

1 **Flexibility in positional behavior, strata use, and substrate utilization**
2 **among Bale monkeys (*Chlorocebus djamdjamensis*) in response to habitat**
3 **fragmentation and degradation**

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23 Running header: Habitat fragmentation impacts positional behavior, strata use, and substrate
24 utilization of Bale monkeys

25 **Abstract:** Studies of the effects of habitat fragmentation and degradation on primate positional
26 behavior, strata use, and substrate utilization offer valuable insights into the behavioral and
27 ecological flexibility of primates whose habitats have undergone extensive anthropogenic
28 disturbance. In this study, we evaluated how positional behavior, strata use, and substrate
29 utilization differed between Bale monkeys (*Chlorocebus djamdjamensis*) – bamboo-eating
30 cercopithecids endemic to the southern Ethiopian Highlands – occupying continuous versus
31 fragmented forests. Bale monkeys in forest fragments (where bamboo had been degraded or
32 eradicated) spent significantly more time on the ground and in understory strata whereas those
33 in continuous forest spent significantly more time in the middle and upper strata. Bale monkeys
34 in forest fragments also spent significantly more time walking and galloping and significantly
35 less time climbing than those in continuous forest. Our results suggest that, unlike the primarily
36 arboreal Bale monkeys in continuous forest, Bale monkeys in forest fragments should be
37 characterized as semi-terrestrial. In response to habitat disturbance in fragments, we observed
38 a greater emphasis on terrestrial foraging and travel among Bale monkeys in these human
39 altered habitats, which may put them at greater risk of predation and conflict with nearby human
40 populations. Bale monkeys in fragments exhibit flexibility in their positional behavioral
41 repertoire and their degree of terrestriality is more similar to their sister taxa in *Chlorocebus*
42 than to Bale monkeys in continuous forest. These findings suggest that habitat alteration may
43 compel Bale monkeys to exhibit semi-terrestrial behaviors crucial for their persistence in
44 human-modified habitats. Our results contribute to a growing body of literature on primate
45 behavioral responses to anthropogenic modification of their habitats and provide information
46 that can contribute to the design of appropriate conservation management plans.

47 **KEYWORDS**

48 Ethiopian Highlands, forest fragment, locomotion, posture, terrestriality

49 **INTRODUCTION**

50 Habitat loss and fragmentation are the greatest threats to biodiversity conservation in the tropics
51 (Crooks et al., 2017; Haddad et al., 2015). Primates are particularly vulnerable to extinction
52 because of their frequent dependence on forests (Almeida-Rocha, Peres, & Oliveira, 2017;
53 Estrada et al., 2017). Habitat destruction and fragmentation impact primates in many ways,
54 including altering their diets, activity budgets, and ranging patterns (Campera et al., 2014;
55 Chaves & Bicca-Marques, 2016; Chaves, Stoner, & Arroyo-Rodríguez, 2011; Chaves, Stoner,
56 & Arroyo-Rodríguez, 2012; Irwin, 2008a, b). Though less often studied, positional behavior
57 (locomotor and postural behaviors) and forest strata and substrate use are also impacted by
58 habitat destruction and fragmentation (Aronsen, 2004; Dagosto & Yamashita, 1998; Zhou, Luo,
59 Wei, & Huang, 2013), and flexibility in positional behavior can be essential to the persistence
60 of forest primate taxa in degraded or isolated habitats. For example, being capable of greater
61 terrestriality in disturbed habitats can be critical to a species' ability to exploit resources in the
62 human matrix areas that often surround forest fragments (Ancrenaz et al., 2014; Eppley, Donati,
63 & Ganzhorn, 2016; Xiang, Huo, Xiao, Quan, & Grueter, 2009).

64 Positional behaviors are influenced by both extrinsic (e.g., ecological factors) (Bitty &
65 McGraw, 2007; Gebo & Chapman, 1995a) and intrinsic factors (e.g., postcranial morphology
66 and anatomy) (Fleagle, 2013; Garber, 2007; Sargis, Terranova, & Gebo, 2008). Habitat
67 structure, food availability, diet, and the presence of predators are the most important ecological
68 factors influencing the positional behavior and strata use of many primate species (Bitty &
69 McGraw, 2007; Cannon & Leighton, 1994; Gebo & Chapman, 1995a; Huang et al., 2015;
70 McGraw, 1998a). The locomotor behavior (movement with gross displacement of the animal)
71 of some species varies among forest types: e.g., red colobus monkeys (*Colobus badius*) (Gebo
72 & Chapman, 1995b), lemurs (Dagosto & Yamashita, 1998), and black-and-gold howlers
73 (*Alouatta caraya*) (Prates & Bicca-Marques, 2008). These differences can often be attributed

74 to variation in forest structure associated with changes in diet and the availability and
75 distribution of food resources (Garber, 1998; McGraw, 1998a; Prates & Bicca-Marques, 2008;
76 Youlatos, 1998b; Youlatos, 2002). Conversely, locomotor behavior is often invariable within
77 species even across forest types. For instance, despite differences in habitat quality, locomotor
78 modes were similar in studies of mustached tamarin monkeys (*Saguinus mystax*) in Peru
79 (Garber & Pruetz, 1995) and five species of cercopithecoid monkeys (*Cercopithecus* spp. and
80 *Colobus* spp.) in Ivory Coast (McGraw, 1996). On the other hand, habitat fragmentation and
81 degradation had variable effects on the feeding and resting postural behaviors of these species
82 due to architectural differences across habitats (Garber & Pruetz, 1995; Gebo & Chapman,
83 1995b; McGraw, 1998a). In particular, feeding posture appears to be most affected by dietary
84 and architectural differences across habitats (Garber, 1998; Gebo & Chapman, 1995b), whereas
85 resting posture seems less likely to be affected by habitat structure (Garber & Pruetz, 1995;
86 McGraw, 1996).

87 On the other hand, positional behavior is also significantly influenced by morphological
88 features such as body size and limb and tail length (Bitty & McGraw, 2007; Fleagle, 2013;
89 Garber, 2007). Smaller species tend to leap and use small substrates more often than larger
90 species. Conversely, larger species tend to climb and bridge and use larger substrates more
91 frequently than smaller species (Bitty & McGraw, 2007; Gebo & Chapman, 1995b). Macaques
92 with long tails are more likely to cross wider forest gaps, suggesting long tails help to balance
93 the body during large gap leaping (Chatani, 2003; Rodman, 1991).

94 African green monkeys, also referred to as savannah monkeys, are comprised of six
95 medium-sized species in the genus *Chlorocebus* including vervets (*C. pygerythrus*), grivets (*C.*
96 *aethiops*), green monkeys (*C. sabaues*), Malbrouck monkeys (*C. cynosuroides*), tanzania monkeys
97 (*C. tantalus*), and Bale monkeys (*C. djambamensis*) (Groves, 2005; Haus et al., 2013). All
98 green monkeys, except Bale monkeys, are widely distributed generalists that inhabit open

99 country and wooded habitats, consume a diverse diet, and are terrestrial or semi-terrestrial
100 (Cardini, Dunn, O'Higgins, & Elton, 2013; Cardini, Jansson, & Elton, 2007; Enstam & Isbell,
101 2007; Isbell, Pruetz, Lewis, & Young, 1998; Kingdon, 2015). More specifically, vervets spent
102 nearly 20% of their time on the ground in a study carried out in riparian and savannah woodland
103 habitats in Kenya (Rose, 1979).

104 Bale monkeys are unusual among *Chlorocebus* spp. in being (1) endemic to the southern
105 Ethiopian Highlands, (2) very arboreal, and (3) found mostly in continuous bamboo forest
106 habitat (Mekonnen, Bekele, Fashing, Hemson, & Atickem, 2010a; Mekonnen, Bekele, Hemson,
107 Teshome, & Atickem, 2010b). Bale monkeys are also unusual among primates in that they
108 consume a diet of up to 81% bamboo (mostly young leaves and shoots) in continuous forests
109 (Mekonnen et al., 2010a; Mekonnen et al., 2018). However, the species was also recently
110 discovered in a few dozen small, isolated fragments where bamboo populations have been
111 degraded (Mekonnen et al., 2012) and the monkeys have responded by greatly diversifying their
112 diets (Mekonnen et al., 2018). Our recent research also found that habitat destruction and
113 fragmentation significantly reduced habitat quality in forest fragments (Mekonnen et al., 2017).
114 In particular, the availability of large trees and density of bamboo was much lower in fragments
115 than in continuous forest whereas the abundance of pioneer tree species, shrubs, graminoids
116 and forbs was higher in fragments (Mekonnen et al., 2017; Mekonnen et al., 2018). In addition
117 to supplementing their diet with graminoids, forbs, and shrubs (Mekonnen et al., 2018), Bale
118 monkeys in fragments were found to exhibit an energy minimization strategy in response to the
119 reduced food availability in this habitat (Mekonnen et al., 2017). Further, the possible
120 hybridization of forest fragment Bale monkey populations with more terrestrial grivets and
121 vervets (Haus et al., 2013; Mekonnen et al., 2012) associated with ecological niche
122 differentiation documented between Bale monkey populations in continuous forest and forest
123 fragments (Mekonnen et al., 2018; Trosvik, Rueness, de Muinck, Moges, & Mekonnen, 2018)

124 may increase the degree of terrestriality and affect the positional behavior of monkeys in
125 fragments.

126 The architectural differences between continuous forest and forest fragment habitats are
127 described in detail in Mekonnen et al. (2017). In particular, plant species diversity was much
128 lower, and dominance much higher, in continuous forest than in fragments. Larger trees and
129 bamboo were more abundant in continuous forest than in fragments, whereas shrubs were more
130 abundant in fragments than in continuous forest. The mean canopy size, height, and DBH
131 (diameter at breast height) of large trees and bamboo were greater in continuous forest than in
132 fragments (Mekonnen et al., 2017). In addition, the monthly food availability indices of bamboo
133 young leaves, non-bamboo young leaves, and fruits were higher in continuous forest than in
134 fragments (Mekonnen et al., 2017; Mekonnen et al., 2018). In sum, changes in habitat type and
135 quality along with associated changes in diet and activity patterns might also be expected to
136 impact the positional behavior and strata and substrate use of Bale monkeys.

137 We therefore aimed to examine the effects of habitat fragmentation and degradation on
138 the locomotor behavior, postural mode, vertical habitat use, and substrate utilization of Bale
139 monkey groups in continuous forest and two forest fragments in the southern Ethiopian
140 Highlands. Specifically, we investigated how Bale monkeys utilize locomotor and postural
141 behaviors in relation to strata and substrate use patterns by testing the following five hypotheses.
142 First, because of the architectural differences between forest types (Mekonnen et al., 2010a;
143 Mekonnen et al., 2017; Mekonnen et al., 2018) as well as the probable past admixture between
144 Bale monkeys in fragments and other more terrestrial *Chlorocebus* spp. (Haus et al., 2013), we
145 hypothesized that Bale monkeys living in forest fragments would be more terrestrial than those
146 in continuous forest (Hypothesis 1). Second, we hypothesized that the locomotor behavior of
147 Bale monkeys would differ between populations living in continuous forest and forest
148 fragments (Hypothesis 2) (Mekonnen et al., 2010a; Mekonnen et al., 2017; Mekonnen et al.,

149 2018). Third, we hypothesized that Bale monkeys in fragments would spend more time engaged
150 in quadrupedal locomotion (galloping, running, and walking), particularly on the ground, than
151 conspecifics in continuous forest (Hypothesis 3). Fourth, we hypothesized that Bale monkeys
152 in fragments would spend less time leaping and climbing than conspecifics in continuous forest
153 (Hypothesis 4). Lastly, we hypothesized that differences in forest type would have little effect
154 on Bale monkey resting posture, but would impact feeding posture, because resting posture is
155 typically less influenced by differences in habitat quality than feeding posture (Hypothesis 5)
156 (Fei et al., 2015; Garber & Pruetz, 1995; McGraw, 1996).

157

158 **METHODS**

159 Permission to carry out this project was granted by the Ethiopian Wildlife Conservation
160 Authority and adhered to the legal requirements of Ethiopia. This project also complied with
161 the American Society of Primatologists Principles for the Ethical Treatment of Primates.

162

163 **Study site**

164 We conducted this study in a continuous forest, Odobullu Forest (06°50'–6°56'N and 40°06'–
165 40°12'E), and in two forest fragments (6°44'–06°45'N and 38°48'–38°51'E), Kokosa and Afursa,
166 in the southern Ethiopian Highlands (Mekonnen et al., 2017). Odobullu Forest (hereafter
167 Continuous forest) is a large forest within which bamboo is abundant. It covers 141 km² at
168 elevations ranging from 1500 to 3300 m asl (Mekonnen et al., 2018). Odobullu consists of four
169 habitat types: mostly bamboo forest and tree-dominated forest but also shrubland and
170 occasional grasslands (Mekonnen et al., 2010b). It is partially protected, and disturbance in the
171 home ranges of our study groups is uncommon due to the steep terrain and remoteness of the
172 area.

173 Kokosa forest fragment (hereafter Patchy fragment) consists mostly of large trees and
174 degraded bamboo set amidst a matrix of human settlement, cultivated land, shrubland, and
175 grazing land. Patchy fragment covers 1.62 km² at elevations ranging from 2534 m to 2780 m
176 asl. Most of the fragment is owned privately by local individuals, though a smaller portion is
177 collectively owned by the local community (Mekonnen et al., 2017). Logging of bamboo by
178 local people is common in the fragment today, though it was dominated by bamboo forest just
179 three decades ago (Mekonnen et al., 2012).

180 Afursa forest fragment (hereafter Hilltop fragment) is set upon a hilltop and is a mix of
181 secondary forest, shrubland, and a *Eucalyptus* plantation with graminoid and forb cover
182 underneath. Bamboo has been nearly eradicated at Hilltop fragment, which covers only 0.34
183 km² at elevations ranging from 2582 m to 2790 m asl. It is surrounded by an anthropogenic
184 matrix of cultivated lands, pastures, and human settlements. Currently, cutting of trees and use
185 of the fragment for grazing are prohibited. However, the edge of the fragment, especially the
186 ground cover underneath the *Eucalyptus* plantation, is used for grazing. Like Patchy fragment,
187 Hilltop fragment was dominated by bamboo forest only three decades ago (Mekonnen et al.,
188 2012). The distance between Hilltop and Patchy fragments is ~9 km and they have been
189 separated by human settlements, grazing land, and agriculture for many decades (Mekonnen et
190 al., 2012). The continuous forest and forest fragments are ~160 km apart (Mekonnen et al.,
191 2017). The continuous forest is characterized by lower annual rainfall and temperature than the
192 forest fragments (Mekonnen et al., 2018). Additional quantitative details about the study areas,
193 groups, and characteristics of home ranges can be found in Table 1 of a previous publication
194 (Mekonnen et al., 2017).

195

196 **Study groups**

197 We studied four groups in total: two groups (Continuous A: 65 individuals; Continuous B: 38
198 individuals) with adjacent, partially overlapping ranges at Odobullu, one group at Kokosa
199 (Patchy: 28 individuals), and one group at Afursa (Hilltop: 23 individuals) (Mekonnen et al.,
200 2017). The home ranges of continuous forest groups (Continuous A vs. Continuous B) consisted
201 of exclusively bamboo forest (53.7% vs 55.6%) and mixed bamboo forest habitats (46.3% vs.
202 44.4%). Alternatively, the home range of fragment groups consisted of variable habitat types.
203 Patchy group's range consisted of five habitat classes: grazing land (37.9%), shrubland (29.5%),
204 mixed bamboo forest (17.1%), tree-dominated forest (8.0%), and cultivated land (7.5%),
205 whereas Hilltop group's range consisted of four habitat classes: shrubland (50.4%), *Eucalyptus*
206 plantation (24.3%), tree-dominated forest (22.7%), and grazing land (2.7%) (Mekonnen et al.,
207 2017). A.M. and two intensively-trained field assistants habituated these groups to human
208 observers from March – June 2013 (Mekonnen et al., 2017).

209

210 **Behavioral data collection**

211 We collected data on positional behavior and strata and substrate use from July 2013 - June
212 2014 using instantaneous scan sampling (Altmann, 1974) conducted at 15-min intervals for up
213 to 5-min duration, typically from 0700-1730. This sampling method is standard in studies of
214 positional behavior because it helps ensure independence of data points (Dagosto, 1994; Fei et
215 al., 2015; Zhu, Garber, Bezanson, Qi, & Li, 2015). During the last two months of the habituation
216 period, AM and the two field assistants practiced accurately determining the monkeys'
217 locomotor and postural modes, strata use, and substrate utilization via visual estimation as well
218 as by using a measuring tape and rangefinder where appropriate (Bitty & McGraw, 2007;
219 Huang et al., 2015; Iurck et al., 2013). Subsequently, we collected 28,583 individual behavioral
220 scan records (hereinafter records) over 234 group follow days (N=12 months; Continuous A:
221 5442 records; Continuous B: 5499 records; Patchy fragment: 10254 records, and Hilltop

222 fragment: 7388 records) (Mekonnen et al., 2017). We collected data on 52 days from
223 Continuous A (mean = 4.3 days; SD \pm 0.7; range 3-5 days per month), 54 days from Continuous
224 B (mean = 4.5 days; SD \pm 0.8; range 3-6 days per month), 61 days from Patchy (mean = 5.1
225 days; SD \pm 0.3; range 5-6 days per month), and 67 days from Hilltop (mean = 5.6 days; SD \pm
226 0.7; range 5-7 days per month).

227 When scanning an individual, we recorded its activity as either feeding, moving, resting,
228 socializing, or vocalizing as described in Table 1 and in greater detail in a previous publication
229 (Mekonnen et al., 2017). During each individual scan, when a monkey was observed traveling,
230 we recorded its locomotor mode. We also recorded postural behaviors for feeding and resting
231 bouts based on body shape and limb position. Our definitions for both locomotor modes and
232 postural behaviors followed Hunt et al. (1996) (Table 1). To investigate the relative use of
233 different strata in the environment (i.e., vertical habitat utilization), we recorded the strata use
234 category for each scan record (Table 1). To examine substrate use patterns, we visually
235 estimated the type, size, inclination, and number of substrate(s) that supported the main weight
236 of the animal during each scan record (Table 1).

237

238 **Data analysis**

239 We calculated the monthly percentage contribution of each locomotor mode, postural behavior,
240 strata use category, and substrate utilization pattern for each Bale monkey group by dividing
241 the monthly contribution of each category of a *locomotor mode*, *postural behavior*, *strata use*
242 *category*, *substrate type*, and *substrate utilization* pattern with their corresponding total
243 contributions. The sampling efforts for all categories summarized in this study are presented in
244 Table S1. We analyzed lifestyle (terrestrial vs. arboreal) from recorded strata use patterns.
245 Lifestyle denotes the general categorization of a species' ecology and behavior depending on
246 the relative proportion of time spent on the ground or in the canopy layer (lower, middle, and

247 upper strata). We categorized a species/population as terrestrial if it spends $\geq 60\%$ of its time on
248 the ground (Isbell et al., 1998; Motsch et al., 2015), semi-terrestrial if it spends 20-59% of its
249 time on the ground, and arboreal if it spends $> 80\%$ of its time in the trees (Motsch et al., 2015).

250 We initially calculated and compared variables for each Bale monkey study group
251 individually and tested for differences among groups using the one-way analysis of variance
252 (ANOVA) model followed by the Tukey honest significant difference (HSD) *post hoc* test.
253 Given that the results for both groups within each habitat type exhibited similar patterns, we
254 combined the two continuous forest groups and the two fragmented forest groups for data
255 analysis. We used a one-way ANOVA to examine differences between continuous forest and
256 fragment groups in the monthly percentage contribution of locomotor and postural modes, strata
257 use, lifestyle, and substrate type, size, inclination, and number. To normalize the data, we
258 implemented logit transformations of proportion data before conducting statistical analysis as
259 recommended by Warton and Hui (2011). We tested all data for normality using Shapiro-Wilk
260 tests and homogeneity of variances using Levene tests. If the assumption of normality and/or
261 homogeneity was violated, we performed a non-parametric Kruskal–Wallis test (e.g., Fei et al.,
262 2015; Manduelli, Harrison, & Thorpe, 2012). We carried out all statistical tests using the
263 programming platform R version 3.3.3 (R Development Core Team, 2016) with significance
264 level set at $P \leq 0.05$. We generated all figures using the ggplot2 package (Wickham, 2009) in
265 R (R Development Core Team, 2016).

266

267 **RESULTS**

268 **Strata use and lifestyle**

269 Overall, and during traveling and feeding, groups in forest fragments spent significantly more
270 time on the ground and in the lower stratum but significantly less time in the middle and upper
271 strata than groups in continuous forest (Table 2; Figure 1A,B,C). During resting, the middle

272 stratum was the most frequently used by all study groups, while the use of other strata varied
273 among groups in continuous forest and forest fragments (Figure 1D). Specifically, groups in
274 continuous forest spent significantly more time in the middle and upper strata, and significantly
275 less time in the lower stratum and on the ground, than groups in forest fragments during resting
276 (Table 2; Figure 1D).

277

278 **Locomotor and postural behavior**

279 Groups in continuous forest spent significantly more time climbing, and significantly less time
280 galloping and walking, than groups in forest fragments. However, groups in continuous forest
281 and forest fragments did not differ in their use of bridging, leaping, or running (Table 2; Figure
282 2). Overall, Bale monkeys in all study groups spent most of their time in a sitting posture and
283 nearly all of their remaining time standing (Figure 3). Groups in continuous forest used a sitting
284 posture significantly more frequently and a standing posture significantly less frequently than
285 groups in forest fragments, particularly during feeding (Table 2; Figure 3). However, during
286 resting, groups in continuous forest and forest fragments both spent nearly all of their time
287 sitting (Table 2; Figure 3).

288

289 **Substrate utilization during arboreal locomotion and postural behavior**

290 **Substrate type:** During locomotion, groups in both continuous forest and forest fragments
291 mostly used branches as supports, though they sometimes used twigs, boughs, lianas, or trunks
292 instead (Table 2; Figure 4A). During feeding, groups in both continuous forest and forest
293 fragments most frequently used twigs. They also sometimes used branches, lianas, boughs, or
294 trunks (Table 2; Figure 4B). During resting, groups in both continuous forest and forest
295 fragments most frequently used branches and twigs, whereas boughs, trunks, and lianas were
296 infrequently used (Figure 4C). However, groups in continuous forest used branches and lianas

297 more frequently, and twigs and trunks less frequently, than groups in forest fragments during
298 resting, though there was no difference in the use of boughs between continuous forest and
299 fragment groups (Table 2).

300

301 **Substrate size:** During locomotion, Bale monkeys in all study groups most often used medium
302 sized supports, followed by small, large, and very large supports (Figure 4D). Furthermore,
303 groups in continuous forest used small and very large substrates more frequently, and medium
304 sized substrates less frequently, than groups in forest fragments (Table 2). However, there was
305 no difference in the use of large substrates between continuous forest and fragment groups
306 (Table 2). During feeding, all groups used small and medium substrates frequently whereas
307 large and very large substrates were rarely used (Figure 4E); there were no significant
308 differences in the sizes of substrates used by groups in continuous and fragmented forests during
309 feeding (Table 2). During resting, the most frequently used substrate size class was medium
310 followed by small and large substrates, whereas very large substrates were rarely used (Figure
311 4F). Groups in forest fragments used medium substrates significantly more, and large and very
312 large substrates significantly less, than groups in continuous forest, but there were no
313 differences in the use of small substrates between continuous forest and fragment groups (Table
314 2).

315

316 **Substrate inclination:** During locomotion, groups in continuous forest more frequently used
317 vertical substrates and less often used oblique substrates than groups in forest fragments (Table
318 2; Figure 5A), but there was no difference in the use of horizontal substrates between continuous
319 forest and fragment groups (Table 2). During feeding and resting, the most frequently used
320 substrate inclination class was horizontal followed by oblique, whereas vertical substrates were
321 not used (Figure 5B, 5C). No significant differences in patterns of substrate inclination use were

322 found between groups in continuous and fragmented forest during feeding (Table 2). During
323 resting, groups in forest fragments used oblique substrates significantly less than groups in
324 continuous forest (Table 2; Figure 5C), but there was no difference in the use of horizontal
325 substrates between continuous forest and fragment groups (Table 2).

326

327 **Substrate number:** During both locomotion (Figure 5D) and resting (Figure 5F), use of a
328 single support was more common, whereas during feeding, use of multiple supports was more
329 common (Figure 5E). However, there was no difference in the use of single and multiple
330 substrates between continuous forest and fragment groups (Table 2).

331

332 **DISCUSSION**

333 Our study revealed that Bale monkeys in fragments exhibit flexibility in their locomotor
334 behavior, feeding posture, degree of terrestriality, and substrate utilization patterns in response
335 to habitat alteration due to habitat fragmentation and degradation. We suggest that the reduction
336 in habitat quality and changes in matrix use patterns in fragments are probably responsible for
337 the shift among Bale monkeys from an arboreal lifestyle in continuous forest to a semi-
338 terrestrial lifestyle in fragments. Our results suggest that locomotor mode, feeding posture, and
339 strata use are strongly influenced by forest fragmentation and associated habitat degradation.
340 Resting posture was not influenced by changes in forest type, suggesting that forest degradation
341 does not impact resting posture to the same degree that it impacts other behaviors.

342

343 **Variation in degree of terrestriality among Bale monkeys across habitats**

344 In this study, Bale monkey groups in forest fragments spent more than one-third of their time
345 on the ground whereas those in continuous forest were observed on the ground only 2% of the
346 time, thus supporting Hypothesis 1 that Bale monkeys living in forest fragments would be more

347 terrestrial than those in continuous forest. We therefore suggest that Bale monkeys in forest
348 fragments fit the semi-terrestrial category (i.e., 20-59% on the ground) occupied by other
349 *Chlorocebus* spp. e.g., *C. pygerythrus* 20% (Rose, 1979) and some *Cercopithecus* spp. [e.g., *C.*
350 *neglectus* 30% (Gautier-Hion, 1988), *C. solatus* 33.7% (Motsch et al., 2015), *C. campbelli* 20%
351 (McGraw, 1998b) and *C. lhoesti* 38% (Struhsaker, 1981)] rather than the arboreal category that
352 best fits the source populations of Bale monkeys in continuous forest (Mekonnen et al., in press).

353 The Bale monkey is peculiar among its sister species in the genus *Chlorocebus* in being
354 primarily arboreal and inhabiting dense continuous forest, thus bearing similarities to most
355 *Cercopithecus* species, which tend to spend >80% of their time in trees: [e.g., *C. ascanius* and
356 *C. mitis* (Gebo & Chapman, 1995a), *C. diana* (McGraw, 2000), *C. nictitans stampflii* (Bitty &
357 McGraw, 2007), and *C. petaurista* (McGraw, 2000)]. Some primates exhibit inter-population
358 variability in levels of arboreality due to differences in ecological factors, such as forest
359 architecture, availability and consumption of food resources (Fei et al., 2015; Houle, Chapman,
360 & Vickery, 2007; Huang et al., 2015; Li, 2007; Zhu et al., 2015), and presence of terrestrial
361 predators (McGraw & Bshary, 2002; Thorpe & Crompton, 2006, 2009). For example, Sumatran
362 orangutans are rarely seen descending to the ground in forests where tigers are present (Thorpe
363 & Crompton, 2006, 2009).

364 Our study suggests that habitat alteration due to fragmentation and degradation may force
365 Bale monkeys in fragments to use the ground frequently. Changes in habitat structure and food
366 availability resulting from anthropogenic activities (e.g., land use, canopy disturbance, and
367 logging) have been demonstrated to increase the degree of terrestriality in several other primates
368 (Ancrenaz et al., 2014; Huang et al., 2015). Here, Bale monkeys in forest fragments also
369 occupied anthropogenically-degraded habitats with disconnected canopies that probably caused
370 them to increase terrestrial activity (Mekonnen et al., 2010a; Mekonnen et al., 2017). In
371 response to habitat alteration due to the reduction in the availability, abundance, mean height,

372 canopy size, and DBH of bamboo and large food tree species in fragments (Mekonnen et al.,
373 2017; Mekonnen et al., 2018), Bale monkeys shifted their feeding from arboreal strata to the
374 ground where shrubs, forbs, and graminoids are mostly available (Mekonnen et al., 2018). In
375 the absence of their primary dietary species and items, several other arboreal primates also
376 increased ground use to exploit terrestrial food sources more intensively (Eppley et al., 2016;
377 Eppley, Verjans, & Donati, 2011; Xiang et al., 2009).

378

379 **Plasticity of positional behavior in response to architectural variability across habitats**

380 Consistent with Hypothesis 2, our results also showed that habitat fragmentation and
381 degradation caused marked differences in locomotor behavior and support use between Bale
382 monkeys in continuous forest and forest fragments. The modification of locomotor modes in
383 forest fragments could represent a strategic response to habitat alteration resulting from
384 fragmentation and degradation. Unlike conspecifics in continuous forest, Bale monkeys in
385 forest fragments often used quadrupedal locomotion (running, walking, and galloping) to cross
386 gaps between fragments consisting of human matrix while traveling and searching for food
387 resources, which supports Hypothesis 3. In particular, Patchy fragment consisted of patches of
388 degraded forest interspersed with grassland and cultivated land, and nearly 75% of the group's
389 range is in human use areas (Mekonnen et al., 2017). Another reason for traveling
390 quadrupedally on the ground could be to minimize locomotor routes and thus energy
391 expenditure (Huang et al., 2015). Consistent with Hypothesis 4, Bale monkeys in fragments
392 spent less time climbing and leaping due to marked differences in habitat quality and canopy
393 structure between fragments and continuous forest. Primates in forest fragments spent less time
394 climbing than those in continuous forest, perhaps because it is energetically expensive to climb
395 vertically, and frequent ascent and descent in a fragmented setting would be energetically
396 unfavorable (Hanna, Schmitt, & Griffin, 2008). Our recent study showed that Bale monkeys in

397 fragments traveled shorter distances per day and spent less time feeding and moving than
398 conspecifics in continuous forest, suggesting that monkeys in fragments adopted a strategy of
399 energy minimization (Mekonnen et al., 2017). Similar to our Patchy group, primates in other
400 studies also spent less time leaping when they traveled through habitats with discontinuous
401 canopies, likely because gaps in fragmented areas are too large to cross via leaping (Lawler,
402 Ford, Wright, & Easley, 2006; Workman & Schmitt, 2012; Zhou et al., 2013).

403 Our results also suggest that habitat fragmentation and degradation affect feeding posture
404 but not resting posture, thus supporting Hypothesis 5. The increase in standing posture while
405 feeding in fragments may be related partly to the dietary shift from bamboo young leaves
406 (commonly consumed while sitting) in continuous forest to the greater consumption of
407 graminoids and forbs in fragments (that are often consumed standing tripedally). In addition,
408 the greater frugivory of Bale monkeys in fragments than by those in continuous forest
409 (Mekonnen et al., 2018) might also have contributed to their greater use of standing postures.
410 Lastly, to reduce the risk of falling, monkeys may frequently use sitting postures while feeding
411 arboreally. Frugivorous species more often feed in a standing posture related to the more mobile,
412 softer, or harder to obtain feeding sources they exploit than folivorous species, which tend to
413 sit while feeding because their food sources are easy to collect and must be chewed for long
414 periods of time (Youlatos, 1998a).

415 Unlike during feeding, resting postural patterns were similar irrespective of habitat type.
416 This finding suggests that the changes to habitat structure in this case simply do not affect
417 resting posture, a result consistent with previous studies of callitrichines and cercopithecids
418 (Garber & Pruetz, 1995; McGraw, 1996). It is striking that Bale monkey groups in both habitats
419 go to the middle strata to rest. This behavior is consistent with the hypothesis that some primates
420 position themselves in places that make them maximally hidden during a period of vulnerability,
421 from both terrestrial and arboreal predators (Grueter, Li, Ren, & Li, 2013). Despite the

422 architectural differences between habitats (continuous versus fragmented canopy), monkeys
423 most frequently used medium to large horizontal branches to rest in well-hidden parts of the
424 tree crown as well as to ensure stability (Grueter et al., 2013; McGraw, 1998a).

425 While feeding arboreally, Bale monkeys most frequently used twigs, followed by branches,
426 for support regardless of forest type, a pattern similar to that reported in other forest primate
427 studies (e.g., Houle et al., 2007; Huang et al., 2015; Youlatos, 2002). Bale monkeys usually
428 used a sitting posture on branches and twigs to free their hands to manipulate food resources
429 such as leaves that are evenly distributed and shoots once they break off. They obtained access
430 to branches and twigs mostly by sitting on branches while pulling or breaking off the terminal
431 branch containing food resources. The frequent use of small-sized, horizontal, and multiple
432 weight-bearing supports while feeding may be associated with keeping their balance and
433 increasing both safety and access to terminal food resources (Iurck et al., 2013; McGraw,
434 1998a).

435

436 **Implications for Bale monkey evolution**

437 Our results suggest that the ancestors of modern Bale monkeys may have used semi-terrestrial
438 locomotion and standing postures. Close relatives such as grivets spend a considerable amount
439 of time on the ground and have evolved morphological adaptations for a terrestrial (Gebo &
440 Sargis, 1994) or semi-terrestrial mode of life (Anapol, Turner, Mott, & Jolly, 2005). They have
441 longer distal fore- and hind limb segments for running and galloping in terrestrial habitats and
442 longer tails for keeping balance during the transition between arboreal strata and the ground
443 (Anapol & Gray, 2003; Anapol et al., 2005; Gebo & Sargis, 1994). Though we have no
444 quantitative data on morphological variation between Bale monkeys in continuous forest and
445 forest fragments, monkeys in fragments appear to exhibit some morphological differences (e.g.,
446 longer tails) from those in continuous forest (Mekonnen et al., 2012). Bale monkeys in

447 fragments have similar terrestrial locomotor modes (running and galloping) to those of grivets
448 that are uncommon among arboreal Bale monkeys in continuous forest. Thus, we propose that
449 the ancestors of the arboreal Bale monkey may have been semi-terrestrial savannah dwelling
450 species (Dolotovskaya et al., 2017) that transitioned to arboreality and adapted to closed
451 canopies in continuous bamboo forest to exploit an available bamboo-based dietary niche
452 (Mekonnen et al., 2010a; Mekonnen et al., 2010b; Mekonnen et al., 2018). As some habitats
453 became fragmented through human disturbance, Bale monkeys in fragments returned to a semi-
454 terrestrial lifestyle. Though terrestrial locomotion may have evolved only once among guenons
455 (Tosi, Melnick, & Disotell, 2004), morphological modifications among terrestrial guenons may
456 have occurred multiple times (Gebo & Sargis, 1994; Sargis et al., 2008). The semi-terrestrial
457 behavior of some Bale monkeys documented in our study may be indicative of an incipient
458 transition from arboreal to semi-terrestrial locomotion. More quantitative and comparative
459 studies on their morphological adaptations are needed to increase our understanding of the shift
460 from arboreality in continuous forest to semi-terrestriality in fragments.

461 On the other hand, recent preliminary phylogenetic evidence from mitochondrial DNA
462 suggests that Bale monkeys in forest fragments are more closely related to their sister
463 *Chlorocebus* taxa, including vervets and grivets (Haus et al., 2013; Mekonnen et al., in press),
464 than to Bale monkeys in continuous forest. These results imply past interspecies gene flow.
465 Therefore, we cannot rule out the possibility that hybridization might have impacted the
466 lifestyle, locomotion, and feeding posture of Bale monkey populations in forest fragments,
467 which are more similar to semi-terrestrial vervets and grivets than to conspecifics in continuous
468 forest. We do acknowledge, however, that we cannot reach a firm conclusion on the impacts of
469 hybridization on the positional behavior and semi-terrestriality of Bale monkeys in forest
470 fragments from a single locus and maternally inherited mtDNA (Mekonnen et al., in press).
471 Thus, further genomic studies using nuclear DNA are required to confirm the hybridization

472 documented from mtDNA (Haus et al., 2013; Mekonnen et al., in press) and to explore the
473 implications of hybridization on the positional behavior and semi-terrestriality of Bale monkey
474 populations in forest fragments.

475

476 **Implications for Bale monkey conservation**

477 In the current study, Bale monkeys were flexible enough to exhibit variation in degree of
478 terrestriality, locomotor modes, and feeding postures to cope with the impacts of habitat
479 alteration resulting from fragmentation and degradation. Semi-terrestrial behavior can increase
480 the efficiency of foraging on nutrient-dense food resources such as forbs, graminoids and crops
481 (Chaves & Bicca-Marques, 2017; Eppley et al., 2016). Further, the ability to cross open forest
482 gaps may enhance the probability of isolated individuals meeting and interbreeding. This, in
483 turn, would help to increase gene flow and reduce the loss of genetic diversity in isolated
484 populations and minimize the impact of habitat fragmentation (Allendorf, Luikart, & Aitken,
485 2013; Ancrenaz et al., 2014). Although the flexibility to adopt a semi-terrestrial lifestyle
486 exhibited by Bale monkey groups in fragments is encouraging, potential threats caused by
487 human-monkey conflict, gastrointestinal parasitic infection, and predation risk [(Mekonnen et
488 al., 2018); Mekonnen, unpublished data] are all likely to increase with greater terrestriality
489 (Chaves & Bicca-Marques, 2017; Eppley et al., 2016; Hussain, Ram, Kumar, Shivaji, &
490 Umopathy, 2013; Xiang et al., 2009), thereby posing challenges to the long-term persistence of
491 these populations. To reduce the threats resulting from semi-terrestriality in forest fragments,
492 our findings suggest it is crucial to incorporate nearby matrix habitats into Bale monkey
493 conservation strategies in fragmented habitats. Restoration efforts in fragmented habitats must
494 also focus on mitigating human monkey-conflict, minimizing edge effects, increasing fragment
495 sizes, and improving connectivity of forest strata (c.f., Anderson, Rowcliffe, & Cowlishaw,
496 2007; Chaves & Bicca-Marques, 2017; Estrada, Raboy, & Oliveira, 2012). In sum, the

497 conservation recommendations resulting from this study would help to protect and restore the
498 remaining fragmented and degraded montane forest habitats and to ensure the future persistence
499 of Bale monkey populations and other wildlife in the human-dominated landscape of the
500 southern Ethiopian Highlands (Mekonnen et al., 2017).

501

502 **ACKNOWLEDGMENTS**

503 This research was supported by grants from the People's Trust for Endangered Species,
504 International Foundation for Science, and Conservation and Research Foundation. This study
505 would not have been possible without generous financial support to Addisu Mekonnen from
506 the Norwegian State Educational Loan Fund (Lånekassen) under the Quota Scholarship
507 program. Peter Fashing thanks the U.S.-Norway Fulbright Foundation for their support during
508 the preparation of this manuscript and San Diego Zoo for their generous support of his long-
509 term research endeavors in Ethiopia. We would like to thank the Centre for Ecological and
510 Evolutionary Synthesis (CEES) at the University of Oslo and Department of Zoological
511 Sciences at Addis Ababa University for logistical support. We are grateful to the Ethiopian
512 Wildlife Conservation Authority, Oromia Region Forest and Wildlife Enterprise, Sidama and
513 West Arsi Zone Agriculture Offices, and Goba, Kokosa, and Arbegona District Agriculture
514 Offices for granting us permission to conduct this study. We are grateful to our research
515 assistants, Mengistu Birhan and Mamar Dilnesa, for their valuable contributions to this project.
516 We also thank Amera Moges and Sewalem Tsehay for their support during the fieldwork. We
517 thank the following local guides and camp attendants: Firdie Sultan, Omer Hajeleye, Hassen
518 Wolle, Jemal Kedir, Mudie Kedir, and Matiyos Yakob. Lastly, we thank the Associate Editor,
519 Donald C. Dunbar, and two anonymous reviewers for many valuable comments that greatly
520 improved the manuscript.

521

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- 779

780 **TABLE 1** Variables and definitions recorded for the study of Bale monkey positional
 781 behavior, strata use and substrate utilization.

No.	Terms	Definitions
1	Activity	
	Feeding	Foraging for or masticating a particular food item (food plant species and animal prey)
	Traveling	Changing spatial position via walking, running, climbing, leaping, or bridging
	Resting	Adopting a stationary posture of sitting or lying down or self-grooming and not engaging in other activities such as feeding, traveling, or socializing
	Socializing	Playing, grooming, or engaging in sexual activity with another individual
	Vocalizing	Uttering audible sounds
2	Locomotor mode	
	Climbing	Upward or downward movement on a vertical or steeply angled substrate/s
	Leaping	Movement between substrates involving free flight in which the hind limbs provide the propulsive force
	Walking	Progression along a substrate in which all four limbs follow a regular pattern of movement
	Running	Rapid progression along a substrate
	Galloping	Movement in which each homologous pair of limbs acts as a unit
	Bridging	A short gap crossing involving active or passive compliance of initial and landing supports
3	Postural mode	
	Sitting	Stationary position where the monkey rests on its hind limbs in a pronograde or semi-pronograde posture
	Quadrupedal stand	Standing posture on four limbs
	Tripedal stand	Standing posture on three limbs
	Bipedal stand	Standing posture on two hind limbs
	Lying	When a ventral, dorsal, or side of the torso support the body
4	Strata use	
	Ground	When a monkey uses the ground as support
	Lower	Shrub and understory layer up to 5 m above the ground
	Middle	Small tree and bamboo layer between 5-15 m high
	Upper	Forest stratum over 15 m high
5	Substrate type	Type of substrate that supports the main weight of the animal
	Trunk	The main woody structure of a tree (does not apply to bamboo)
	Bough	The major branch that occurs between the trunk and a branch of a tree (does not apply to bamboo)
	Branch	Branch of a tree between a bough and a twig (> 2 cm in diameter) also including stems and branches of bamboo
	Twig	Small terminal branches less than 2 cm in diameter on trees and bamboo
	Liana	Vines and climbers

6	Substrate size	
	Small	Small and flexible supports < 2 cm in diameter
	Medium	Supports between 2 - 10 cm in diameter
	Large	Supports between 10 - 20 cm in diameter
	Very large	Supports >20 cm in diameter
7	Substrate inclination	
	Horizontal	Angle between $0 \pm 22.5^\circ$
	Oblique	Angle between 22.5° and 67.5°
	Vertical	Angle $\geq 67.5^\circ$ to 90°
8	Substrate number	
	Single	Only a single support
	Multiple	Two or more main weight-bearing supports

782 *Definitions for locomotor and postural modes were adapted from Hunt et al. (1996), strata use
783 from Huang et al. (2015), and substrate type, inclination, and size from Bitty and McGraw
784 (2007); Iurck et al. (2013), and number from Iurck et al. (2013).
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787 **TABLE 2** Comparison of percentage strata use, positional behaviors, and substrate utilization
 788 between Bale monkey groups in continuous forest (CF, Continuous A and Continuous B) and
 789 fragmented forests (FF, Patchy and Hilltop) using One-Way ANOVA or Kruskal–Wallis test.
 790 Variables are described in the methods section and Table 1.

No.	Features	Variables	CF (%)	FF (%)	df=1, F-value	LS
1	Strata use					
1.1	Overall	Ground	2.3	36.5	41.87	***
		Lower	4.3	24.1	35.29	***
		Middle	74.2	37.4	98.18	***
		Upper	19.2	2.1	30.49	***
1.2	Travel	Ground	3.0	43.3	59.73	***
		Lower	3.3	22.4	55.30	***
		Middle	64.5	33.5	39.77	***
		Upper	29.3	0.8	145.60	***
1.3	Feeding	Ground	2.4	42.2	86.24	***
		Lower	4.9	23.5	67.60	***
		Middle	80.1	31.2	96.88	***
		Upper	12.6	3.1	15.26	***
1.4	Resting	Ground	1.5	11.2	61.59	***
		Lower	2.9	31.3	69.89	***
		Middle	69.1	56.0	8.72	***
		Upper	26.6	1.5	74.48	***
2	Locomotion					
2.1	Locomotor mode	Climbing	50.3	24.5	38.72	***
		Leaping	31.4	21.5	2.03	<i>ns</i>
		Walking	12.4	23.2	7.68	**
		Running	4.5	10.9	0.31	<i>ns</i>
		Gallop	0.0	13.4	377.20	***
		Bridging	1.5	2.6	0.50	<i>ns</i>
3	Postural mode					
3.1	Feeding (F)	Sitting	97.7	88.3	^a 24.50	***
		Standing	2.3	11.7	^a 24.50	***
3.2	Resting (R)	Sitting	100.0	98.7	^a 0.73	<i>ns</i>
		Standing	0.0	1.3	^a 0.73	<i>ns</i>
3.3	F + R	Sitting	98.2	90.9	^a 24.20	***
		Standing	1.8	9.0	^a 23.40	***
4	Substrate type					
4.1	Locomotion	Trunk	2.3	15.0	33.24	***
		Bough	6.3	2.9	26.05	***
		Branch	61.4	62.6	0.05	<i>ns</i>
		Twig	27.7	19.2	6.40	**
		Liana	2.3	0.3	17.99	***
4.2	Feeding	Trunk	0.0	3.5	119.7	***
		Bough	0.8	0.5	7.59	**

		Branch	33.6	32.5	0.05	<i>ns</i>
		Twig	61.8	63.0	0.19	<i>ns</i>
		Liana	3.7	0.6	13.75	***
4.5	Resting	Trunk	1.2	3.3	36.87	***
		Bough	4.6	1.9	3.70	<i>ns</i>
		Branch	73.85	62.9	8.90	**
		Twig	10.6	31.1	19.02	***
		Liana	9.9	0.9	27.79	***
5	Substrate size					
5.1	Locomotion	Small	30.0	21.4	5.95	*
		Medium	44.2	59.2	14.59	***
		Large	19.4	15.8	0.499	<i>ns</i>
		Very large	6.4	3.7	4.57	*
5.2	Feeding	Small	64.9	60.9	0.723	<i>ns</i>
		Medium	32.2	36.3	1.01	<i>ns</i>
		Large	2.3	2.3	0.868	<i>ns</i>
		Very large	0.6	0.2	0.832	<i>ns</i>
5.3	Resting	Small	20.5	23.6	2.33	<i>ns</i>
		Medium	58.2	70.5	12.69	***
		Large	16.5	4.7	10.36	**
		Very large	4.8	1.2	8.33	**
6.1	Substrate inclination					
6.1	Locomotion	Horizontal	41.7	35.0	3.39	<i>ns</i>
		Oblique	18.3	56.3	57.27	***
		Vertical	40.0	8.7	13.47	***
6.2	Feeding	Horizontal	81.7	68.5	1.06	<i>ns</i>
		Oblique	18.1	31.4	1.07	<i>ns</i>
		Vertical	0.1	0.1	0.52	<i>ns</i>
6.3	Resting	Horizontal	51.4	77.2	1.06	<i>ns</i>
		Oblique	48.2	22.8	14.92	***
7.1	Substrate number					
7.1	Locomotion	Single	68.7	74.6	2.20	<i>ns</i>
		Multiple	31.3	25.4	2.20	<i>ns</i>
7.2	Feeding	Single	33.5	31.7	0.102	<i>ns</i>
		Multiple	66.5	68.3	0.102	<i>ns</i>
7.3	Resting	Single	77.4	66.5	6.53	*
		Multiple	22.6	33.5	6.53	*

791 The last column shows the level of significance (LS) with significant difference, $P < 0.001$ (***); P
792 < 0.01 (**); $P < 0.05$ (*); *ns* (no significance).

793 ^a Kruskal–Wallis test (χ^2) for postural mode statistical tests.

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797 **Figure legends**

798 **FIGURE 1** The proportion of time spent using different forest strata among Bale monkey
799 groups in continuous forest (Continuous A, [Cont_A] and Continuous B, [Cont_B]) and forest
800 fragments (Patchy and Hilltop) during A) overall behavioral activity, B) traveling, C) feeding,
801 and D) resting among four Bale monkey study groups.

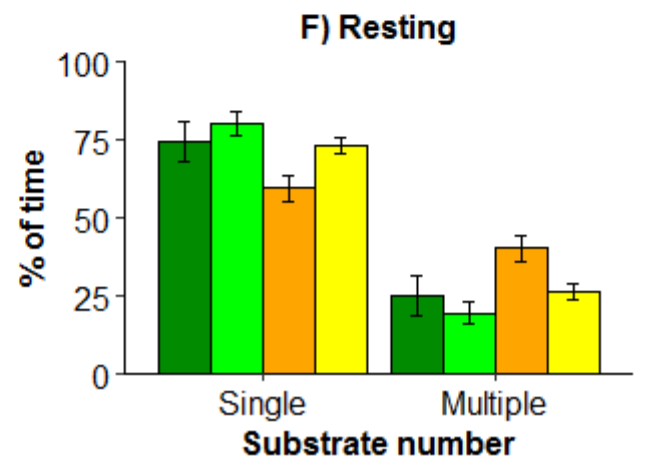
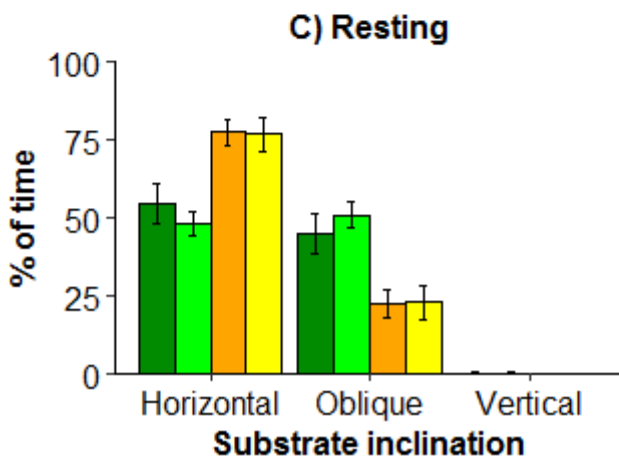
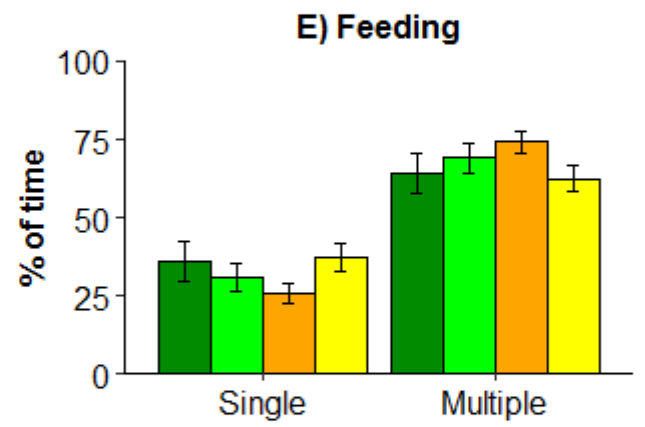
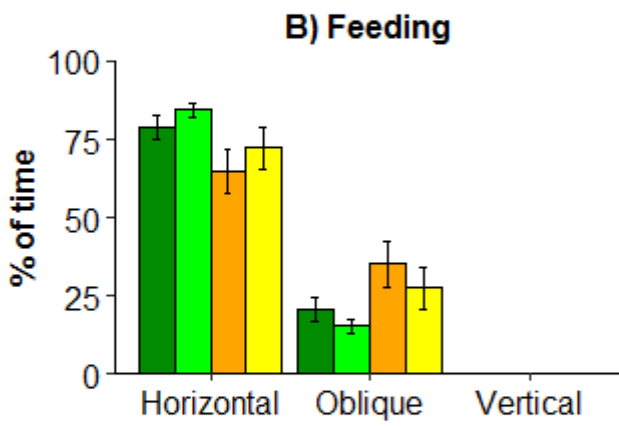
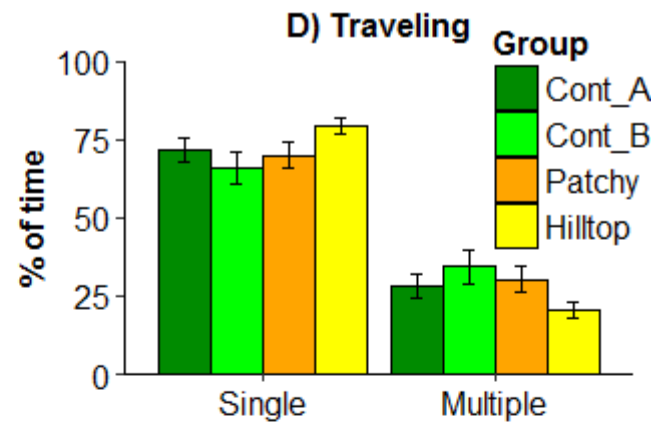
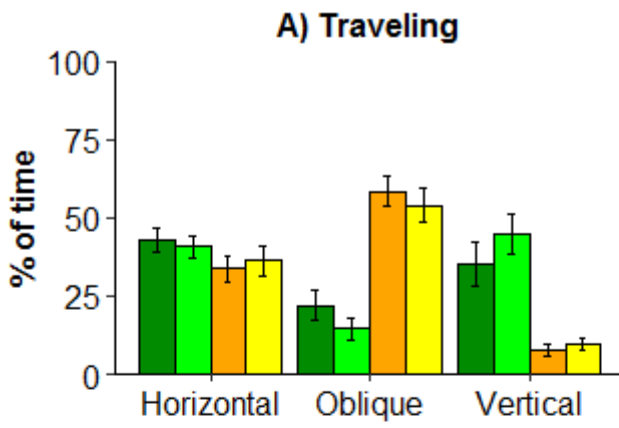
802 **FIGURE 2** The proportion of time spent adopting different locomotor modes during travel
803 among the four Bale monkey study groups in continuous forest (Continuous A, [Cont_A] and
804 Continuous B, [Cont_B]) and forest fragments (Patchy and Hilltop).

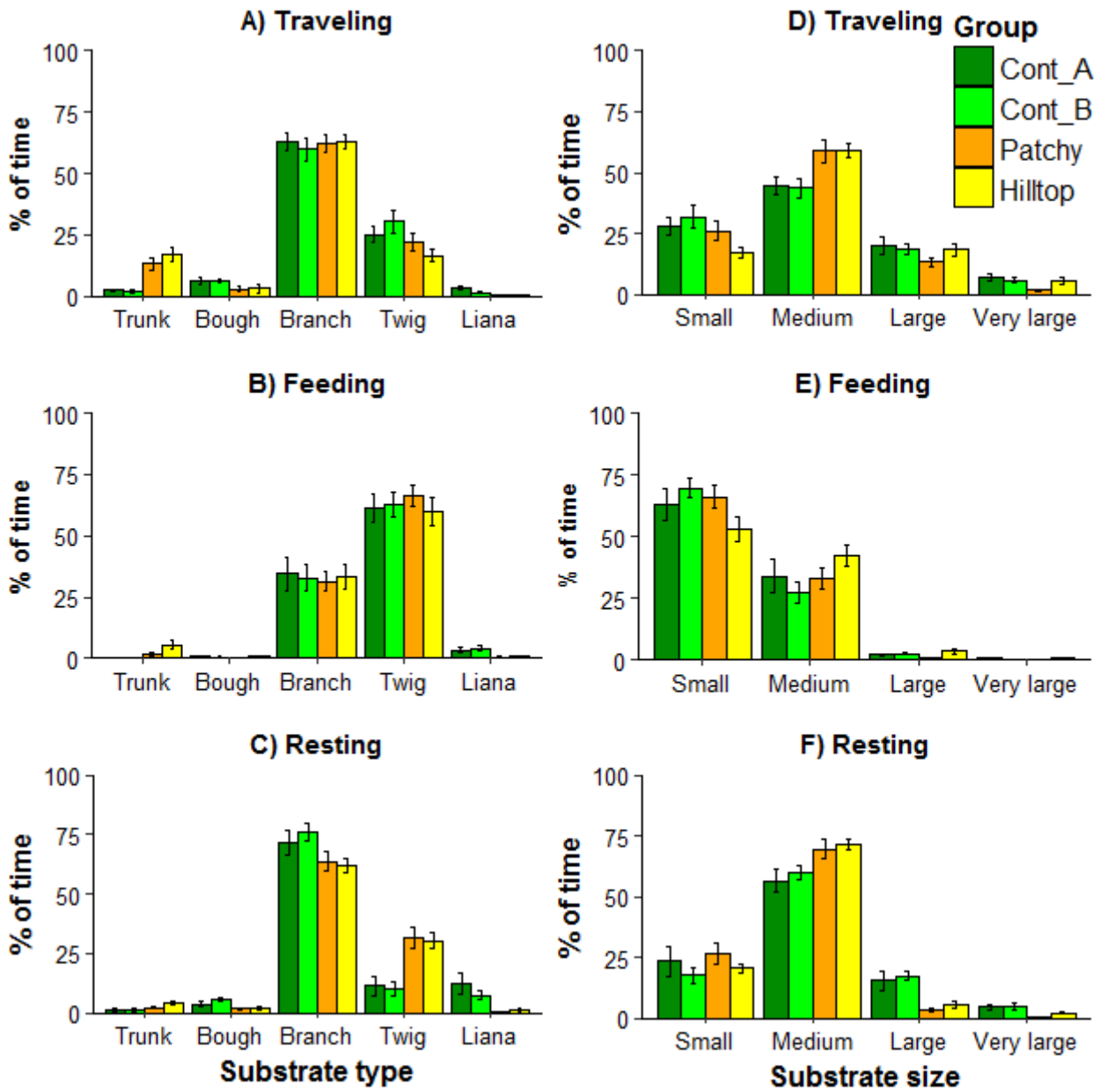
805 **FIGURE 3** Posture use among the four Bale monkey study groups in continuous forest
806 (Continuous A, [Cont_A] and Continuous B, [Cont_B]) and forest fragments (Patchy and
807 Hilltop) during A) feeding and resting combined, B) feeding, and C) resting.

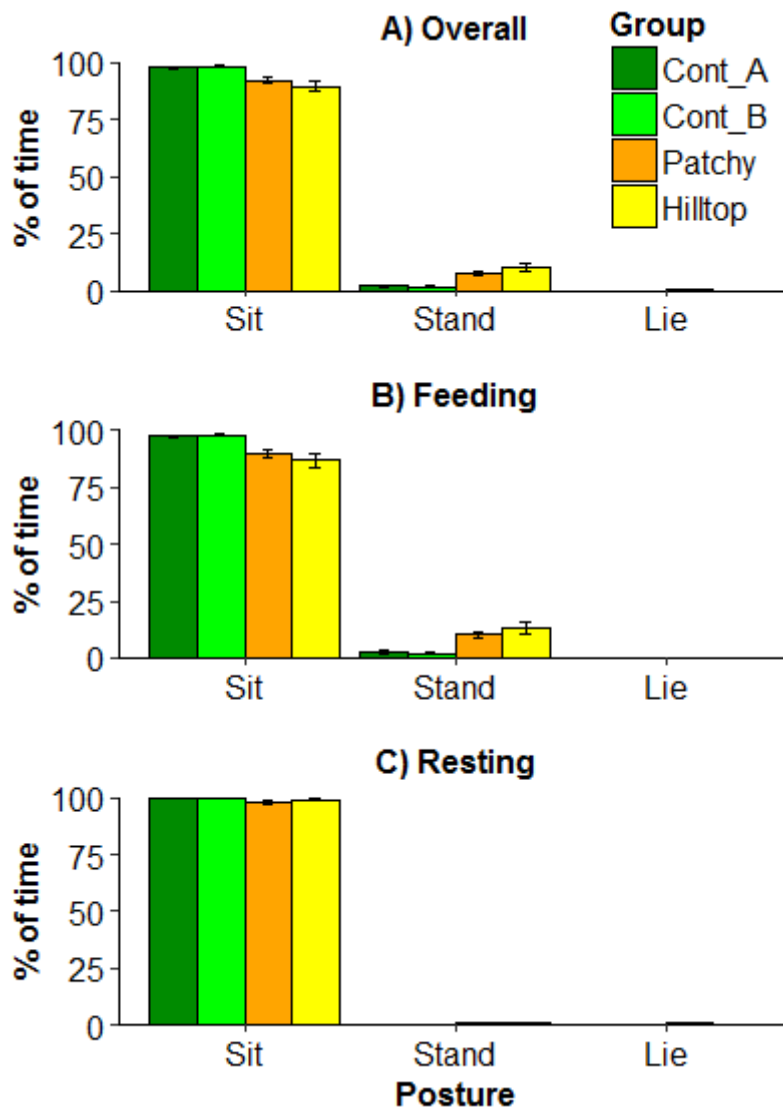
808 **FIGURE 4** Substrate type (left) and size (right) used among the four Bale monkey study groups
809 in continuous forest (Continuous A, [Cont_A] and Continuous B, [Cont_B]) and forest
810 fragments (Patchy and Hilltop) during locomotion (A and D), feeding (B and E), and resting (C
811 and F).

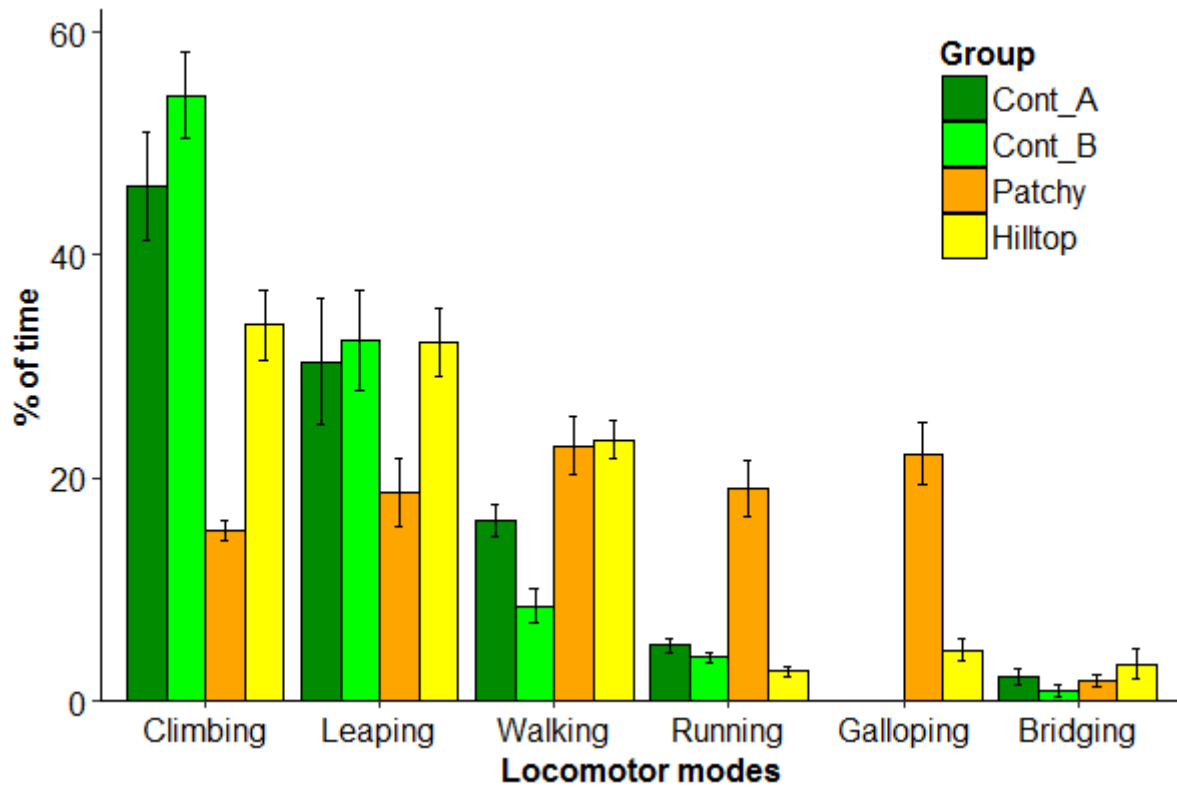
812 **FIGURE 5** Utilization of substrate inclination (left) and number (right) among the four Bale
813 monkey study groups in continuous forest (Continuous A, [Cont_A] and Continuous B,
814 [Cont_B]) and forest fragments (Patchy and Hilltop) during locomotion (A and D), feeding (B
815 and E), and resting (C and F).

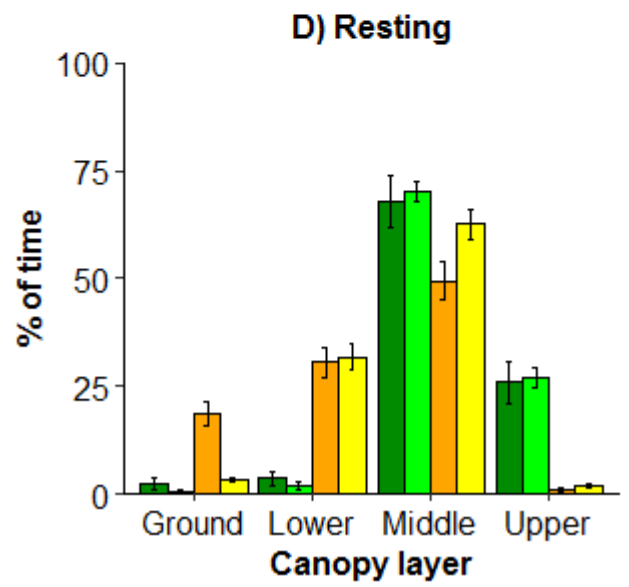
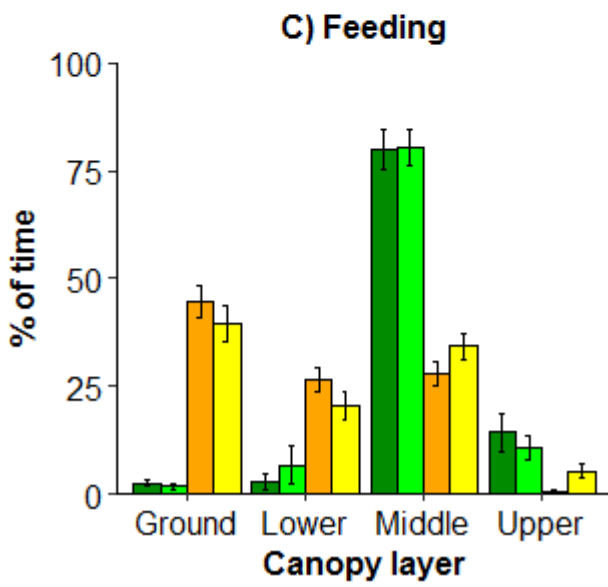
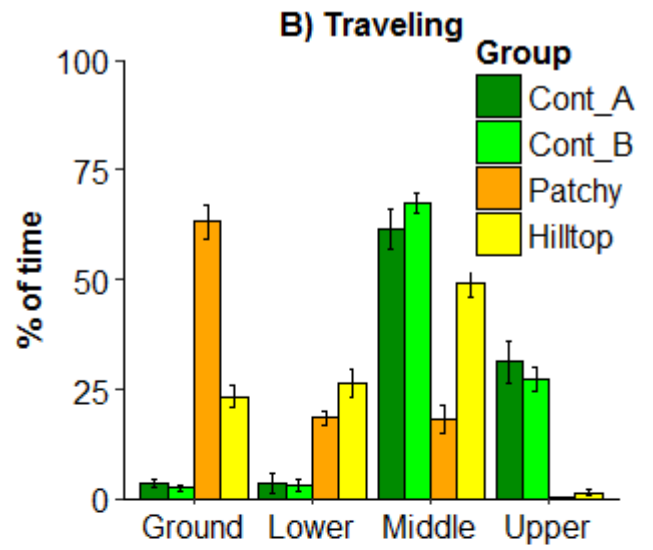
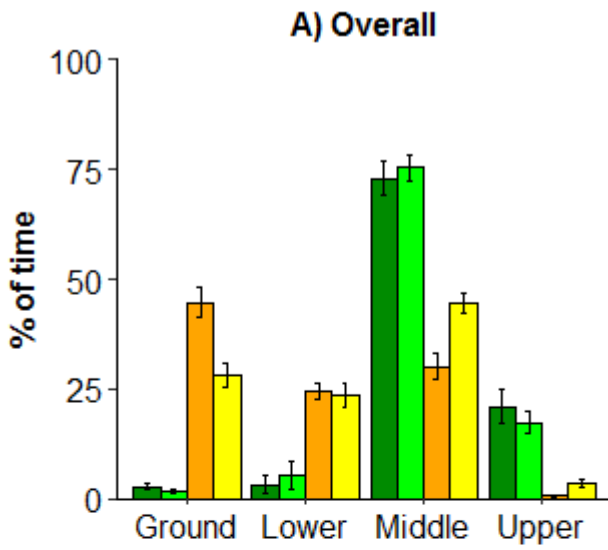
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