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3   **Impacts of Habitat Loss and Fragmentation on the Activity Budget, Ranging**

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5   **Ecology and Habitat Use of Bale Monkeys (*Chlorocebus djamdjamensis*) in the**

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7   **Southern Ethiopian Highlands**

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47   19   Running header: Habitat Fragmentation Impact the Ecology of Bale monkey
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24 **Abstract:** Understanding the extent to which primates in forest fragments can adjust

25 behaviorally and ecologically to changes caused by deforestation is essential to designing

26 conservation management plans. During a 12-month period, we studied the effects of habitat loss

27 and degradation on the Ethiopian endemic, bamboo specialist, Bale monkey (*Chlorocebus*

28 *djamdjamensis*) by comparing its habitat quality, activity budget, ranging ecology and habitat use

29 in continuous forest and two fragments. We found that habitat loss and fragmentation resulted in

30 major differences in vegetation composition and structure between forest types. We also found

31 that Bale monkeys in continuous forest spent more time feeding and traveling and less time

32 resting and socializing than monkeys in fragments. Bale monkeys in continuous forest also had

33 higher movement rates (m/hr) than monkeys in fragments. Bale monkeys in continuous forest

34 used exclusively bamboo and mixed bamboo forest habitats while conspecifics in fragments used

35 a greater variety of habitats including human use areas (i.e., matrix). Our findings suggest that

36 Bale monkeys in fragments use an energy minimization strategy to cope with the lower

37 availability of the species' primary food species, bamboo (*Arundinaria alpina*). We contend that

38 Bale monkeys may retain some of the ancestral ecological flexibility assumed to be characteristic

39 of the genus *Chlorocebus*, within which all extant species except Bale monkeys are regarded as

40 ecological generalists. Our results suggest that, like other bamboo eating primates (e.g., the

41 bamboo lemurs of Madagascar), Bale monkeys can cope with a certain threshold of habitat

42 destruction. However, the long-term conservation prospects for Bale monkeys in fragments

43 remain unclear and will require further monitoring to be properly evaluated.

44 **Key words: Bale monkey; bamboo; ecological flexibility; forest fragment; habitat loss**

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46   **INTRODUCTION**

47   Habitat loss and fragmentation are the primary threats to biodiversity in the tropics [Haddad

48   et al., 2015]. Among mammals, nonhuman primates are particularly threatened by tropical

49   deforestation [Cowlishaw and Dunbar, 2000; Irwin, 2016]. Currently, more than half of the

50   world's primate species are vulnerable to extinction because of anthropogenic habitat

51   modifications [Estrada et al., 2012; Marsh et al., 2013]. Many species are increasingly reliant on

52   human modified landscapes [Arroyo-Rodríguez and Fahrig, 2014].

53   The persistence of primates in small and isolated forest fragments depends on their

54   behavioral and ecological flexibility [Onderdonk and Chapman, 2000]. Some primates persist in

55   forest fragments by adopting an *energy maximizing strategy,* spending more time feeding and

56   less time resting (e.g., *Ateles geoffroyi*: [Chaves et al., 2011]), or by traveling longer distances

57   per day (*Propithecus edwardsi*: [Gerber et al., 2012]) than conspecifics in continuous forest.

58   Conversely, many other primates survive in forest fragments by using an *energy minimizing*

59   *strategy,* spending less time feeding, more time resting and less time traveling (e.g., *Chiropotes*

60   *satanas*: [Boyle and Smith, 2010], *Alouatta seniculus*: [Palma et al., 2011], *Colobus vellerosus*:

61   [Wong and Sicotte, 2007], or by traveling shorter distances per day (*Propithecus diadema*:

62   [Irwin, 2008], *Eulemur collaris*: [Campera et al., 2014]) than their counterparts in continuous

63   forest. There are also some primate taxa that have proven largely incapable of persisting in small,

64   isolated fragments, ultimately resulting in widespread local extirpation (e.g., *Ateles geoffroyi*:

65   [Estrada and Coates-Estrada, 1996]; *Trachypithecus pileatus*: [Sharma et al., 2014]). Generally,

66   the smaller the fragment size, the higher the probability of extirpation. Species with specialized

67   habitat and dietary requirements, limited geographic range, larger body size and larger home

68   range needs are also particularly vulnerable to extinction [Harcourt, 2006; Benchimol and Peres,

69   2013]. However, the long-term persistence of primates in forest fragments also depends on

70   several additional factors including the level of anthropogenic disturbance, hunting pressure,

71   patch quality, matrix type and level of protection [Benchimol and Peres, 2013].

72   Successful conservation of threatened species in forest fragments depends on basic

73   knowledge of the species' ecology and subsequent implementation of appropriate conservation

74   management strategies [Marsh, 2003]. Research on critically endangered Tana River mangabeys

75   (*Cercocebus galeritus*) identified a link between fragment size and mangabey abundance

76   [Wieczkowski, 2004] and quantified competition between humans and mangabeys over forest

77   products [Kinnaird, 1992], factors that were subsequently incorporated into management plans

78   for the species and its fragmented habitat [Wieczkowski, 2005]. Unfortunately, similar studies of

79   behavioral and ecological responses to habitat loss and fragmentation are still lacking for many

80   threatened species, including the enigmatic Bale monkey (*Chlorocebus djamdjamensis*). The

81   Bale monkey is endemic to the montane forests of the southern Ethiopian Highlands and is

82   unusual among primates in occupying a bamboo specialist niche, consuming a diet of 77%

83   bamboo in intact forest [Mekonnen et al., 2010a; Mekonnen and Jaffe, 2016]. Until recently, it

84   was among the least studied primates in Africa [Mekonnen et al., 2010a; Mekonnen et al.,

85   2010b] and is currently classified as Vulnerable by the IUCN [Butynski et al., 2008].

86   As for many other tropical primates [Marsh, 2003], much of the Bale monkey's historical

87   geographic range has been converted into agricultural land, grazing land and human settlements,

88   leaving many populations in small and isolated forest fragments [Mekonnen et al., 2012]. With

89   its specialized habitat (montane bamboo forest) and dietary (bamboo) requirements and its

90   narrow geographic range (southern Ethiopia) [Butynski et al., 2008; Mekonnen et al., 2010a;

91   Mekonnen et al., 2010b], the Bale monkey may consequently be at high risk of extinction due to

92   the increasing habitat loss and fragmentation across much of its range [Mekonnen et al., 2012].

93   The Bale monkey's high degree of specialization is unique among its sister species, including the

94   vervet (*Chlorocebus pygerythrus*) and grivet (*C. aethiops*) monkeys, which are able to exploit

95   many different habitat types and consume a variety of diets [Isbell et al., 1998; Enstam and

96   Isbell, 2007]. The recent discovery of Bale monkey populations in several heavily-disturbed

97   forest fragments lacking bamboo suggests that the species may be capable of greater habitat

98   flexibility [Mekonnen et al., 2012] than previously thought [Carpaneto and Gippoliti, 1994;

99   Butynski et al., 2008; Mekonnen et al., 2010a]. Thus, despite their tendency towards

100   specialization in continuous forest, the possibility that Bale monkeys retain some of the

101   ecological flexibility characteristic of other members of the *Chlorocebus* genus warrants more

102   detailed evaluation.

103   The main purpose of this study was to examine how bamboo habitat loss and fragmentation

104   influence habitat quality, activity budget, home range use, movement rates and habitat use of

105   Bale monkeys in continuous forest and forest fragments. In particular, we (1) tested the

106   hypothesis that fragmentation would reduce habitat quality for Bale monkeys; (2) evaluated

107   whether Bale monkeys adopt an energy minimizing or maximizing strategy in forest fragments;

108   and (3) assessed how flexible Bale monkeys are behaviorally and ecologically in forest

109   fragments. Our results suggest that forest fragments are indeed of lower quality than intact

110   habitat, and that Bale monkeys manage to persist in fragments by using a wider variety of habitat

111   types (including matrix) and by adopting an energy minimizing strategy. Based on this study, we

112   recommend continued monitoring of Bale monkeys in forest fragments to evaluate their long-

113   term viability in these suboptimal habitats [cf., Chapman et al., 2013] as well as the development

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114   of conservation and management programs that protect not only the fragments but the access of

115   Bale monkeys to the surrounding matrix as well.

116

117   **METHODS**

118   **Study Site and Habitat Characteristics**

119   Based on the availability and disturbance status of bamboo (*Arundinaria alpina*), the species

120   which dominates the diet of Bale monkeys in continuous forest [Mekonnen et al., 2010a], we

121   selected three study sites: a continuous forest with intact bamboo (Odobullu Forest), a forest

122   fragment with degraded bamboo (Kokosa Forest) and a forest fragment with nearly eradicated

123   bamboo (Afursa Forest; Fig. 1). Odobullu Forest (hereafter Continuous forest) is a large forest

124   (14,100 ha) with a high density of bamboo that lies east of Bale Mountains National Park

125   [Mekonnen et al., 2010a]. Odobullu consists of four habitat types including bamboo forest, tree-

126   dominated forest, shrubland and grassland [Mekonnen et al., 2010b]. It is partially protected by

127   the privately owned hunting company, Ethiopian Rift Valley Safari, though legal bamboo harvest

128   is practiced by the local community in some sections of the forest [Mekonnen et al., 2010a].

129   However, disturbance is uncommon within the home ranges of our two study groups at Odobullu

130   because of the difficult terrain and inaccessibility of the area.

131   Kokosa forest fragment (hereafter Patchy fragment) consists of several "islands" of degraded

132   bamboo and large trees amidst a matrix of human settlements, cultivated land, shrubland and

133   grazing land. Only a portion of the 162 ha fragment is owned by the community while most of

134   the fragment is owned by private individuals. Selective cutting of bamboo is common in the

135   fragment. This forest fragment was dominated by bamboo forest as recently as three decades ago

136   [Mekonnen et al., 2012].

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137   Afursa forest fragment (hereafter Hilltop fragment) consists of 34 ha of secondary forest,

138   shrubland/bushland and *Eucalyptus* on a hilltop where bamboo has been nearly eradicated.

139   Hilltop fragment is surrounded by an anthropogenic matrix consisting of cultivated land, pastures

140   and human settlements. Currently, tree cutting and grazing in this fragment are forbidden by the

141   district government. However, the edge of the fragment, especially a portion consisting of a

142   *Eucalyptus* plantation with an understory of graminoids and forbs, is used for grazing of

143   livestock. Hilltop fragment was also dominated by bamboo forest three decades ago [Mekonnen

144   et al., 2012]. The distance between Hilltop and Patchy fragments is 9 km and they have been

145   separated from each other by human settlement, grazing land and agriculture for many decades

146   [Mekonnen et al., 2012]. The distance between the continuous forest and forest fragments is

147   ~160 km (Fig. 1).

148

149   **Study Groups**

150   We selected four Bale monkey groups in the three forests for detailed study: two adjacent

151   groups in the continuous forest at Odobullu (Continuous A and Continuous B), one group in

152   Patchy fragment and one group in Hilltop fragment. We habituated each group to human

153   observers for four months (from March-June 2013) by following them from dawn to dusk on a

154   near daily basis. Group sizes varied among the study groups: Continuous A: 65 individuals,

155   Continuous B: 38 individuals, Patchy fragment: 28 individuals and Hilltop fragment: 23

156   individuals. We determined the sizes of our study groups by opportunistically counting them

157   when they crossed gaps in the forest canopy or, in the case of fragment groups, descended to the

158   ground. During these counts, we were unable consistently to determine the age-sex category of

159   each individual and did not recognize animals individually.

160

Vegetation Description and Food Availability

162   We examined vegetation composition and structure along 2-4 randomly selected transects

163 200-750 m long and 5 m wide within the home range of each study group. We sampled large

164 trees in 50 m x 10 m vegetation quadrats (24 in Continuous forest, 27 in Patchy fragment and 24

165 quadrats in Hilltop fragment). We sampled only 12 quadrats for each of the continuous forest

166 groups because of the high homogeneity of bamboo forest habitats [Mekonnen et al., 2010a;

167 Eppley et al., 2015]. In each vegetation quadrat, AM, with the help of two research assistants,

168 measured and recorded the following variables for all large trees with a diameter at breast height

169 (DBH) ≥ 10 cm: species name, growth form, DBH (cm) (using caliper or tape measure), height

170 (m) (Nikon 550 range finder) and canopy size/diameter (m) (tape measure). We randomly

171 selected 50% of the vegetation quadrats for each group within which we counted and identified

172 to species level all plants ≥ 2 m tall. We felt this was necessary because the monkeys depend not

173 only on large trees but also on bamboo, shrubs and forbs. We classified plant growth forms into

174 six categories: bamboo, large trees (≥ 10 cm DBH), small trees (≥ 2 m tall and < 10 cm DBH),

175 shrubs, lianas (including climbers and epiphytes), and forbs. We collected unidentified plant

176 species and pressed them for later identification by professional botanists at the National

177 Herbarium, Addis Ababa University.

178   In each group's home range, we quantified species richness, stem density, and species

179 diversity for all plants ≥ 2 m tall and trees ≥ 10 cm DBH. We quantified plant species diversity

180 using the Shannon-Wiener index of diversity, *H′*, dominance index, *D* and evenness index, *J*

181 [Krebs, 1999]. We also assessed plant species richness and similarity. Plant species similarity

182 was calculated by the Sorensen's (*S*) index of similarity coefficient using EstimateS [Colwell,

183   2013]. To estimate the biomass of each large tree species, we calculated the basal area (BA) of

184   each tree from the DBH recorded using the following formula (BA $= [0.5 \times \text{DBH}]^2 \times \pi$)

185   [Fashing, 2001b].

186   To evaluate temporal changes in the availability of potential food resources over an annual

187   cycle, we carried out monthly phenological assessments of 8 plant species we anticipated would

188   be important in the diets of Bale monkeys based on preliminary observations of the four groups

189   in this study as well as the results from an earlier 8-month study of the species in continuous

190   forest [Mekonnen et al., 2010a]. We marked and identified 10-15 individuals of each species

191   within or near the vegetation transects for monthly monitoring, including trees ($\geq$ 10 cm DBH),

192   bamboo (*Arundinaria alpina*) and shrubs. After visual inspection (using binoculars when

193   necessary), we assigned each individual plant a relative abundance score for each of its potential

194   food items (young leaves, mature leaves, flowers, ripe fruits and shoots). Relative abundance

195   score ranged from 0 (item absent from plant) to 8 (plant fully laden with item, though keeping in

196   mind that different species may have different densities of an item, especially fruits, when fully

197   laden) at intervals of 1.

198   We analysed phenological data from five tree species (*Canthium oligocarpum, Dombeya*

199   *torrida, Galiniera saxifraga, Hagenia abyssinica,* and *Ilex mitis*), two shrubs (*Rubus apetalus*

200   and *Bothriocline schimperi*) and bamboo (*A. alpina*). These species accounted for 92.6% of the

201   overall diet for Continuous A; 93.4% for Continuous B, 50.9% for Patchy fragment and 44.5%

202   for Hilltop fragment. The lower contribution of monitored plants to the diets of fragment groups

203   resulted from them consuming much less bamboo as well as a greater variety of food species,

204   including difficult to monitor grasses and herbs [cf., Fashing et al., 2014], than continuous forest

205   groups [Mekonnen et al., in prep]. We calculated the monthly mean phenological scores for

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206 young leaves, fruits, flowers, and shoots for each individual plant species. We calculated a

207 monthly food availability index (FAI) for each plant part by multiplying the mean phenology

208 scores of species *i* with the mean basal area of species *i* and density of the corresponding species

209 *i* per ha [Fashing, 2001b].

210

Activity Budget

212 After two months of practice data collection, AM collected activity data with the help of two

213 well-trained research assistants from July 2013 through June 2014. From ca 0700 to 1730, these

214 data were collected via instantaneous scans [Altmann, 1974] of up to 5 minutes length every 15

215 minutes. The activity recorded for each individual was the first activity that lasted for ≥ 3

216 seconds once it came into view. During scans, we collected data for up to the first 5 adults or

217 juveniles but not from infants. We scanned the group each time from left to right to avoid

218 possible biases towards eye-catching activities like grooming, agonism and mating. During

219 scans, we recorded individuals as performing one of the following behaviors: feeding (foraging

220 for or masticating food items), moving (any locomotor behavior), resting (inactive), socializing

221 (playing, grooming, engaging in agonistic or sexual activity) or vocalizing. We obtained a total

222 of 28,583 individual behavioral scan records during 2085 h of observation (Continuous A = 441;

223 Continuous B = 432; Patchy fragment = 601; Hilltop fragment = 611) over 234 group follow

224 days (Continuous A = 52; Continuous B = 54; Patchy fragment = 61; Hilltop fragment = 67)

225 lasting 6.0 (incomplete but usable day) – 10.5 h (complete day).

226 We calculated the proportions of time spent on different activities by dividing the number of

227 behavioral records for each activity category with the total number of activity records. We used

228 the behavioral records of the group to calculate the activity budgets per day and averaged within

229   each month to construct monthly activity budgets for each study group (mean ± SD records;

230   Continuous A = 453.5 ± 81.7; Continuous B = 458.3 ± 139.0; Patchy fragment = 854.5 ± 135.2;

231   Hilltop fragment = 615.7 ± 113.6). The grand mean proportions of the monthly budgets provided

232   the annual activity budgets for the entire study period. We combined social behaviors (agonism,

233   grooming, playing and sexual activity) in our data analyses because some of these behaviors

234   accounted for <1% of the total activity budget.

235

236   **Spatial Analysis: Home Range and Movement Rate**

237   We also recorded the location of the estimated geographic center of the group [Fashing,

238   2001a] and elevation using a handheld Garmin GPSMap 62s Geographic Positioning System

239   (GPS) at 15-minute intervals. We recorded GPS locations even if activity data were not recorded

240   owing to poor visibility as long as we confirmed the group's location via cues such as distinctive

241   tree movements or vocalizations.

242   For spatial analysis, we used a combination of ArcGIS 10.3 [ESRI, 2011], Home Range

243   Tools (HRT) version 2.0 [Rodgers et al., 2015], Geospatial Modeling Environment (GME)

244   Version 0.7.3 [Beyer, 2015] and R [R Development Core Team, 2015]. We modelled home

245   range using Home Range Tools (HRT) in ArcGIS 10.3 using all GPS locations recorded. We

246   used fixed Kernel Density Estimations (KDEs) which measure utilization distribution [Worton,

247   1989; Seaman and Powell, 1996]. We used an *ad hoc* bandwidth estimator, which minimizes

248   over-smoothing of the reference bandwidth (h_{ref}), that performs better for large sample sizes and

249   clumped GPS locations [Kie et al., 2010]. In this study, we defined home range as *ad hoc* fixed

250   KDE with 95% isopleths (contour lines) and core areas with 50% isopleths. In addition, we

251   modelled home range using the Minimum Convex Polygon (MCP) method to enable comparison

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252 with earlier studies [Harris et al., 1990]. We calculated MCP (90%, 95% and 100% MCPs) using

253 fixed mean points [Rodgers et al., 2015]. To estimate home range and core area overlap between

254 adjacent groups, we used ArcGIS analysis tools to intersect the corresponding home ranges and

255 core areas of adjacent groups. We defined home range overlap as the percentage of the area

256 shared by adjacent groups relative to the total home range used by each group. To assess the

257 influence of patch effect in each group's home range, we calculated a shape index (perimeter-to-

258 area ratio) of 95% KDE by dividing its perimeter (m) by the square root of home range size (m^2)

259 multiplied by π. Shape index values usually vary from 1 (more circular) to >5 (more elongated

260 and irregular) [Forman and Godron, 1986]. A shape index value indicates the patch area exposed

261 to the edge [Helzer and Jelinski, 1999].

262   To estimate hourly movement rates (MVRs, m/h), we used complete days as well as

263 incomplete days with group follows of $\geq$ 7 hrs. We first converted the consecutive GPS locations

264 of each study group to point shapefile in ArcGIS 10.3 and measured daily path length using two

265 commands in GME (*convert.pointstolines* and *addlength*). We calculated hourly movement rate

266 (m/hr) by dividing the daily path length (m) by the total time traveled (hr) per day. The mean of

267 the 12 monthly MVRs provided the mean annual MVR for each group.

268

Habitat Use

270   During the scan sampling at 15-minute intervals, we also recorded the habitat type occupied

271 by the majority of the group. We categorized habitats as bamboo forest, mixed-bamboo forest,

272 tree-dominated forest, shrubland, cultivated land, grazing land, or *Eucalyptus* plantation. In

273 bamboo forest, bamboo accounts for $\geq$50% of the stem density and large trees are scarce. Mixed-

274 bamboo forest is a habitat consisting of 10-49% bamboo as well as many large trees. In tree-

275   dominated forest, large trees account for >50% the canopy cover and bamboo accounts for <10%

276   of the stem density. Shrubland consists of ≥50% of shrubs, predominantly *Rubus apetalus*,

277   *Bothriocline schimperi* and *Jasminum abyssinicum*, and relatively few trees. Cultivated land is

278   used for cultivation, especially enset (*Ensete ventricosum*) and home gardens. Grazing land is

279   covered by graminoids and forbs and exploited by livestock. *Eucalyptus* plantation consists

280   primarily of *Eucalyptus* sp. with or without a graminoid and forb understory. To examine matrix

281   use patterns, we also categorized the locations occupied by most of the group members during

282   scans as matrix (human use areas used for cultivation, plantation, and grazing) or forest (all other

283   areas).

284   Within each group's 95% KDE home range, we calculated habitat selection ratios by

285   dividing the frequency of observed use (% of scans in each habitat type) by the frequency of

286   expected use (% of home range area accounted for by each habitat type) [Manly et al., 2002]. To

287   obtain the frequency of expected use, the habitat types within each home range were classified

288   using high resolution Google Earth images (continuous forest: 18 January 2014; forest

289   fragments: 24 January 2014) of the study area in ArcGIS 10.3 [Pebsworth et al., 2012; Kelley,

290   2013] and ground-truthed with the GPS and habitat type data collected during group follows. A

291   habitat selection ratio close to 1 indicates no selectivity for that habitat, < 1 indicates a habitat is

292   avoided and > 1 indicates a habitat is selected.

293

Statistical Analyses

295   All statistical tests were carried out using the statistical software R version 3.2.3 [R

296   Development Core Team, 2015] with significance level $P \leq 0.05$ unless otherwise stated. We

297   tested all data for normality using the Shapiro-Wilk test and homogeneity of variances using the

298 Levene test (P > 0.05). We initially calculated and compared all the variables for each Bale

299 monkey study group individually and examined the differences using a one-way ANOVA model

300 followed by Tukey's HSD *post hoc* test. When the results for the two continuous forest or the

301 two forest fragment groups showed the same general patterns, we then combined them into a

302 single continuous forest or forest fragment category unless otherwise stated. To examine

303 differences across groups in general habitat characteristics and monthly movement rates, we used

304 a one-way ANOVA after we log transformed the data to fit the assumption of normality. We also

305 used a one-way ANOVA test for differences in monthly activity budgets among groups in

306 continuous forest and forest fragments. We performed logit transformations of proportion data

307 prior to statistical analysis to normalize the data as recommended by Warton and Hui [2011].

308 Permission to conduct this research was granted by the Ethiopian Wildlife Conservation

309 Authority. This study complied with the American Society of Primatologists's Principles for the

310 Ethical Treatment of Nonhuman Primates and adhered to the legal requirements of Ethiopia.

311

312 **RESULTS**

313 **Habitat Description and Resource Availability**

314 Plant species richness was higher in the fragments (Patchy: 35 species; Hilltop: 47 species)

315 than in the continuous forest (Continuous A: 23 species; Continuous B: 19 species). The ranges

316 of the two continuous groups had a higher plant species similarity index (19 shared species;

317 Sorensen's S = 0.91) than the ranges of the two fragment groups (28 shared species; Sorensen's

318 S = 0.68). Plant species diversity and evenness were much higher and dominance much lower in

319 fragmented forest than continuous forest (Table I). Bamboo dominated (85.9% of stems ≥ 2 m

320 tall, n = 6217) in continuous forest, but accounted for only 39.6% of stems (n = 1341) in Patchy

14

321   fragment and 1.6% of stems (n = 37) in Hilltop fragment. The density of bamboo was nearly 5-

322   times greater in Continuous forest than in Patchy fragment and 170-times greater in Continuous

323   Forest than in Hilltop fragment (Table I). Large trees ($\geq$ 10 cm DBH) were also more abundant

324   in Continuous forest (mean = 198.3 stems/ha) than in the fragments (mean = 138.1 stems/ha).

325   However, shrubs were far more abundant in fragments (mean = 979.2 stems/ha) than in

326   continuous forest (mean = 65.0 stems/ha) (Table I).

327   The basal area of large ($\geq$ 10 cm DBH) food trees was nearly 3-times higher in continuous

328   forest (mean = 2292.0 cm^2/ha) than in fragments (mean = 780.2 cm^2/ha) (Table I). Further, Bale

329   monkeys had significantly higher monthly food availability indices of bamboo young leaves

330   (ANOVA: F = 544.00, df = 1, P < 0.001), non-bamboo young leaves (ANOVA: F = 17.17, df =

331   1, P < 0.001), and fruits (ANOVA: F = 4.19, df = 1, P = 0.05) in continuous forest than in forest

332   fragments.

333

Activity Budget

334

335   Bale monkeys in all study groups spent most of their time feeding (51.5-56.2%), followed by

336   moving (17.5-25.3%), resting (12.0-18.1%), socializing (2.8-12.7%) and vocalizing (0.3-4.8%)

337   (Fig. 2). Groups in continuous forest spent significantly more time feeding (55.5% vs. 52.3%;

338   ANOVA: F = 4.9, df = 1, P < 0.001), moving (24.7% vs. 18.6%; ANOVA: F = 34.1, df = 1, P <

339   0.001) and vocalizing (4.6% vs 0.6%; ANOVA: F = 181.3, df = 1, P < 0.001) and significantly

340   less time resting (12.2% vs. 17.6%; ANOVA: F = 30.4, df = 1, P < 0.001) and socializing (2.9%

341   vs. 10.9%; ANOVA: F = 57.4, df = 1, P < 0.001) than groups in forest fragments.

342

Spatial Analysis

343

344   The 95% KDE home ranges were 39.9 ha for Patchy fragment group, 26.1 ha for Continuous

345   group A, 15.9 ha for Continuous group B and 15.8 ha for the Hilltop fragment group (Fig. 3;

346   Table II). Home range overlap between the continuous forest groups was 7.5 ha (Fig. 3). The

347   Patchy and Hilltop fragment groups each overlapped with one adjacent group, although we did

348   not carry out a systematic study to determine the amount of overlap. The Patchy fragment group

349   had a larger annual core area than groups at the other sites (Fig. 3; Table II). The two adjacent

350   continuous forest groups had only 0.1 ha overlap of their core areas. We found that the Patchy

351   fragment group had a higher perimeter-to-area ratio (5.8) than the other groups (Continuous A:

352   4.1; Continuous B: 2.6; Hilltop: 2.2) because of its extremely elongated and irregularly shaped

353   home range. Bale monkeys in continuous forest had a significantly higher movement rate (Mean

354   = 121.2 ± 6.4 m/hr) than monkeys in forest fragments (Mean = 94.5 ± 5.1 m/hr) (ANOVA: F =

355   16.77, df = 1, $P < 0.001$) (Table III).

356

357   **Habitat Use**

358   The home ranges of continuous forest groups consisted solely of bamboo and mixed-bamboo

359   forest habitats while Patchy fragment group used five and Hilltop fragment group four habitat

360   types (Fig. 4; Table IV). Continuous A used both bamboo and mixed bamboo forest in

361   accordance with their respective availabilities in its home range. However, Continuous B used

362   the bamboo forest significantly more than expected based on its percentage representation in the

363   home range. Patchy fragment group used mixed-bamboo forest and shrubland more than

364   expected while using grassland, tree-dominated forest and cultivated land less than expected.

365   Hilltop fragment group used shrubland and tree-dominated forest more than expected, and

366   *Eucalyptus* plantation and grazing land habitats less than expected (Table IV). Overall, Patchy

367   fragment group spent far more time in matrix habitat than the other groups (Patchy: 73.5%;

368   Hilltop: 26.9%; Continuous A; 0% and Continuous B: 0%).

369

370   **DISCUSSION**

371   **Impacts of Fragmentation and Bamboo Loss on Habitat Quality**

372   Habitat loss and fragmentation resulted in major differences in habitat characteristics,

373   vegetation composition and structure in our montane forest study sites in southern Ethiopia. Our

374   results are consistent with those from studies of tropical forests elsewhere which have shown that

375   fragmentation leads to reduction in the availability of large food trees, changes in tree

376   composition and diversity, and reduction in overall habitat quality [Laurance et al., 2000;

377   Arroyo-Rodríguez et al., 2007]. In our study, although fragments had higher plant species

378   richness, Bale monkey groups in continuous forest had access to a greater abundance of both

379   bamboo and large food trees, suggesting that the continuous forest was of much higher habitat

380   quality than the forest fragments. In Malagasy forests, which also contain primate bamboo

381   specialists (bamboo lemurs: *Hapalemur* spp.), habitat destruction has also been demonstrated to

382   increase plant species richness, but lower the density of food plants, leading to reduced overall

383   habitat quality for lemurs in forest fragments [Tan, 1999; Grassi, 2006]. Furthermore,

384   fragmentation-induced reduction in habitat quality may lower carrying capacity and group size,

385   adversely affecting the long-term viability of primates occupying fragments [Arroyo-Rodríguez

386   and Mandujano, 2006]. In our study, group size was indeed much lower in forest fragments

387   (mean=25.5 individuals, n=2 groups) than in continuous forest (51.5 individuals, n=2 groups),

388   though we lack the population density data necessary to evaluate the possibility of differences in

389   Bale monkey carrying capacity between forest types [cf., Butynski, 1990].

390

Are Bale Monkeys in Forest Fragments Energy Minimizers?

392   Our study suggests that Bale monkeys in fragments adopt an energy minimization strategy.

393   Specifically, they spent more time resting, less time feeding and moving, and traveled at a slower

394   rate than conspecifics in continuous forest. They also socialized more in fragmented forests,

395   though most Bale monkey social behavior consists of grooming, which is not believed to be a

396   very energetically demanding activity [Russell and Phelps, 2013]. The apparent energy

397   conservation strategy of Bale monkeys in fragments may be a response to the lower overall food

398   availability at these sites. A number of primates adopt a similar strategy to cope with the limited

399   abundance, density and quality of food resources in fragments, including several other folivores,

400   *Colobus vellerosus* [Wong and Sicotte, 2007], *Alouatta palliata* [Dunn et al., 2009], and *Alouatta*

401   *seniculus* [Palma et al., 2011], and at least one granivore, *Chiropotes satanas* [Boyle and Smith,

402   2010]. Another proximate factor that may contribute to primates adopting an energy

403   conservation strategy in fragments is that ambient temperatures are often higher there than in

404   nearby continuous forests [Silva and Ferrari, 2009; Korstjens et al., 2010]. Indeed, mean daily

405   temperature averaged a full two degrees higher in forest fragments (16.7 $^{\circ}$C SE $\pm$ 0.4) than in

406   continuous forest (14.7 $^{\circ}$C SE $\pm$ 0.2) during our study [Mekonnen et al. in prep.], perhaps

407   contributing to the greater time spent resting and slower rates of movement among Bale monkeys

408   inhabiting fragments. However, we cannot rule out the possibility that the monkeys in the hotter

409   forest fragments are more active during what are presumably the coolest times of day, earlier in

410   the morning and later in the evening than our observation hours (typically 0700-1730). Lastly, it

411   is often the case, including in our study, that primates in continuous forest live in considerably

412   larger groups than conspecifics in fragments [Marsh, 2003], raising the possibility that increased

413   scramble competition [Isbell, 1991] might also contribute to increases in the proportion of time

414   spent foraging and moving by Bale monkeys and other primates in continuous forest.

415

How Ecologically Flexible are Bale Monkeys?

417   Habitat loss and degradation affect plant species richness, diversity and structure in forest

418   fragments consequently modifying the natural habitat and availability of food resources for

419   species [Marsh, 2003]. Forest fragments generally consist of islands of disturbed vegetation

420   surrounded by areas of intensive human use [Benchimol and Peres, 2013]. Bale monkeys in

421   forest fragments proved able to use the surrounding human matrix, with the group in Patchy

422   fragment, in particular, spending nearly ¾ of its time in matrix habitat. Groups in fragments also

423   supplemented their diets with alternative food resources to bamboo including shrubs, forbs,

424   graminoids, and even cultivated foods; most of these items were never consumed by groups in

425   continuous forest [Mekonnen et al., in prep]. These findings suggest that Bale monkeys in forest

426   fragments are capable of much greater ecological flexibility than was previously believed

427   [Carpaneto and Gippoliti, 1994; Butynski et al., 2008; Mekonnen et al., 2010a].

428   Intriguingly, the sister taxa to Bale monkeys, the five other species of *Chlorocebus* (two of

429   whom - *C. aethiops* and *C. pygerythrus* - also occur in Ethiopia), are renowned for their

430   ecological flexibility, inhabiting a variety of habitats including shrublands, grasslands,

431   woodlands and riverine forests as well as human matrix areas [Isbell et al., 1998; Zinner et al.,

432   2002; Enstam and Isbell, 2007]. While Bale monkeys do not match the other *Chlorocebus* taxa in

433   degree of plasticity of diet or habitat use [Enstam and Isbell, 2007], our study suggests that they

434   retain at least some of the ancestral ecological flexibility we assume to be characteristic of the

435   genus *Chlorocebus*. However, given recent morphological [some individuals in fragments

436 exhibit intermediate physical characteristics between Bale monkeys and grivets: Mekonnen et

437 al., 2012] and genetic [mitochondrial DNA haplotypes suggest continuous and fragment

438 populations form two different clades: Mekonnen et al., in prep.] evidence, it is also possible that

439 a recent history of hybridization with other *Chlorocebus* taxa has contributed to the ecological

440 plasticity of Bale monkeys in fragments that we documented.

441   Our results show that Bale monkeys can cope with a certain threshold of habitat destruction.

442 This flexibility stands in stark contrast to the case of the giant panda (*Ailuropoda melanoleuca*)

443 of China, another bamboo specialist, which shows few signs of being able to cope with intensive

444 disturbance of its habitat. Indeed, 99% of the diet of the giant panda consists of bamboo and it

445 has never been observed to occur outside of thick bamboo forest [Schaller, 1985; Reid and

446 Jinchu, 1991]. Conversely, the other major primate bamboo specialists, the bamboo lemurs

447 (*Hapalemur aureus*, *H. griseus*, and *H. simus*) of Madagascar, are able to exploit modified

448 habitats and subsist on a mix of bamboo and other food resources, including human crops, in

449 logged and degraded forests [Tan, 1999; Grassi, 2006; Tan, 2006]. These patterns suggest that

450 bamboo-eating primates are more flexible than carnivora (i.e., pandas) that subsist on bamboo

451 for whom the bamboo eating adaptation may be a more ancient adaptation. Nevertheless, it

452 remains unclear whether even the more ecologically versatile bamboo lemurs and Bale monkeys,

453 can persist over the long-term in such small and isolated forest fragments particularly if their

454 exploitation of human crops within the nearby matrix results in conflict with local communities

455 [Tan, 2006; Mekonnen et al., 2012].

456

457 **Implications for Conservation and Management**

458   Bale monkeys in fragments have smaller group sizes, experience lower bamboo availability,

459   and appear to adopt a strategy of energy minimization. Long-term monitoring of Bale monkeys

460   in fragments will be essential to determining if life in fragments is an evolutionarily viable

461   strategy for the species or if these adjustments are having negative fitness consequences [cf.,

462   Chapman et al., 2013]. If population declines are occurring in fragments, the possibility of

463   connecting isolated patches to ensure metapopulation connectivity should be explored [Foster et

464   al., 2016]. In light of recent genetic evidence that fragmented populations form a separate clade

465   from continuous populations [Mekonnen et al., in prep.], as many remaining fragments as

466   possible containing Bale monkeys should be protected. We recommend that Bale monkey habitat

467   restoration programs should focus first on increasing fragment sizes, minimizing edge effects

468   and incorporating matrix habitats into management plans [cf., Anderson et al., 2007] now that

469   our study has demonstrated that Bale monkeys in fragments can and do exploit adjacent areas of

470   matrix. In sum, the conservation actions we recommend would help to conserve the important

471   remaining tropical montane forest habitats of southern Ethiopia and minimize the future

472   extinction risk of isolated populations of Bale monkeys and other wildlife in the human

473   dominated landscapes of the region.

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666 **TABLES**

667 **TABLE I. Characteristics of the Bale monkey study sites, groups, habitats and home ranges in southern Ethiopia.**

Characteristics of study sites and groups	Continuous A	Continuous B	Patchy fragment	Hilltop fragment	df, F, P-Value
Forest/ fragment size (ha)	14100	14100	162	34	
Group size	65	38	28	23	
Mean elevation (m asl) (Range)	2758 (2617-2893)	2751 (2628-2842)	2650 (2544-2780)	2706 (2582-2790)	
Distance to the nearest village (m)	6000	6000	0	0	
Habitat quality					
Total species richness ≥ 2 m tall	23	19	35	47	
All plant species diversity index, Shannon-Weaver H'	0.78	0.68	2.17	3.13	
All plant species evenness index, J	0.09	0.10	0.25	0.48	
All plant species dominance index, D	0.72	0.76	0.21	0.08	
Large tree species richness ≥ 10 cm DBH	9.00	7.00	14.00	12.00	
Large tree species diversity index, Shannon-Weaver H'	1.17	1.10	1.58	1.61	
Large tree species evenness index, J	0.36	0.43	0.35	0.42	
Large tree species dominance index, D	0.48	0.50	0.32	0.25	
Bamboo stem density per ha	7720.00	4713.33	1332.74	37.22	
Large tree stem density per ha	236.67	160.00	137.04	139.18	
Shrub stem density per ha	93.33	36.67	878.49	1079.94	
Small tree density per ha	340.00	140.00	831.36	529.91	

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Lianas density per ha	693.33	266.67	208.55	368.54	
Forbs density per ha	26.67	93.33	0.00	157.22	
Total stem density per ha (N)	9110.00	5410.00	3388.47	2312.00	
Characteristics of home ranges (large trees ≥10 cm DBH and bamboo, mean ± SE)					
Number of large trees measured (N)	142	96	185	167	
DBH of large trees (cm)	33.20 ± 2.03	31.88 ± 2.40	23.68 ± 1.20	38.27 ± 1.06	3, 37.0***
Height of large trees (m)	18.49 ± 0.53	19.04 ± 0.63	11.11 ± 0.42	22.13 ± 0.94	3, 67.4***
Canopy size of large trees (m)	6.07 ± 0.32	7.10 ± 0.39	3.93 ± 0.12	4.78 ± 0.17	3, 35.9***
Basal area of large trees (cm^2/ha)	2208.83 ± 392.38	2046.29 ± 424.08	480.91 ± 59.54	1079.52 ± 63.19	3, 76.0***
DBH of food trees (cm)	33.64 ± 2.12	34.90 ± 2.74	22.64 ± 1.16	41.37 ± 1.46	3, 37.7***
Height of food trees (m)	18.62 ± 0.59	19.41 ± 0.71	11.01 ± 0.45	15.72 ± 0.70	3, 60.7***
Canopy size of food trees (m)	6.12 ± 0.35	7.34 ± 0.46	3.88 ± 0.11	5.46 ± 0.22	3, 36.9***
Basal area of food trees (cm^2/ha)	2213.29 ± 412.84	2370.68 ± 501.11	433.99 ± 60.22	1263.51 ± 91.57	3, 77.9***
DBH of bamboo stems (cm)	4.23 ± 0.04	4.05 ± 0.05	2.14 ± 0.04	-	2, 670.7***
Height of bamboo stems (m)	7.64 ± 0.08	6.78 ± 0.13	4.37 ± 0.08	-	2, 59.6***

668   The last column shows the *P*-value for One-Way ANOVA tests across four group home ranges with significant difference, P <0.001

669   (***)

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671

32

672   **TABLE II. Annual home range and core area comparison between the four Bale monkey study groups**

Forest type	Group	No of days	*No. GPS points	Annual Home Range (ha)				Core Area (ha)	Group size
				95% KDE*	100% MCP	95% MCP	90% MCP	50% KDE*	
Continuous forest									
	Continuous A	56	1488	26.1	37.6	26.9	22.6	5.9	65
	Continuous B	57	1496	15.9	22.2	17.0	15.3	4.0	38
Fragment									
Patchy fragment	Patchy fragment	61	2296	39.9	78.8	71.7	70.2	8.8	28
Hilltop fragment	Hilltop fragment	67	2241	15.8	18.7	15.0	13.4	5.2	23

673   *Results were similar when the analysis was done using only 1488 randomly selected GPS points for each group, with little variation

674   within repeated randomly selected samples.

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680 **Table III. Mean movement rates (m/hr) of the four Bale monkey study groups.**

Forest	Group	No. of days	Mean No. GPS points per day	Movement rate (m/hr) Mean	SE	Range
Continuous						
	Continuous A	44	29.0	128.5	7.7	94.1-188.8
	Continuous B	41	29.0	113.8	5.0	94.9-146.1
Fragment						
Patchy fragment	Patchy fragment	58	38.4	102.7	6.9	67.1-130.9
Hilltop fragment	Hilltop fragment	61	34.4	86.3	3.3	62.3-110.9

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686   **TABLE IV. Differences in the total area of available habitat types (ha) and their percentage representations, observed use**

687   **(observed number of habitat records), expected use (expected number of habitat records) and selection ratio of each habitat**

688   **calculated within the 95% KDE home ranges of each study group.**

Group	Habitat types	Area (ha)	Area (%)	Observed use	Expected use	Selection ratio	Habitat selection status
Continuous A	Bamboo forest	14.00	53.67	715	704	1.02	No selection
	Mixed-bamboo forest	12.09	46.33	596	607	0.98	No selection
Continuous B	Bamboo forest	8.85	55.56	832	745	1.12	Selected
	Mixed-bamboo forest	7.08	44.44	509	596	0.85	Avoided
Patchy fragment	Mixed-bamboo forest	6.82	17.08	466	380	1.23	Selected
	Tree-dominated forest	3.18	7.96	139	177	0.78	Avoided
	Shrubland	11.80	29.54	933	657	1.42	Selected
	Cultivated land	2.99	7.49	163	167	0.98	No selection
	Grazing land	15.15	37.93	524	844	0.62	Avoided
Hilltop fragment	Tree-dominated forest	3.58	22.66	503	469	1.07	Selected
	Shrubland	7.96	50.38	1255	1043	1.20	Selected
	Grazing land	0.42	2.66	0	55	0.00	Avoided
	Eucalyptus plantation	3.84	24.30	312	503	0.62	Avoided

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692 **FIGURE LEGENDS**

693 Fig. 1. Map of the study sites showing continuous and fragmented forests in southern Ethiopian

694 Highlands

695 Fig. 2. The proportion of time members of the four Bale monkey study groups spent engaging in

696 different activities (N=12 months, mean±SE; Continuous A 5442 scans on 52 days; Continuous

697 B 5499 scans on 54 days; Patchy fragment 10254 scans on 61 days, and Hilltop fragment 7388

698 scans on 67 days).

699 Fig. 3. Annual home ranges (ha) and core areas (ha) of Bale monkey groups in continuous and

700 fragmented forests: open line (95% MCP), orange (95 % KDE home range), light green (50%

701 KDE core area), red crossbars (95% KDE overlap between Continuous A and Continuous B),

702 and dark green (50% core area overlap between Continuous A and Continuous B).

703 Fig. 4. Map of available habitats in the home ranges of the Bale monkey study groups.

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706   **FIGURES**
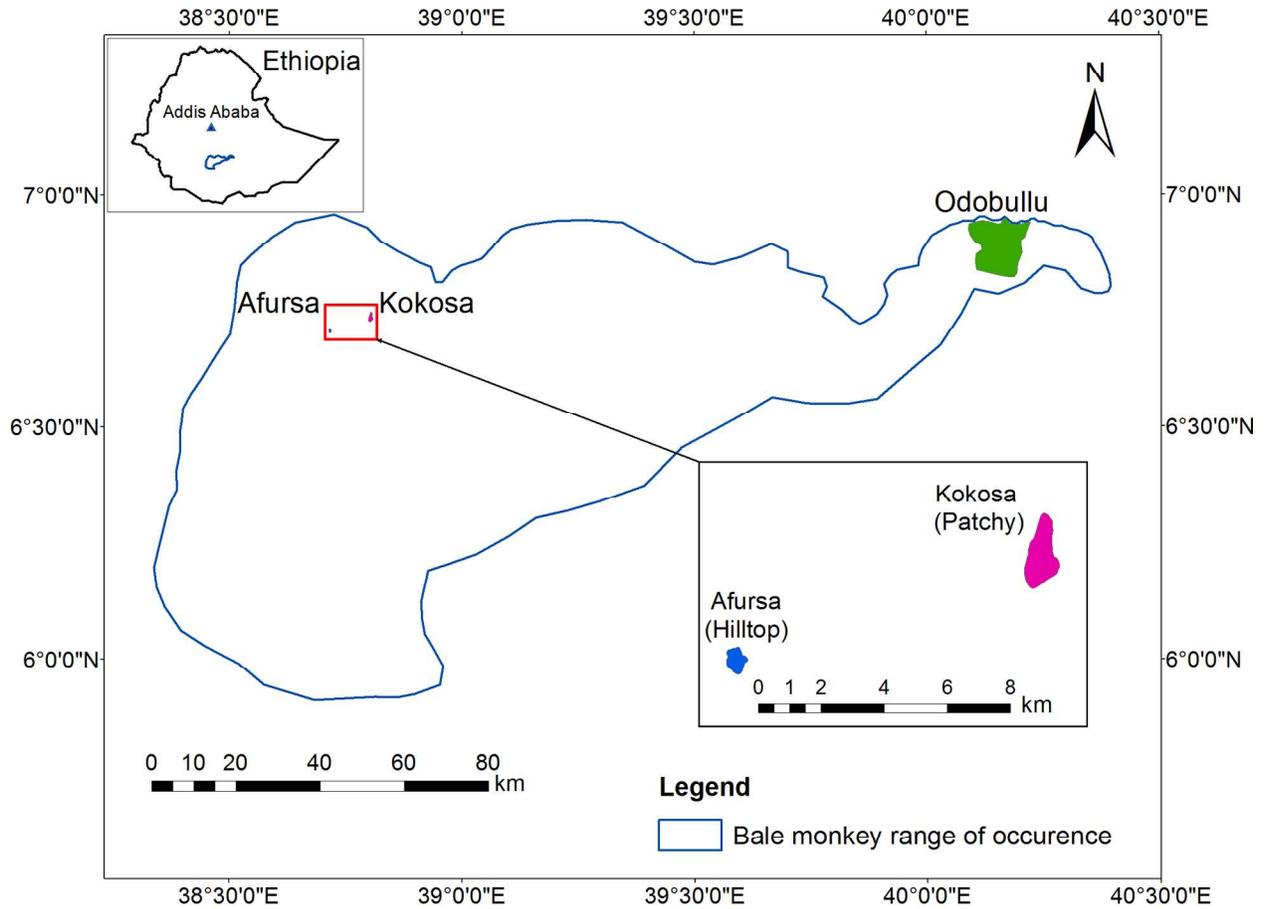
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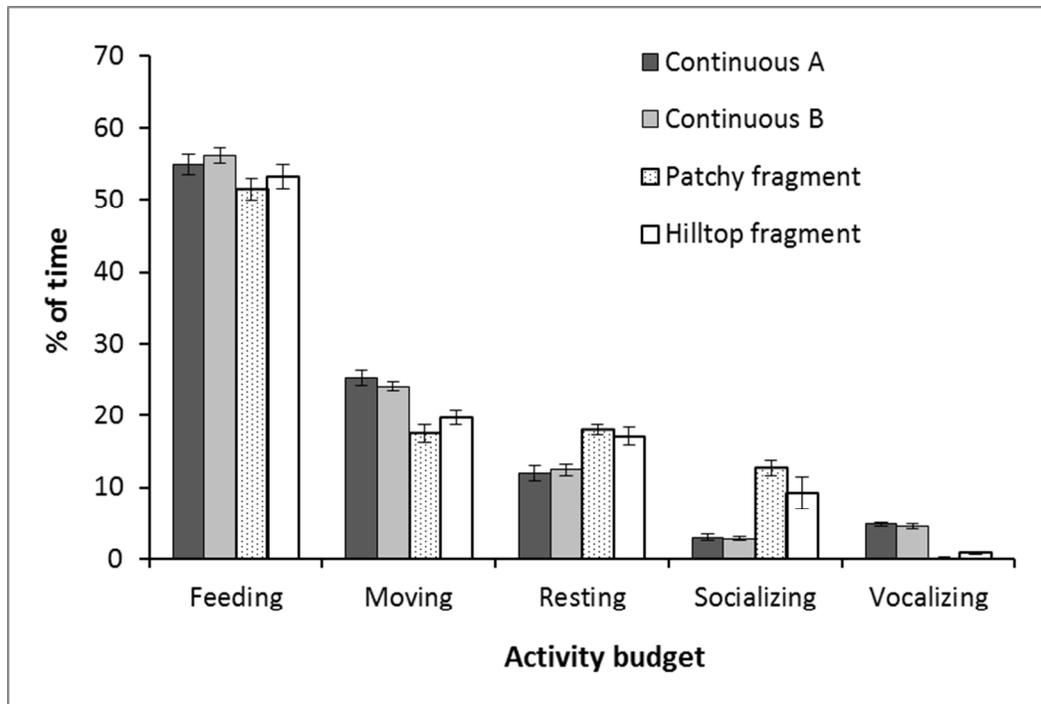
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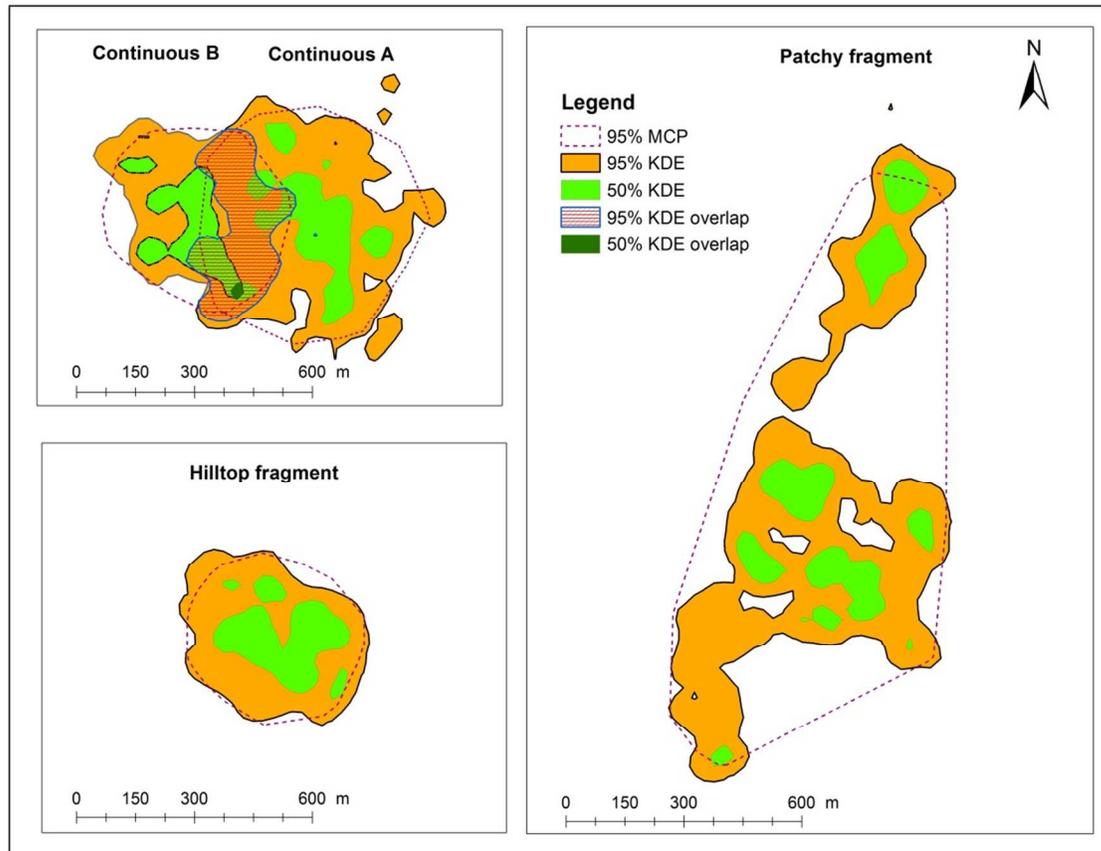
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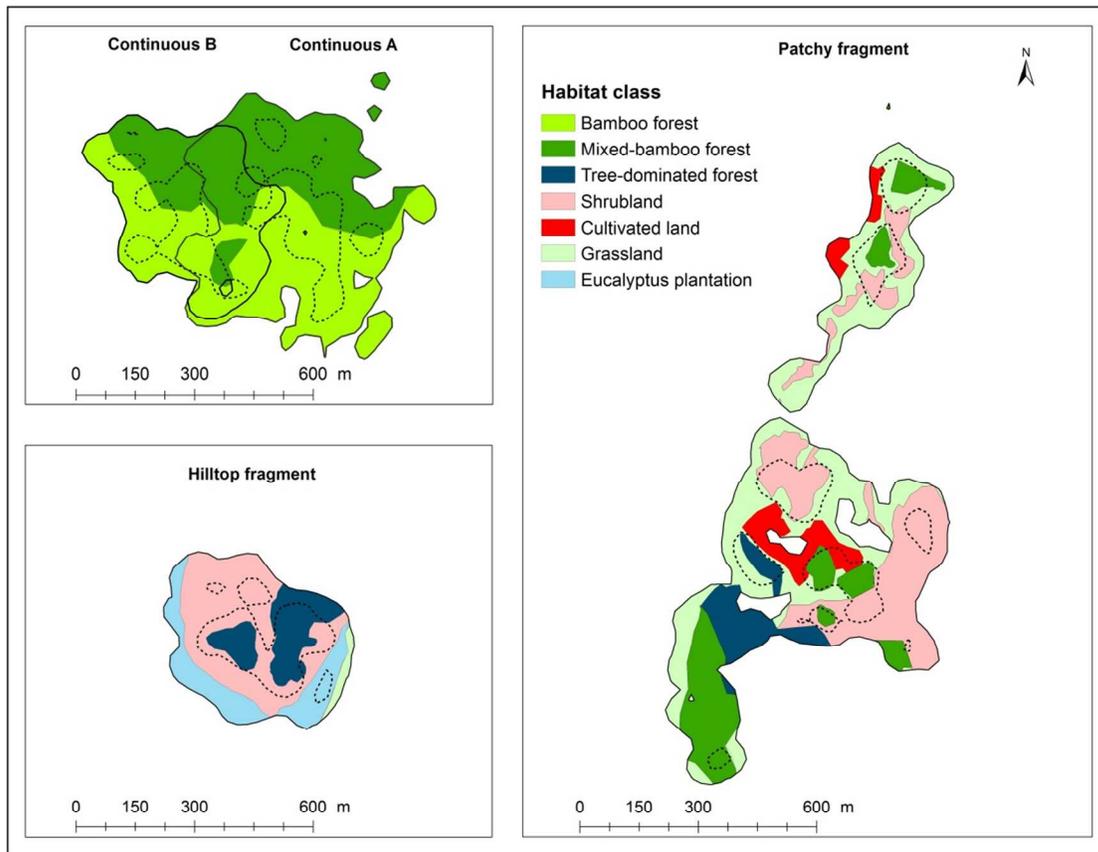
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