [1103–1621 m]) (Mann-Whitney U

392   test with Bonferroni adjustment, $n1 = 38$, $n2 = 2,244$, $z = 2.7$, $p < 0.017$; Fig. 2c).

393   The vegetation of some bed trees was not clear, because we could not identify the

394   species of some bed trees, and some bed clusters straddled two vegetations. However,

395   vegetation was clearly identified in 321 beds of 150 bed clusters within the quadrats. Of

396   those beds, 175 (54.5%) were located in forests and 146 (45.5%) were in woodlands. If

397   the grassland area was excluded, the proportions of forest and woodland in the

398   remaining areas were 5.8% and 94.2%, respectively, indicating that more beds were

399   located in forests than expected given the proportion of the forest area (χ^2-test, $df = 1$, χ^2

400    $= 1394.4$, $p < 0.05$). In addition, 135 new and recently made beds in 65 bed clusters

401   revealed that more beds were located in forests than expected during both the dry (χ^2

402   test, $df = 1$, $\chi^2 = 504.6$, $p < 0.05$) and rainy (χ^2 test, $df = 1$, $\chi^2 = 888.4$, $p < 0.05$) seasons

403   (Fig. 3).

404   However, the proportion of beds in forests during the rainy season was not greater

405   than that during the dry season (χ^2 test, $df = 1$, $\chi^2 = 1.9$, n.s.). Additionally, we compared

406   the actual and expected number of beds during each season based on leaf availability.

407   The density of trees with a DBH ≥5 cm was 0.09 trees/m^2 in forests and 0.02 trees/m^2 in

408   woodlands (see below). The proportion of mature unwithered leaves in each tree with

409   DBH ≥5 cm was 77.7% in forests and 87.9% in woodlands during the rainy season, and

410   66.0% in forests and 86.2% in woodlands during the rainy season. These findings

411   indicate that (amount available leaves in forests) : (amount available leaves in

412   woodlands) = 24.6% : 75.4% during the dry season, and 22.0% : 78.0% during the rainy

413   season, respectively. Comparison between the ratio of number of beds to the amount

414   available leaves in forests and woodlands revealed that more beds were located in

415   forests than expected during both the dry (χ^2 test, $df = 1$, $\chi^2 = 88.3$, $p < 0.05$) and rainy

416   (χ^2 test, $df = 1$, $\chi^2 = 169.5$, $p < 0.05$) seasons (Fig. 3).

417   Among the bed clusters in woodlands, the farthest one was 614 m from the nearest

418   evergreen forest. We found more bed clusters at the site closer to the forest (Kendall

419   rank correlation test, $n = 7$, $\tau = -0.67$, $z = -2.1$, $p < 0.05$; Fig. 4). The distance between

420   bed clusters and the nearest evergreen forest during the dry season (92 ± 74 m [7–313

421   m]) was shorter than that during the rainy season (184 ± 121 m [16–614 m]) (Mann-

422   Whitney U test, $n1 = 37$, $n2 = 30$, $z = -3.8$, $p < 0.05$; Fig. 5).

423

424   Feeding Tree and Sleeping Tree

425

426   Table 3 shows data on the feeding and sleeping trees of chimpanzees. We identified

427   the species of 719 sleeping trees in which beds were new and recently made.

428   Chimpanzees made beds in 28 different tree species. Of these, they fed on fruits or

429   legumes of 14 species, based on direct observation and fecal analyses (Yoshikawa and

430   Ogawa unpublished data). If we divide the year into four periods according to the

431   phenology of fruits and legumes, chimpanzees made 593 beds in feeding trees when

432   they fed on the fruits or legumes of that tree; however, this number did not significantly

433   differ from that expected by chance (χ^2 test, expected number = 573.4, $df = 1$, $\chi^2 = 3.3$,

434   n.s.).

435   Along two 5-km bed and vegetation line transects at Nguye, we recorded 16

436   chimpanzee beds in seven quadrats during the 1-year monitoring period. Among the 664

437   quadrats (166 × four periods), the number of feeding trees within the vegetation transect

438   line in quadrats with beds (2.7 ± 2.5 [0–4]) did not significantly differ from the number

439   found in quadrats without beds (3.0 ± 2.7 [0–18]) (Mann-Whitney U test, $n1$=7, $n2$=657,

440   z=-0.98, n.s.).

441

442   Vegetation

443

444   We recorded 443 trees with a DBH ≥5 cm in two 50 × 50-m quadrats in forests at

445   Bhukalai and Nguye and 232 trees in 100 × 100-m quadrats in a woodland at Nguye

446   (Ogawa et al. 2007). After reanalyzing the data, we found that trees in forests were

447   denser (0.09 trees/m^2) than those in woodlands (0.02 trees/m^2) (χ^2 test, df = 1, χ^2 = 22.7,

448   $p < 0.05$). Additionally, trees ≥10 m in height were denser in forests (0.05 trees/m^2) than

449   in woodlands (0.02 trees/m^2) (χ^2 test, df = 1, χ^2 = 101.1, $p < 0.05$). Trees ≥20 m in height

450   were also denser in forests (0.02 trees/m^2) than in woodlands (0.01 trees/m^2) (χ^2 test,

451   df=1, χ^2 = 16.4, $p < 0.05$), although the average tree height in forests (14.1 ± 7.9 m [3–

452   35 m]) was shorter than was that in woodlands (17.9 ± 6.1 m [2–25 m]) (Mann-Whitney

453   U test, $n1$ = 356, $n2$ = 195, z =6.9, $p < 0.05$).

454   We recorded 3815 trees with a DBH ≥5 cm in 104,000 m^2 on slopes at Nguye,

455   Bhukalai, and Nkondwe, and 1976 trees in 48,000 m^2 in flatlands at Shangwa, Mfuwazi,

456   and Issa Basin (Table 1). Deciduous woodlands, evergreen forests, and grasslands

457   occupied 91.2%, 3.2%, and 5.6% of the transect area, respectively. Trees on slopes

458   (0.037 trees/m^2) were less dense than were those in flatlands (0.041 trees/m^2) (χ^2 test, df

459   = 1, χ^2 = 17.7, $p < 0.05$). However, trees on slopes (9.4 ± 6.5 m [1–32]) were taller than

460   were those in flatlands (8.8 ± 5.3 m [1–34]) (Mann-Whitney U test, $n1$ = 3815, $n2$ =

461   1976, $z = 2.7$, $p < 0.05$). Additionally, trees ≥ 10 m in height were denser on slopes

462   (0.014 trees/m^2) than in flatlands (0.013 trees/m^2) (χ^2 test, $df = 1$, $\chi^2 = 5.8$, $p < 0.05$).

463   Trees ≥ 20 m were also denser on slopes (0.003 trees/m^2) than in flatlands (0.002

464   trees/m^2), but the difference was not significant (χ^2 test, $df = 1$, $\chi^2 = 0.5$, n.s.).

465

466   **Discussion**

467

468   Quadrats with chimpanzee beds contained a higher proportion of forest than did

469   quadrats without beds. In addition, chimpanzees made beds in forests at a

470   disproportionately high frequency given the overall percentage of the area that was

471   covered by forests, similar to previous studies in Ugalla (Ogawa et al. 2007; Stewart and

472   Pruetz 2013). Although some deciduous trees lose their leaves during the dry season,

473   however, the proportion of beds in forests during the rainy season was not greater than

474   that during the dry season. Moreover, the comparison of available sleeping trees

475   according to tree density and seasonal change of mature unwithered leaves showed that

476   chimpanzees slept in forests more frequently than expected during both the dry and

477   rainy seasons. This finding indicates that the following factors other than the availability

478   of sleeping trees might influence the distribution of chimpanzee beds. One of the

479   possible factors is that chimpanzees may have slept in forests more often because

480   forests are safer than woodlands. It may be also possible that chimpanzees select forests

481   because they had more preferred tree species or because forest trees had more desirable

482   sleeping locations, as chimpanzees chose certain tree species and certain locations in the

483   trees for sleeping (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013;

484   Ogawa et al. 2007).

485

486   In areas with few to no predators, chimpanzees sometimes construct ground beds

487   (Koops et al. 2012). However, chimpanzees in Ugalla did not construct beds on the

488   ground (Hernandez-Aguilar 2006, 2009; Ogawa et al. 2007), suggesting that the

489   predation risk was high in this area. If chimpanzees on the ground in woodlands

490   encounter carnivores in the daytime and evening before arriving at a sleeping site, they

491   may have to run away on the ground due to low density and wide spaces between trees.

492   Furthermore, it may be more difficult for chimpanzees to monitor the movements of

493   terrestrial carnivores in the woodlands because of the high and abundant grasses; for

494   example, lions can hide in bushes when they hunt (Ogutu and Dublin 2004). Woodlands

495   would also likely be dangerous at night. This is supported by the fact that chimpanzees

496   in Ugalla form larger sub-groups at night than in the daytime (Ogawa et al. 2007),

497   assuming that chimpanzees form large sub-groups to reduce predation risk, although

498   several other factors, such as food patch size and number of estrous females, may affect

499   sub-group size (Matsumoto-Oda et al. 1998). If a carnivore can climb a tree,

500   chimpanzees have difficulty passing through branches because the canopy is open in

501   woodlands.

502   In contrast to the woodlands, the forests had more trees with DBH ≥5 cm, more

503   trees with DBH ≥5 cm and ≥10 m in height, and more trees with DBH ≥5 cm and ≥20 m

504   in height. The intervals between trees were narrow, and the canopy was closed. If a

505   carnivore climbs a tree containing sleeping chimpanzees in a forest, the chimpanzees

506   are likely to pass through branches more easily and escape from the carnivore.

507   Chimpanzees make higher tree beds if the predation risk is high (Pruetz et al. 2008),

508   which is similar to other primates (Reichard 1998; Von Hippel 1998). Chimpanzees at

509   Issa in Ugalla made beds higher and at more peripheral locations within the tree than

510   did chimpanzees in Fongoli that had no predators (Stewart and Pruetz 2013). These

511   observations suggest that chimpanzees may choose safer places to reduce predation risk.

512   As well as choosing safer places in a tree, chimpanzees may choose forests for their

513   sleeping sites to reduce predation risk because forests should be safer than woodlands;

514   thus supporting the predation pressure hypothesis. Direct evidence of predation pressure

515   in the forests and woodlands in future studies can contribute to a better understanding of

516   the predation pressure hypothesis.

517

518   Feeding efficiency is another potential factor affecting the choice of chimpanzee

519   sleeping   sites.   Chimpanzees   in   Ugalla   chose   *Monopetalanthus   richardsiae*,

520   *Brachystegia bussei*, and *Pterocarpus tinctoriusas* as sleeping trees more frequently

521   than expected from the density of the trees, and chimpanzees also feed on legumes of

522   these trees (Ogawa et al. 2007). However, our study did not show that chimpanzees

523   made more beds in or near their feeding trees during the period in which they actually

524   fed on the fruits or legumes of that tree. Chimpanzees in Ugalla were more likely to

525   sleep in forests, but they ate fruits and other parts of plants in both woodlands and

526   forests (Hernandez-Aguilar 2006; Schoeninger et al. 1999; Yoshikawa and Ogawa

527   unpublished data). Thus, the present study did not provide evidence to support the

528   feeding efficiency hypothesis. This may be because the selection of sleeping sites is

529   heavily influenced by predation pressure, as the predation risk is high in Ugalla.

530   However, lack of evidence supporting the feeding efficiency hypothesis does not

531   necessarily mean that the distribution of food resources is unrelated to sleeping site

532   selection. An examination of feeding trees within a wider area around the sleeping trees

533   may reveal a relationship between sleeping trees and feeding trees, as previously

534   reported (Furuichi and Hashimoto 2004).

535

536   The fact that chimpanzees made more beds in forests than expected indicates that water

537   availability influenced the distribution of sleeping sites, as most available water in

538   Ugalla was found in the evergreen forests along streams. Additionally, water is not

539   readily available in the flatlands, and is restricted to the valley forests along slopes and

540   the small patchy forests under escarpments in slopes during the dry season, whereas

541   numerous pools exist in the woodlands and grasslands of the flatlands during the rainy

542   season (Itani 1979; Kano 1972; Moore 1992, 1994; Ogawa et al. 1999, 2007). Although

543   beds were not aggregated close to water pools at Issa (Hernandez-Aguilar 2006, 2009),

544   when chimpanzees constructed beds in woodlands, more beds were located in

545   woodlands that were closer to forests, and chimpanzees made beds closer to the forest

546   during the dry season than during the rainy season. Furthermore, quadrats containing

547   beds were located along steeper slopes than quadrats without beds during the dry season.

548   These results indicate that chimpanzees preferred to sleep in or near forests and on

549   slopes to obtain water from the forest valleys during the dry season.

550   The low correlation between the proportion of forests and slope of the ground and

551   the best model in the GLMM analysis indicated that the fact that the chimpanzees

552   frequently slept along slopes was not a byproduct of more forests being present along

553   slopes and chimpanzee preference for forests. Similarly, chimpanzees did not shun

554   flatland sleeping sites because of human activities, as chimpanzees also made few beds

555   in the flatlands at Mfuwazi and Issa Basin, where permanent human habitation is absent.

556   Chimpanzees may have chosen slopes as sleeping sites to reduce the risk of predation

557   because trees on the slopes were taller, and trees with ≥10 m in height were denser than

558   trees in the flatlands. Chimpanzees may sleep along slopes to facilitate vocal

559   communication with other chimpanzees (Piel and Moore 2007). During the rainy season,

560   however, chimpanzees slept in gently sloping locations rather than along steep slopes.

561   Neither the predation pressure hypothesis nor the vocal communication hypothesis

562   could explain the seasonal differences in the relation between bed sites and slopes.

563   Seasonal changes in the relationship between bed sites and slopes is best explained by

564   the water availability hypothesis, although more direct data on water availability are

565   needed to confirm this hypothesis.

566

567   Previous studies have shown that chimpanzees adjusted the height of themselves and

568   their beds in trees according to the temperature of the air (Samson and Hunt 2012;

569   Takemoto 2004). However, we found no significant relationship between bed sites and

570   altitude during the dry season, and the altitude in quadrats with beds was 10 m higher

571   than that in quadrats without beds during the rainy season. High altitude sites generally

572   provide warmer temperatures (Salomons 2001), although there is no data in Ugalla.

573   Thus, our evidence did not support the hypothesis that chimpanzees selected warm

574   sleeping sites within their home range to facilitate thermoregulation. Data on

575   temperature, humidity, and other factors are needed to test the physical comfort

576   hypothesis.

577

578   Our findings provide insight into the possible habitat use of early hominins as they

579   likely faced problems similar to those faced by chimpanzees in the savanna woodland

580   areas (Moore 1992). Early hominins were under constant threat of predation pressure by

581   carnivores (Hart and Sussman 2005). Although habitat use in woodlands is also

582   important, forests provide crucial vegetation for chimpanzees in open habitats (e.g.,

583   both the savanna woodland area in Tanzania and the grassland-forest mosaic area in

584   Senegal) (McGrew et al. 1981; Moore 1992; Pruetz and Bertolani 2009: Stewart and

585   Pruetz 2013). The habitats of hominins preceding *Homo erectus* also included forests

586   (White et al. 2009). As long as early hominins constructed beds in trees, as do

587   chimpanzees (Sept 1998), they may have used forests as safe sleeping sites, possibly to

588   avoid the risk of predation. Moreover, early hominins may have preferred to live in or

589   near forests and on slopes, possibly to obtain water from the valleys. Until hominins

590   began to use vessels or other inventions to keep or obtain drinking water, they could not

591   have changed their ranging patterns, similar to savanna chimpanzees.

592

593   Factors affecting sleeping site selection by chimpanzees vary with the conditions of

594   each study site (Basabose and Yamagiwa 2002; Furuichi and Hashimoto 2004; Koops et

595   al. 2012; Pruetz et al. 2008; Stanford and O'Malley 2008; Stewart et al. 2007). Although

596   the present study found no evidence to support the feeding efficiency and physical

597   comfort hypotheses, our findings supported the predation pressure and water availability

598   hypotheses. Chimpanzees selected forests as their sleeping sites, possibly to reduce the

599   risk of predation. Chimpanzees preferred to sleep in or near forests and on slopes during

600   the dry season, possibly to obtain drinking water. Although further surveys are needed

601   to provide more direct evidence, our findings on the distribution of chimpanzee beds

602   suggests that predation pressure and water availability are important factors in the

603   selection of sleeping site by chimpanzees in the Ugalla savanna woodland area.

604

624

625 **References**

626

627 Anderson JR (1998) Sleep, sleeping sites, and sleep-related activities: Awakening to

628   their significance. Am J Primatol 46: 63-75

629 Baldwin P, Sabater J, McGrew W, Tutin C (1981) Comparisons of nests made by

630   different populations of chimpanzees (*Pan troglodytes*). Primates 22: 474-486

631 Badrian N, Randal A, Susman RL (1981) Preliminary observations on the feeding

632   behavior of *Pan paniscus* in the lomako forest of central Zaïre. Primates 22(2):

633   173-181

634 Basabose AK, Yamagiwa J (2002) Factors affecting nesting site choice in chimpanzees

635   at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. Int J

636   Primatol 23: 263–282

637 Boesch C (1991) The effects of leopard predation on grouping patterns in forest

638   chimpanzees. Behaviour 117: 3-4

639 Chapman CA, Chapman LJ, Mclaughlin RL (1989) Multiple central place foraging by

640   spider monkeys: travel consequences of using many sleeping sites. Oecologia 9:

641   506-511

642 Day RT, Elwood RW (1999) Sleeping site selection by the golden-handed tamarin

643   *Saguinus midas midas*: the role of predation risk, proximity to feeding sites, and

644   territorial defense. Ethology 105: 1035-1051

645 Goodall J (1962) Nest building behavior in the free ranging chimpanzee. Annals of the

646   New York Academy of Sciences 102: 455-467

647 Furuichi T, Hashimoto C (2004) Botanical and topographical factors influencing nest-

648   site selection by chimpanzees in Kalinzu Forest, Uganda. Int J Primatol 25: 755-

649   765

650 Hamilton WJ (1982) Baboon sleeping site preferences and relationships to primate

651   grouping patterns. Am J Primatol 3: 41-53

652 Hanschel P, Abernethy, K., White, L. (2005) Leopard food habits in the Lope National

653   Park, Gabon, Central Africa. Afr J Ecol 43: 21-28

654 Hansell M (2005) Animal architecture. Oxford University Press, Oxford

655 Hart D, Sussman RW (2005) Man the hunted: Primates, predators, and human evolution.

656   Westview, New York

657 Hausfater G, Meade BJ (1982) Alternation of sleeping groves by yellow baboons

658   (*Papio cynocephalus*) as a strategy for parasite avoidance. Primates 23: 287-297

659 Hernandez-Aguilar RA (2006) Ecological and nesting patterns of chimpanzees (*Pan*

660   *troglodytes*) in Issa, Ugalla, western Tanzania. Ph.D. thesis, University of Southern

661   California

662 Hernandez-Aguilar RA (2009) Chimpanzee nest distribution and site reuse in a dry

663   habitat: implications for early hominin ranging. J Hum Evol 57: 350-364

664 Hernandez-Aguilar RA, Moore J, Stanford CB (2013) Chimpanzee nesting patterns in

665   savanna habitat: Environmental influences and preferences. Am J Primatol 75:

666   979-994

667 Inskipp T (2005) Chimpanzee (*Pan troglodytes*). In: Caldecott J, Miles L (eds) World

668   atlas of great apes and their conservation. University of California Press, Berkeley,

669   pp 53–81

670 Kano T (1972) Distribution and adaptation of the chimpanzee on the eastern shore of

671   Lake Tanganyika. Kyoto Univ Afr Stud 7: 37-129

672 Kappeler PM (1998) Nests, tree holes, and the evolution of primate life histories. Am J

673   Primatol 46: 7–33

674 Koops K, McGrew WC, de Vries H, Matsuzawa T (2012) Nest-building by

675   chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains:

676　　　antipredation, thermoregulation, and antivector hypotheses. Int J Primatol 33: 356-
677　　　380

678　MacKinnon J (1974) The behaviour and ecology of wild orangutans (*Pongo pygmaeus*).
679　　　Animal Behavour 22: 3-74

680　Matsumoto-Oda A, Hosaka K, Huffman MA, Kawanaka K (1998) Factors affecting
681　　　party size in chimpanzees of the Mahale Mountains. Int J Primatol 19: 999-1011

682　Moore J (1992) "Savanna" chimpanzees. In: Nishida T, McGrew WC, Marler P,
683　　　Pickford M, de Waal FBM (eds) Topics in primatology, vol.1: Human origins.
684　　　University of Tokyo Press, Tokyo, pp 99-118

685　Moore J (1994). Plants of the Tongwe east reserve (Ugalla), Tanzania. Tropics 3: 333-
686　　　340

687　McGrew WC, Baldwin PJ, Tutin CEG (1981) Chimpanzees in a hot, dry, and open
688　　　habitat: Mt. Assirik, Senegal, West Africa. J Hum Evol 10: 227-244

689　Nakazawa N, Hanamura S, Inoue E, Nakatsukasa M, Nakamura M (2013) A leopard ate
690　　　a chimpanzee: first evidence from east Africa. J Hum Evol 65: 334-7

691　Nishida T (1968) The social group of wild chimpanzees in the Mahali mountains.
692　　　Primates 9: 167-224

693　Ogawa H, Takahashi H (2003) Triadic positions of Tibetan macaques huddling at a
694　　　sleeping site. Int J Primatol 24: 591-606

695　Ogawa H, Idani G, Kanamori M (1999) Chimpanzee habitat in the savanna woodland,
696　　　Ugalla, Tanzania. Primate Research 15(2): 135-146

697　Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A (2007) Sleeping parties
698　　　and nest distribution of chimpanzees in the savanna woodland area, Ugalla,
699　　　Tanzania. Int J Primatol 28: 1397-1412

700 Ogutu JO, Dublin HT (2004) Spatial dynamics of lions and their prey along an
701　　　environmental gradient. Afr J Ecol 42: 8-22

702 Piel AK, Moore J (2007) Locating elusive animals: using a passive acoustic system to
703　　　study savanna chimpanzees at Ugalla, western Tanzania. Am J Phys Anthropol 44:
704　　　189

705 Pruetz JD, Fulton SJ, Marchant LF, McGrew WC, Schiel M, Waller M (2008) Arboreal
706　　　nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes*
707　　　*verus*) in southeastern Senegal. Am J Primatol 70: 393–401

708 Pruetz JD, Bertolani P (2009) Chimpanzee (*Pan troglodytes verus*) behavioral responses
709　　　to stresses associated with living in a savanna-mosaic environment: implications
710　　　for hominin adaptations to open habitats. Paleoanthropol 252-262.

711 R Development Core Team (2011) R: A language and environment for statistical
712　　　computing. R Foundation for statistical computing. Vienna, Austria, URL:
713　　　http://www.r-project.org/

714 Reichard U (1998) Sleeping site, sleeping places, and presleep behavior of gibbons
715　　　(*Hylobates lar*). Am J Primatol 46: 35-62

716 Rudicell RS, Piel AK, Stewart F, Moore DL, Learn GH, Li YY, Takehisa J, Pintea L,
717　　　Shaw GM, Moore J, Sharp PM, Hahn BH (2011) High prevalence of Simian
718　　　Immunodeficiency Virus infection in a community of savanna chimpanzees. J Virol
719　　　85: 9918–9928

720 Salomons, EM (2001) Computational atmospheric acoustics (1st ed.). Kluwer
721　　　Academic Publishers.

722 Samson DR, Hunt KD (2012) A thermodynamic comparison of arboreal and terrestrial
723　　　sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the
724　　　Toro-Semliki Wildlife Reserve, Uganda. Am J Primatol 74: 811-818.

725 Sept J (1998) Shadows on a changing landscape: Comparing nesting patterns of

726   hominids and chimpanzees since their last common ancestor. Am J Primatol 46:

727   85–101

728 Schoeninger M, Moore J, Sept J (1999) Subsistence strategies of two "savanna"

729   chimpanzee populations: the stable isotope evidence. Am J Primatol 49: 297-314

730 Sharman MJ (1982) Feeding, ranging and social organization of the Guinea baboon.

731   Ph.D. thesis, University of St. Andrews

732 Smith AC, Knogge C, Huck M, Löttker P, Buchanan-Smith HM, Heymann EW (2007)

733   Long-term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*)

734   and mustached tamarins (*S. mystax*): effects of foraging, thermoregulation,

735   predation, and resource defense constraints. Am J Phys Anthropol 134: 340-353

736 Stanford CB, O'Malley R (2008) Sleeping tree choice by Bwindi chimpanzees. Am J

737   Primatol 70: 642–649

738 Stewart FA, Pruetz JD, Hansell MH (2007) Do chimpanzees build comfortable nests?

739   Am J Primatol 69: 930–939

740 Stewart FA, Piel, AK, McGrew WC (2011) Living archaeology: Artefacts of specific

741   nest site fidelity in wild chimpanzees. J Hum Evol 61: 388-395

742 Stewart FS, Pruetz JD (2013) Do chimpanzee nests serve an anti-predatory function?

743   Am J Primatol 9999: 1-12

744 Sutton JEG, Roberts AD (1968) Uvinza and its salt industry. Azania 3: 45–869

745 Suzuki A (1969) An ecological study of chimpanzees in a savanna woodland. Primates

746   10: 103-148

747 Takemoto H (2004) Seasonal change in terrestriality of chimpanzees in relation to

748   microclimate in the tropical forest. Am J Phys Anthropol 124: 81–92

749 Tsukahara T (1993) Lions eat chimpanzees: the first evidence of predation by lions on
750   wild chimpanzees. Am J Primatol 29: 1-11

751 Von Hippel FA (1998) Use of sleeping trees by black and white colobus monkeys
752   (*Colobus guereza*) in the Kekamega forest, Kenya. Am J Phys Anthropol 45: 281-
753   290

754 Wada K, Tokida E, Ogawa H (2007) The influence of snowfall, temperature and social
755   relationships on sleeping clusters of Japanese monkeys during winter in Shiga
756   Heights. Primates 48: 130-139

757 White TD, Ambrose SH, Suwa G, Su DF, DeGusta D, Bernor RL, Boisserie JR, Brunet
758   M, Delson E, Frost S, Garcia N, Giaourtsakis IX, Haile-Selassie Y, Howell FC,
759   Lehmann T, Likius A, Pehlevan C, Saegusa H, Semprebon G, Teaford M, Vrba E
760   (2009) Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus*
761   *ramidus*. Science 326(5949): 67-93

762 Yoshikwa M, Ogawa H, Sakamaki T, Idani G (2008) Population density of
763   chimpanzees in Tanzania. Pan Africa News 15: 17-20

764 Zuberbühler K, Jenny D (2002) Leopard predation and primate evolution. J Hum Evol
765   43: 873-886

766

767   **Fig. 1** The Ugalla study area in Tanzania

768

769   **Fig. 2** Conditions in quadrats containing chimpanzee beds in Ugalla

770

771   **Figure legend**

772   (a) Percentage of evergreen forest area, (b) slope angle of the ground, and (c) altitude

773   are compared between the 60×60-m quadrats containing new or recently made

774   chimpanzee beds and the quadrats without beds. Dry: during the dry season. Rainy:

775   during the rainy season. With beds: quadrats containing beds. Without beds: quadrats

776   without beds. Asterisks indicate significance at $p < 0.05$.

777

778   **Fig. 3** Number of beds in forests and woodlands in Ugalla

779

780   **Figure legend**

781   Recorded: number of beds recorded by bed surveys. Expected: number of beds expected

782   based on relative leaf availability estimated by area, tree density (trees/m^2), and

783   proportion of mature unwithered leaves in each tree in forests and woodlands (see text).

784   Forest: beds in forests. Woodland: beds in woodlands. Dry: during the dry season.

785   Rainy: during the rainy season. Asterisks indicate significance at $p < 0.05$.

786

787   **Fig. 4** Location of bed clusters in woodlands in Ugalla

788

789   **Figure legend**

790   Numbers of bed clusters in woodlands are shown with the distance between each bed

791   cluster and the edge of the nearest evergreen forest with area $\geq$10,000 m^2.

792

793   **Fig. 5** Distance between bed clusters and the nearest forest in Ugalla

794

795   **Figure legend**

796   The distance (m) between bed clusters and the nearest evergreen forest during the dry

797   season and the rainy season are shown. Dry: during the dry season. Rainy: during the

798   rainy season. An asterisk indicates significance at $p < 0.05$.

Table 1 Study sites and surveys in the Ugalla area

Site name	Location		Bed line transect		Vegetation line transect					
	Latitude	Longitude	Distance (km)	Date (dd/mm/yy)	Area	Vegetation [1]	Altitude		Topography [2]	Date (dd/mm/yy)
							Lowest	Highest		
Mfuwazi	05°12' S	30°38' E	28.0	09/08/1995 & 09-11/08/2008	2km×4m	W & F	1,040	1,050	F	10/08/2008
Nguye (Ngya)	05°13' S	30°28' E	153.8	23-29/07/2001, 31/07-20/08/2003,	5km×4m	W & F	1,120	1,260	H	25-29/12/2007 [3]
				25/12/2007-04/01/2008,	5km×4m	W & F	1,120	1,260	H	30/12/2007-04/01/2008 [3]
				& 31/12/2010-09/03/2011	100m×100m	W	1,140	1,140	H	18/08/1997
					50m×50m	F	1,110	1,110	H	01-04/11/1995
Mufombosi	05°15' S	30°39' E	40.7	02-05/08/1997	-	-	-	-		-
Bhukalai (Mogogwesi)	05°27' S	30°44' E	47.8	02-26/08/1996	4km×4m	W & F	1,240	1,370	H	23−30/08/1995
					4km×4m	W & F	1,260	1,400	H	07−08/08/1996
					50m×50m	F	1,300	1,300	H	01-04/09/1995
Mtongesi	05°28' S	30°48' E	52.6	11-13/08/1997	-	-	-	-	-	-
Bukombe	05°32' S	31°00' E	55.7	08-10/08/1997	-	-	-	-	-	-
Shangwa	05°36' S	30°45' E	43.4	10-14/08/1996	4km×4m	W & F	1,490	1,510	F	11−13/08/1996
Issa Basin	05°38' S	30°46' E	52.1	23-27/02/2003 & 11-13/08/2008	2km×4m	W & F	1,100	1,110	F	12/08/2008
Nkondwe	05°56' S	30°57' E	13.3	20-22/08/2008	4km×4m	W & F	1,170	1,320	H	15−1608/1996
					4km×4m	W & F	1,170	1,380	H	23−26/08/2008
Niamansi [4]	05°57' S	30°58' E	8.5	31/08-02/09/2005	4km×4m	W & F	1,120	1,180	F	31/08-01/09/2005
					4km×4m	W & F	1,140	1,200	F	25-26/08/2008

(1) W: Woodland, F: Forest
(2) F: Flatland, H: Hill
(3) Along these transect lines, we monitored chimpanzee beds for 1 year beginning on 4th Jan. 2008, and seasonal changes in leaves for 1 year beginning on 1st Sept. 2010.
(4) The bed and vegetaion transects in Niamansi were not included in the analysis, because this area is outside the distribution of chimpanzees.

Table 2 Factors affecting sleeping site selection by chimpanzees in Ugalla

Predictor variable	Coefficient	SE	Wald χ^2 index	p value	Coefficient*	SE*
% of evergreen forest	0.480	0.201	568.1	<0.05	0.468	0.063
Angle of the ground	0.332	0.041	65.4	<0.05	0.373	0.020
Altitude	0.286	0.052	30.3	<0.05	-	-

*: Coefficient and standard error (SE) in the selected model

Table 3 Sleeping trees and feeding trees of chimpanzees in the Ugalla area

| Species | Feeding part | Number of sleeping trees | | | | Total |
| | | Dry season | | Rainy season | | |
		May-July	Aug.-Oct.	Nov.-Jan.	Feb.-April	
Albizia glaberrima and/or *amara*			3	8		11
Anisophyllea pomifera and/or *boehn*	Fruit		<u>1</u>			1
Brachystegia boehmii			1		4	5
Brachystegia bussei	Legume	<u>0</u>	19	5	1	25
Brachystegia spiciformis	Legume	<u>0</u>	17			17
Combretum moll					1	1
Combretum zeyheri					2	2
Craibia grandiflora and/or microcarpa			4		4	8
Ficus spp.	Legume	<u>0</u>	<u>3</u>	<u>0</u>	<u>0</u>	3
Garcinia huillensis	Fruit		<u>1</u>			1
Garcinia volkensii	Fruit		<u>2</u>			2
Isoberlinia angolensis	Legume	<u>0</u>	5			5
Julbernardia paniculata			3			3
Julbernardia unijugata	Legume	<u>65</u>	<u>182</u>	6	4	257
Maesa lanceolata			7			7
Markhamia obtusifolia				1		1
Monopetalanthus richadsiae	Legume	<u>37</u>	<u>281</u>	17		335
Multidentia crassa	Fruit	<u>0</u>	<u>1</u>	<u>0</u>	<u>0</u>	1
Pachystela brevipes			5			5
Parinari curatelliifolia	Fruit	<u>0</u>	<u>4</u>	<u>0</u>	<u>0</u>	4
Pericopsis angolensis			3			3
Pseudospondias microcarpa	Fruit		<u>0</u>	<u>0</u>	1	1
Pterocarpus tinctorius	Legume	<u>0</u>	<u>1</u>	<u>2</u>	1	4
Syzygium guineense	Fruit		<u>7</u>	<u>6</u>		13
Techlea trichocarpa			1			1
Temnocalyx sp.			1			1
Trichilia dregeana			1			1
Vitex ferruginea			1			1
Total		102	554	45	18	719

The number of trees in which beds were new or recently made are listed.

Old and disintegrating beds were also recorded in *Albizia versicolor*, *Annona senegalensis*,
Brachystegia microcarpa, *Brachystegia microphylla*, and *Embelia schimperi*.

Underlined: The period when chimpanzees fed on fruits or legumes of the tree.

Fig. 1 The Ugalla study area in Tanzania

Fig. 2 Conditions in quadrats containing chimpanzee beds in Ugalla
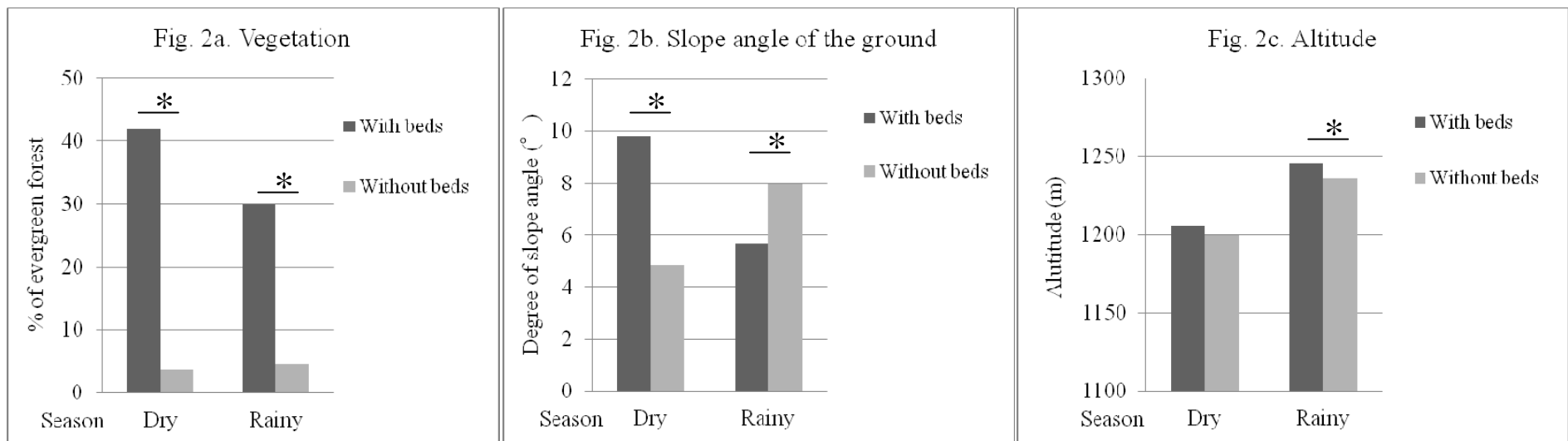
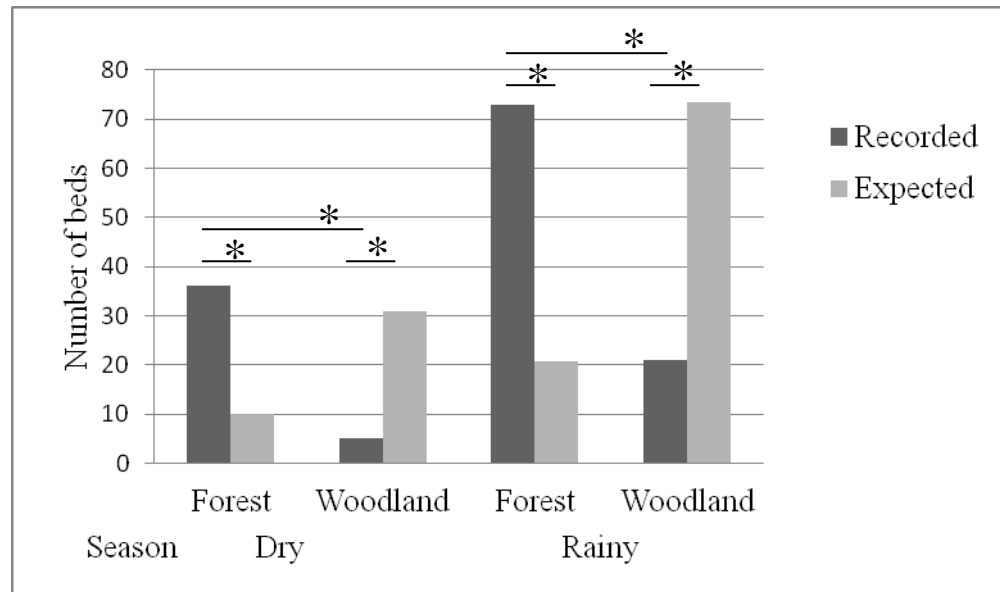**Fig. 3** The number of beds in forests and woodlands in Ugalla

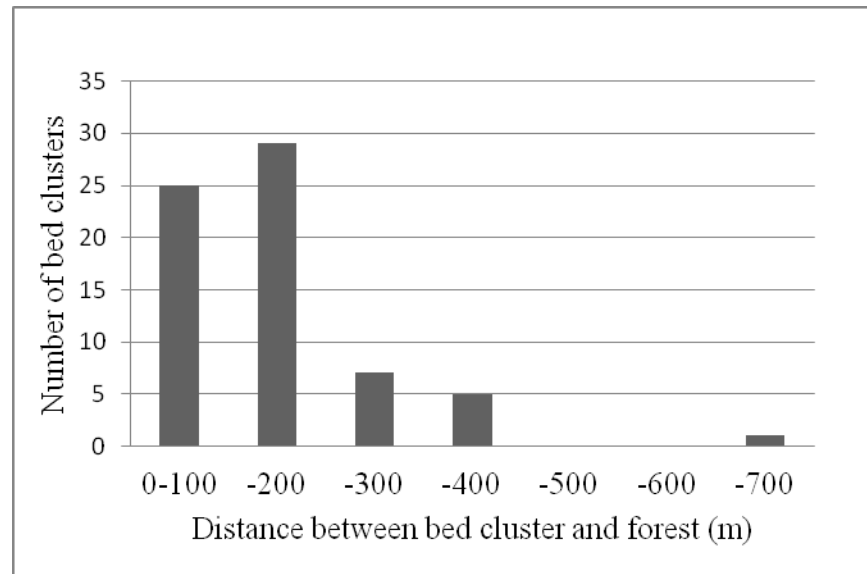**Fig. 4** Location of bed clusters in woodlands in Ugalla

Fig. 5 Distance between bed clusters and the nearest forest in Ugalla