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

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

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

KEYWORDS

Ethiopian Highlands, forest fragment, locomotion, posture, terrestriality

INTRODUCTION

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

Positional behaviors are influenced by both extrinsic (e.g., ecological factors) (Bitty & McGraw, 2007; Gebo & Chapman, 1995a) and intrinsic factors (e.g., postcranial morphology and anatomy) (Fleagle, 2013; Garber, 2007; Sargis, Terranova, & Gebo, 2008). Habitat structure, food availability, diet, and the presence of predators are the most important ecological factors influencing the positional behavior and strata use of many primate species (Bitty & McGraw, 2007; Cannon & Leighton, 1994; Gebo & Chapman, 1995a; Huang et al., 2015; McGraw, 1998a). The locomotor behavior (movement with gross displacement of the animal) of some species varies among forest types: e.g., red colobus monkeys (*Colobus badius*) (Gebo & Chapman, 1995b), lemurs (Dagosto & Yamashita, 1998), and black-and-gold howlers (*Alouatta caraya*) (Prates & Bicca-Marques, 2008). These differences can often be attributed to variation in forest structure associated with changes in diet and the availability and distribution of food resources (Garber, 1998; McGraw, 1998a; Prates & Bicca-Marques, 2008; Youlatos, 1998b; Youlatos, 2002). Conversely, locomotor behavior is often invariable within species even across forest types. For instance, despite differences in habitat quality, locomotor modes were similar in studies of mustached tamarin monkeys (*Saguinus mystax*) in Peru (Garber & Pruetz, 1995) and five species of cercopithecid monkeys (*Cercopithecus* spp. and *Colobus* spp.) in Ivory Coast (McGraw, 1996). On the other hand, habitat fragmentation and degradation had variable effects on the feeding and resting postural behaviors of these species due to architectural differences across habitats (Garber & Pruetz, 1995; Gebo & Chapman, 1995b; McGraw, 1998a). In particular, feeding posture appears to be most affected by dietary and architectural differences across habitats (Garber, 1998; Gebo & Chapman, 1995b), whereas resting posture seems less likely to be affected by habitat structure (Garber & Pruetz, 1995; McGraw, 1996).

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

African green monkeys, also referred to as savannah monkeys, are comprised of six medium-sized species in the genus *Chlorocebus* including vervets (*C. pygerythrus*), grivets (*C. aethiops*), green monkeys (*C. sabaeus*), Malbrouck monkeys (*C. cynosuros*), tantalus monkeys (*C. tantalus*), and Bale monkeys (*C. djamdjamensis*) (Groves, 2005; Haus et al., 2013). All green monkeys, except Bale monkeys, are widely distributed generalists that inhabit open country and wooded habitats, consume a diverse diet, and are terrestrial or semi-terrestrial (Cardini, Dunn, O'Higgins, & Elton, 2013; Cardini, Jansson, & Elton, 2007; Enstam & Isbell, 2007; Isbell, Pruetz, Lewis, & Young, 1998; Kingdon, 2015). More specifically, vervets spent nearly 20% of their time on the ground in a study carried out in riparian and savannah woodland habitats in Kenya (Rose, 1979).

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

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

We therefore aimed to examine the effects of habitat fragmentation and degradation on the locomotor behavior, postural mode, vertical habitat use, and substrate utilization of Bale monkey groups in continuous forest and two forest fragments in the southern Ethiopian Highlands. Specifically, we investigated how Bale monkeys utilize locomotor and postural behaviors in relation to strata and substrate use patterns by testing the following five hypotheses. First, because of the architectural differences between forest types (Mekonnen et al., 2010a; Mekonnen et al., 2017; Mekonnen et al., 2018) as well as the probable past admixture between Bale monkeys in fragments and other more terrestrial *Chlorocebus* spp. (Haus et al., 2013), we hypothesized that Bale monkeys living in forest fragments would be more terrestrial than those in continuous forest (Hypothesis 1). Second, we hypothesized that the locomotor behavior of Bale monkeys would differ between populations living in continuous forest and forest fragments (Hypothesis 2) (Mekonnen et al., 2010a; Mekonnen et al., 2017; Mekonnen et al., 2018). Third, we hypothesized that Bale monkeys in fragments would spend more time engaged in quadrupedal locomotion (galloping, running, and walking), particularly on the ground, than conspecifics in continuous forest (Hypothesis 3). Fourth, we hypothesized that Bale monkeys in fragments would spend less time leaping and climbing than conspecifics in continuous forest (Hypothesis 4). Lastly, we hypothesized that differences in forest type would have little effect on Bale monkey resting posture, but would impact feeding posture, because resting posture is typically less influenced by differences in habitat quality than feeding posture (Hypothesis 5) (Fei et al., 2015; Garber & Pruetz, 1995; McGraw, 1996).

METHODS

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

Study site

We conducted this study in a continuous forest, Odobullu Forest (06°50'–6°56'N and 40°06'–40°12'E), and in two forest fragments (6°44'–06°45'N and 38°48'–38°51'E), Kokosa and Afursa, in the southern Ethiopian Highlands (Mekonnen et al., 2017). Odobullu Forest (hereafter Continuous forest) is a large forest within which bamboo is abundant. It covers 141 km^2 at elevations ranging from 1500 to 3300 m asl (Mekonnen et al., 2018). Odobullu consists of four habitat types: mostly bamboo forest and tree-dominated forest but also shrubland and occasional grasslands (Mekonnen et al., 2010b). It is partially protected, and disturbance in the home ranges of our study groups is uncommon due to the steep terrain and remoteness of the area.

Kokosa forest fragment (hereafter Patchy fragment) consists mostly of large trees and degraded bamboo set amidst a matrix of human settlement, cultivated land, shrubland, and grazing land. Patchy fragment covers 1.62 km^2 at elevations ranging from 2534 m to 2780 m asl. Most of the fragment is owned privately by local individuals, though a smaller portion is collectively owned by the local community (Mekonnen et al., 2017). Logging of bamboo by local people is common in the fragment today, though it was dominated by bamboo forest just three decades ago (Mekonnen et al., 2012).

Afursa forest fragment (hereafter Hilltop fragment) is set upon a hilltop and is a mix of secondary forest, shrubland, and a *Eucalyptus* plantation with graminoid and forb cover underneath. Bamboo has been nearly eradicated at Hilltop fragment, which covers only 0.34 km^2 at elevations ranging from 2582 m to 2790 m asl. It is surrounded by an anthropogenic matrix of cultivated lands, pastures, and human settlements. Currently, cutting of trees and use of the fragment for grazing are prohibited. However, the edge of the fragment, especially the ground cover underneath the *Eucalyptus* plantation, is used for grazing. Like Patchy fragment, Hilltop fragment was dominated by bamboo forest only three decades ago (Mekonnen et al., 2012). The distance between Hilltop and Patchy fragments is ~9 km and they have been separated by human settlements, grazing land, and agriculture for many decades (Mekonnen et al., 2012). The continuous forest and forest fragments are ~160 km apart (Mekonnen et al., 2017). The continuous forest is characterized by lower annual rainfall and temperature than the forest fragments (Mekonnen et al., 2018). Additional quantitative details about the study areas, groups, and characteristics of home ranges can be found in Table 1 of a previous publication (Mekonnen et al., 2017).

Study groups

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

Behavioral data collection

We collected data on positional behavior and strata and substrate use from July 2013 - June 2014 using instantaneous scan sampling (Altmann, 1974) conducted at 15-min intervals for up to 5-min duration, typically from 0700-1730. This sampling method is standard in studies of positional behavior because it helps ensure independence of data points (Dagosto, 1994; Fei et al., 2015; Zhu, Garber, Bezanson, Qi, & Li, 2015). During the last two months of the habituation period, AM and the two field assistants practiced accurately determining the monkeys' locomotor and postural modes, strata use, and substrate utilization via visual estimation as well as by using a measuring tape and rangefinder where appropriate (Bitty & McGraw, 2007; Huang et al., 2015; Iurck et al., 2013). Subsequently, we collected 28,583 individual behavioral scan records (hereinafter records) over 234 group follow days (N=12 months; Continuous A: 5442 records; Continuous B: 5499 records; Patchy fragment: 10254 records, and Hilltop fragment: 7388 records) (Mekonnen et al., 2017). We collected data on 52 days from Continuous A (mean = 4.3 days; SD ± 0.7; range 3-5 days per month), 54 days from Continuous B (mean = 4.5 days; SD ± 0.8; range 3-6 days per month), 61 days from Patchy (mean = 5.1 days; SD ± 0.3; range 5-6 days per month), and 67 days from Hilltop (mean = 5.6 days; SD ± 0.7; range 5-7 days per month).

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

Data analysis

We calculated the monthly percentage contribution of each locomotor mode, postural behavior, strata use category, and substrate utilization pattern for each Bale monkey group by dividing the monthly contribution of each category of a *locomotor mode, postural behavior, strata use category*, *substrate type*, and *substrate utilization* pattern with their corresponding total contributions. The sampling efforts for all categories summarized in this study are presented in Table S1. We analyzed lifestyle (terrestrial vs. arboreal) from recorded strata use patterns. Lifestyle denotes the general categorization of a species' ecology and behavior depending on the relative proportion of time spent on the ground or in the canopy layer (lower, middle, and upper strata). We categorized a species/population as terrestrial if it spends ≥60% of its time on the ground (Isbell et al., 1998; Motsch et al., 2015), semi-terrestrial if it spends 20-59% of its time on the ground, and arboreal if it spends >80% of its time in the trees (Motsch et al., 2015).

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

RESULTS

Strata use and lifestyle

Overall, and during traveling and feeding, groups in forest fragments spent significantly more time on the ground and in the lower stratum but significantly less time in the middle and upper strata than groups in continuous forest (Table 2; Figure 1A,B,C). During resting, the middle stratum was the most frequently used by all study groups, while the use of other strata varied among groups in continuous forest and forest fragments (Figure 1D). Specifically, groups in continuous forest spent significantly more time in the middle and upper strata, and significantly less time in the lower stratum and on the ground, than groups in forest fragments during resting (Table 2; Figure 1D).

Locomotor and postural behavior

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

Substrate utilization during arboreal locomotion and postural behavior

Substrate type: During locomotion, groups in both continuous forest and forest fragments mostly used branches as supports, though they sometimes used twigs, boughs, lianas, or trunks instead (Table 2; Figure 4A). During feeding, groups in both continuous forest and forest fragments most frequently used twigs. They also sometimes used branches, lianas, boughs, or trunks (Table 2; Figure 4B). During resting, groups in both continuous forest and forest fragments most frequently used branches and twigs, whereas boughs, trunks, and lianas were infrequently used (Figure 4C). However, groups in continuous forest used branches and lianas more frequently, and twigs and trunks less frequently, than groups in forest fragments during resting, though there was no difference in the use of boughs between continuous forest and fragment groups (Table 2).

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

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

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

DISCUSSION

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

Variation in degree of terrestriality among Bale monkeys across habitats

In this study, Bale monkey groups in forest fragments spent more than one-third of their time on the ground whereas those in continuous forest were observed on the ground only 2% of the time, thus supporting Hypothesis 1 that Bale monkeys living in forest fragments would be more terrestrial than those in continuous forest. We therefore suggest that Bale monkeys in forest fragments fit the semi-terrestrial category (i.e., 20-59% on the ground) occupied by other *Chlorocebus* spp. e.g., *C. pygerythrus* 20% (Rose, 1979) and some *Cercopithecus* spp. [e.g., *C. neglectus* 30% (Gautier-Hion, 1988), *C. solatus* 33.7% (Motsch et al., 2015), *C. campbelli* 20% (McGraw, 1998b) and *C. lhoesti* 38% (Struhsaker, 1981)] rather than the arboreal category that best fits the source populations of Bale monkeys in continuous forest (Mekonnen et al., in press).

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

Our study suggests that habitat alteration due to fragmentation and degradation may force Bale monkeys in fragments to use the ground frequently. Changes in habitat structure and food availability resulting from anthropogenic activities (e.g., land use, canopy disturbance, and logging) have been demonstrated to increase the degree of terrestriality in several other primates (Ancrenaz et al., 2014; Huang et al., 2015). Here, Bale monkeys in forest fragments also occupied anthropogenically-degraded habitats with disconnected canopies that probably caused them to increase terrestrial activity (Mekonnen et al., 2010a; Mekonnen et al., 2017). In response to habitat alteration due to the reduction in the availability, abundance, mean height, canopy size, and DBH of bamboo and large food tree species in fragments (Mekonnen et al., 2017; Mekonnen et al., 2018), Bale monkeys shifted their feeding from arboreal strata to the ground where shrubs, forbs, and graminoids are mostly available (Mekonnen et al., 2018). In the absence of their primary dietary species and items, several other arboreal primates also increased ground use to exploit terrestrial food sources more intensively (Eppley et al., 2016; Eppley, Verjans, & Donati, 2011; Xiang et al., 2009).

Plasticity of positional behavior in response to architectural variability across habitats

Consistent with Hypothesis 2, our results also showed that habitat fragmentation and degradation caused marked differences in locomotor behavior and support use between Bale monkeys in continuous forest and forest fragments. The modification of locomotor modes in forest fragments could represent a strategic response to habitat alteration resulting from fragmentation and degradation. Unlike conspecifics in continuous forest, Bale monkeys in forest fragments often used quadrupedal locomotion (running, walking, and galloping) to cross gaps between fragments consisting of human matrix while traveling and searching for food resources, which supports Hypothesis 3. In particular, Patchy fragment consisted of patches of degraded forest interspersed with grassland and cultivated land, and nearly 75% of the group's range is in human use areas (Mekonnen et al., 2017). Another reason for traveling quadrupedally on the ground could be to minimize locomotor routes and thus energy expenditure (Huang et al., 2015). Consistent with Hypothesis 4, Bale monkeys in fragments spent less time climbing and leaping due to marked differences in habitat quality and canopy structure between fragments and continuous forest. Primates in forest fragments spent less time climbing than those in continuous forest, perhaps because it is energetically expensive to climb vertically, and frequent ascent and descent in a fragmented setting would be energetically unfavorable (Hanna, Schmitt, & Griffin, 2008). Our recent study showed that Bale monkeys in fragments traveled shorter distances per day and spent less time feeding and moving than conspecifics in continuous forest, suggesting that monkeys in fragments adopted a strategy of energy minimization (Mekonnen et al., 2017). Similar to our Patchy group, primates in other studies also spent less time leaping when they traveled through habitats with discontinuous canopies, likely because gaps in fragmented areas are too large to cross via leaping (Lawler, Ford, Wright, & Easley, 2006; Workman & Schmitt, 2012; Zhou et al., 2013).

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

Unlike during feeding, resting postural patterns were similar irrespective of habitat type. This finding suggests that the changes to habitat structure in this case simply do not affect resting posture, a result consistent with previous studies of callitrichines and cercopithecids (Garber & Pruetz, 1995; McGraw, 1996). It is striking that Bale monkey groups in both habitats go to the middle strata to rest. This behavior is consistent with the hypothesis that some primates position themselves in places that make them maximally hidden during a period of vulnerability, from both terrestrial and arboreal predators (Grueter, Li, Ren, & Li, 2013). Despite the architectural differences between habitats (continuous versus fragmented canopy), monkeys most frequently used medium to large horizontal branches to rest in well-hidden parts of the tree crown as well as to ensure stability (Grueter et al., 2013; McGraw, 1998a).

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

Implications for Bale monkey evolution

Our results suggest that the ancestors of modern Bale monkeys may have used semi-terrestrial locomotion and standing postures. Close relatives such as grivets spend a considerable amount of time on the ground and have evolved morphological adaptations for a terrestrial (Gebo & Sargis, 1994) or semi-terrestrial mode of life (Anapol, Turner, Mott, & Jolly, 2005). They have longer distal fore- and hind limb segments for running and galloping in terrestrial habitats and longer tails for keeping balance during the transition between arboreal strata and the ground (Anapol & Gray, 2003; Anapol et al., 2005; Gebo & Sargis, 1994). Though we have no quantitative data on morphological variation between Bale monkeys in continuous forest and forest fragments, monkeys in fragments appear to exhibit some morphological differences (e.g., longer tails) from those in continuous forest (Mekonnen et al., 2012). Bale monkeys in fragments have similar terrestrial locomotor modes (running and galloping) to those of grivets that are uncommon among arboreal Bale monkeys in continuous forest. Thus, we propose that the ancestors of the arboreal Bale monkey may have been semi-terrestrial savannah dwelling species (Dolotovskaya et al., 2017) that transitioned to arboreality and adapted to closed canopies in continuous bamboo forest to exploit an available bamboo-based dietary niche (Mekonnen et al., 2010a; Mekonnen et al., 2010b; Mekonnen et al., 2018). As some habitats became fragmented through human disturbance, Bale monkeys in fragments returned to a semi-terrestrial lifestyle. Though terrestrial locomotion may have evolved only once among guenons (Tosi, Melnick, & Disotell, 2004), morphological modifications among terrestrial guenons may have occurred multiple times (Gebo & Sargis, 1994; Sargis et al., 2008). The semi-terrestrial behavior of some Bale monkeys documented in our study may be indicative of an incipient transition from arboreal to semi-terrestrial locomotion. More quantitative and comparative studies on their morphological adaptations are needed to increase our understanding of the shift from arboreality in continuous forest to semi-terrestriality in fragments.

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

Implications for Bale monkey conservation

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

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TABLE 1 Variables and definitions recorded for the study of Bale monkey positional 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±22.5°
	Oblique	Angle between 22.5° and 67.5°
	Vertical	Angle ≥ 67.5° to 90°
8	**Substrate number**	
	Single	Only a single support
	Multiple	Two or more main weight-bearing supports

*Definitions for locomotor and postural modes were adapted from Hunt et al. (1996), strata use from Huang et al. (2015), and substrate type, inclination, and size from Bitty and McGraw (2007); Iurck et al. (2013), and number from Iurck et al. (2013).

TABLE 2 Comparison of percentage strata use, positional behaviors, and substrate utilization between Bale monkey groups in continuous forest (CF, Continuous A and Continuous B) and fragmented forests (FF, Patchy and Hilltop) using One-Way ANOVA or Kruskal–Wallis test. 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	*ns*
		Walking	12.4	23.2	7.68	**
		Running	4.5	10.9	0.31	*ns*
		Galloping	0.0	13.4	377.20	***
		Bridging	1.5	2.6	0.50	*ns*
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	*ns*
		Standing	0.0	1.3	^{a}0.73	*ns*
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	*ns*
		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	*ns*
		Twig	61.8	63.0	0.19	*ns*
		Liana	3.7	0.6	13.75	***
4.5	Resting	Trunk	1.2	3.3	36.87	***
		Bough	4.6	1.9	3.70	*ns*
		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	*ns*
		Very large	6.4	3.7	4.57	*
5.2	Feeding	Small	64.9	60.9	0.723	*ns*
		Medium	32.2	36.3	1.01	*ns*
		Large	2.3	2.3	0.868	*ns*
		Very large	0.6	0.2	0.832	*ns*
5.3	Resting	Small	20.5	23.6	2.33	*ns*
		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	*ns*
		Oblique	18.3	56.3	57.27	***
		Vertical	40.0	8.7	13.47	***
6.2	Feeding	Horizontal	81.7	68.5	1.06	*ns*
		Oblique	18.1	31.4	1.07	*ns*
		Vertical	0.1	0.1	0.52	*ns*
6.3	Resting	Horizontal	51.4	77.2	1.06	*ns*
		Oblique	48.2	22.8	14.92	***
7.1	**Substrate number**					
7.1	Locomotion	Single	68.7	74.6	2.20	*ns*
		Multiple	31.3	25.4	2.20	*ns*
7.2	Feeding	Single	33.5	31.7	0.102	*ns*
		Multiple	66.5	68.3	0.102	*ns*
7.3	Resting	Single	77.4	66.5	6.53	*
		Multiple	22.6	33.5	6.53	*

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

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

Figure legends

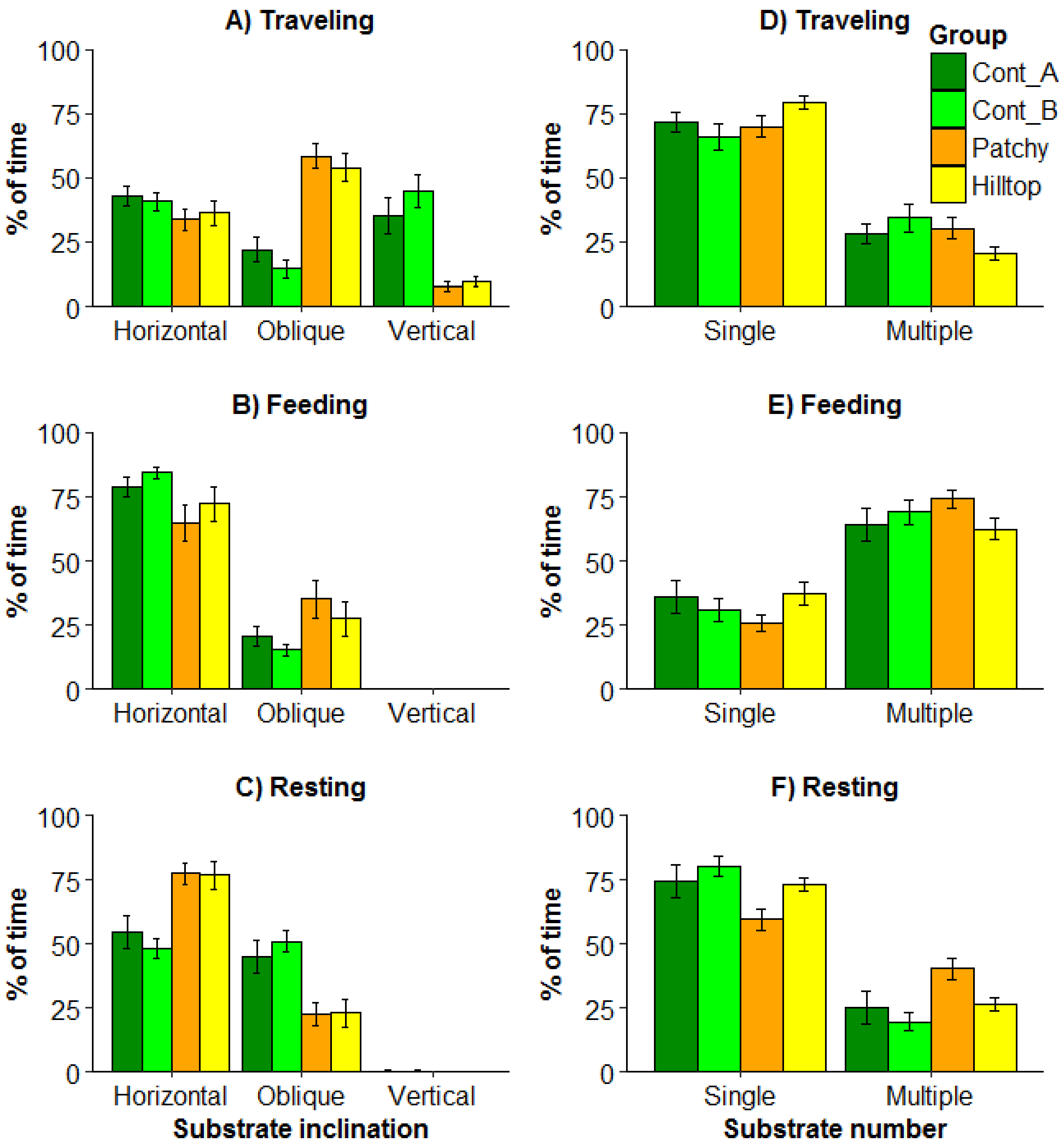
FIGURE 1 The proportion of time spent using different forest strata among Bale monkey groups in continuous forest (Continuous A, [Cont_A] and Continuous B, [Cont_B]) and forest fragments (Patchy and Hilltop) during A) overall behavioral activity, B) traveling, C) feeding, and D) resting among four Bale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

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

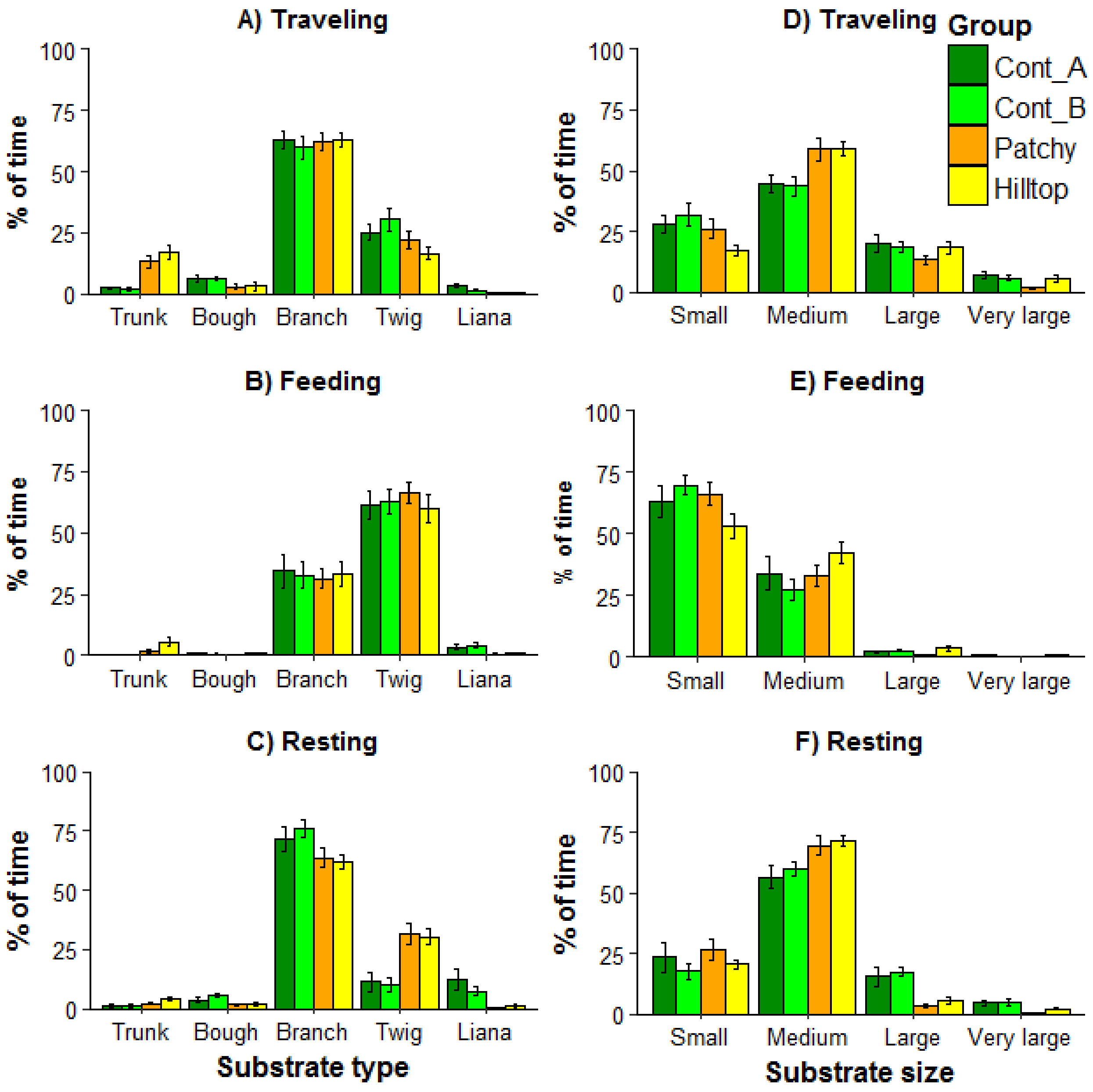
FIGURE 3 Posture use among the four Bale monkey study groups in continuous forest (Continuous A, [Cont_A] and Continuous B, [Cont_B]) and forest fragments (Patchy and Hilltop) during A) feeding and resting combined, B) feeding, and C) resting.

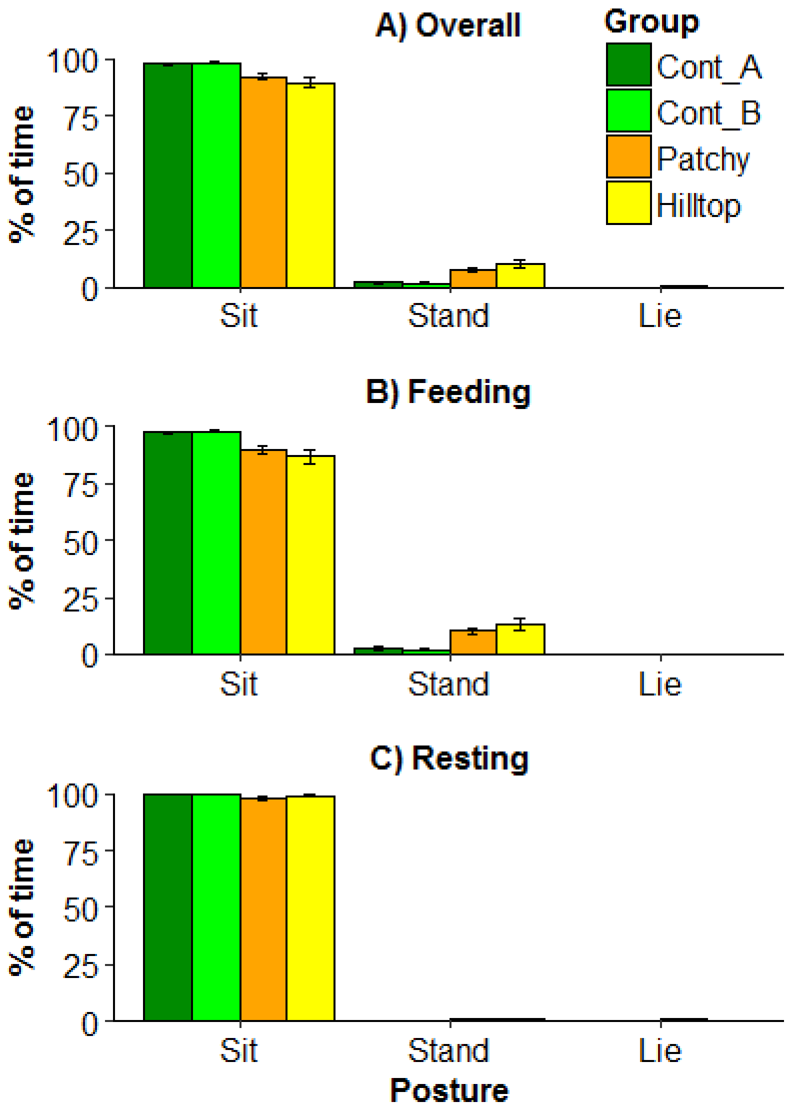
FIGURE 4 Substrate type (left) and size (right) used among the four Bale monkey study groups in continuous forest (Continuous A, [Cont_A] and Continuous B, [Cont_B]) and forest fragments (Patchy and Hilltop) during locomotion (A and D), feeding (B and E), and resting (C and F).

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

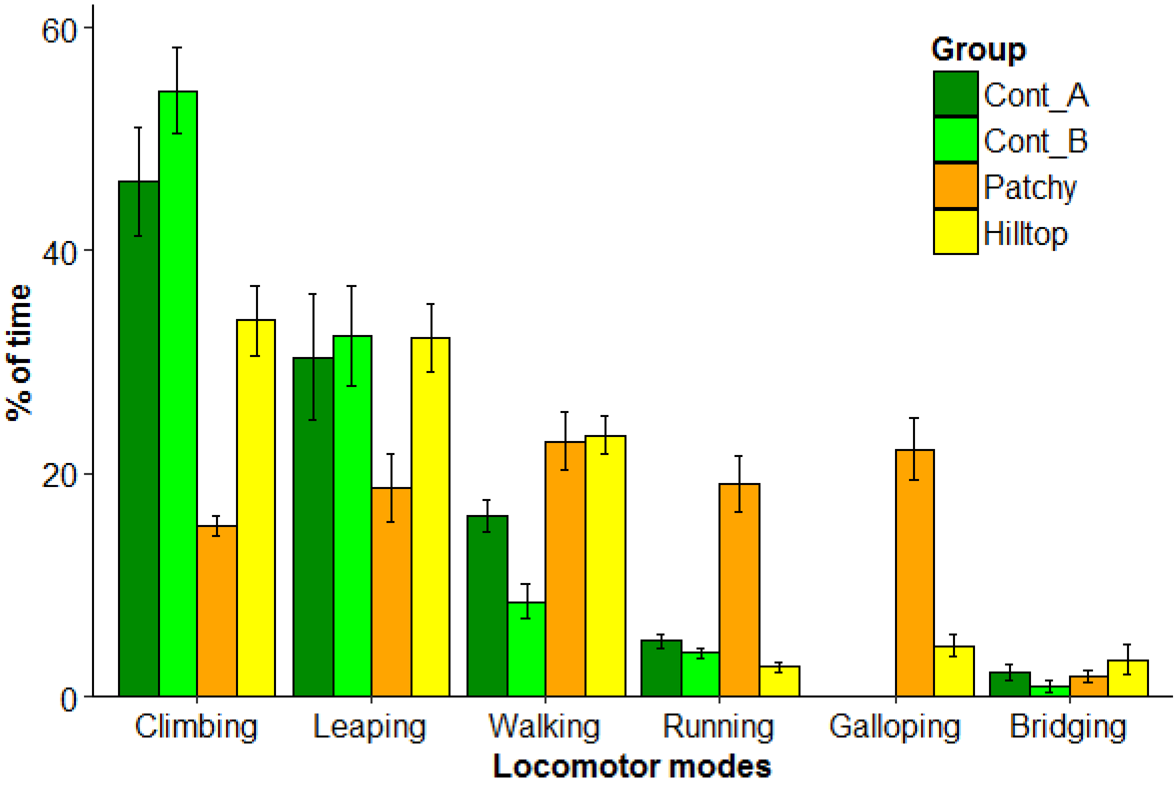

A) Traveling
B) Feeding
C) Resting
D) Traveling
E) Feeding
F) Resting
% of time
0
25
50
75
100
Horizontal
Oblique
Vertical
Single
Multiple
Substrate inclination
Substrate number
Group
Cont_A
Cont_B
Patchy
Hilltop

817

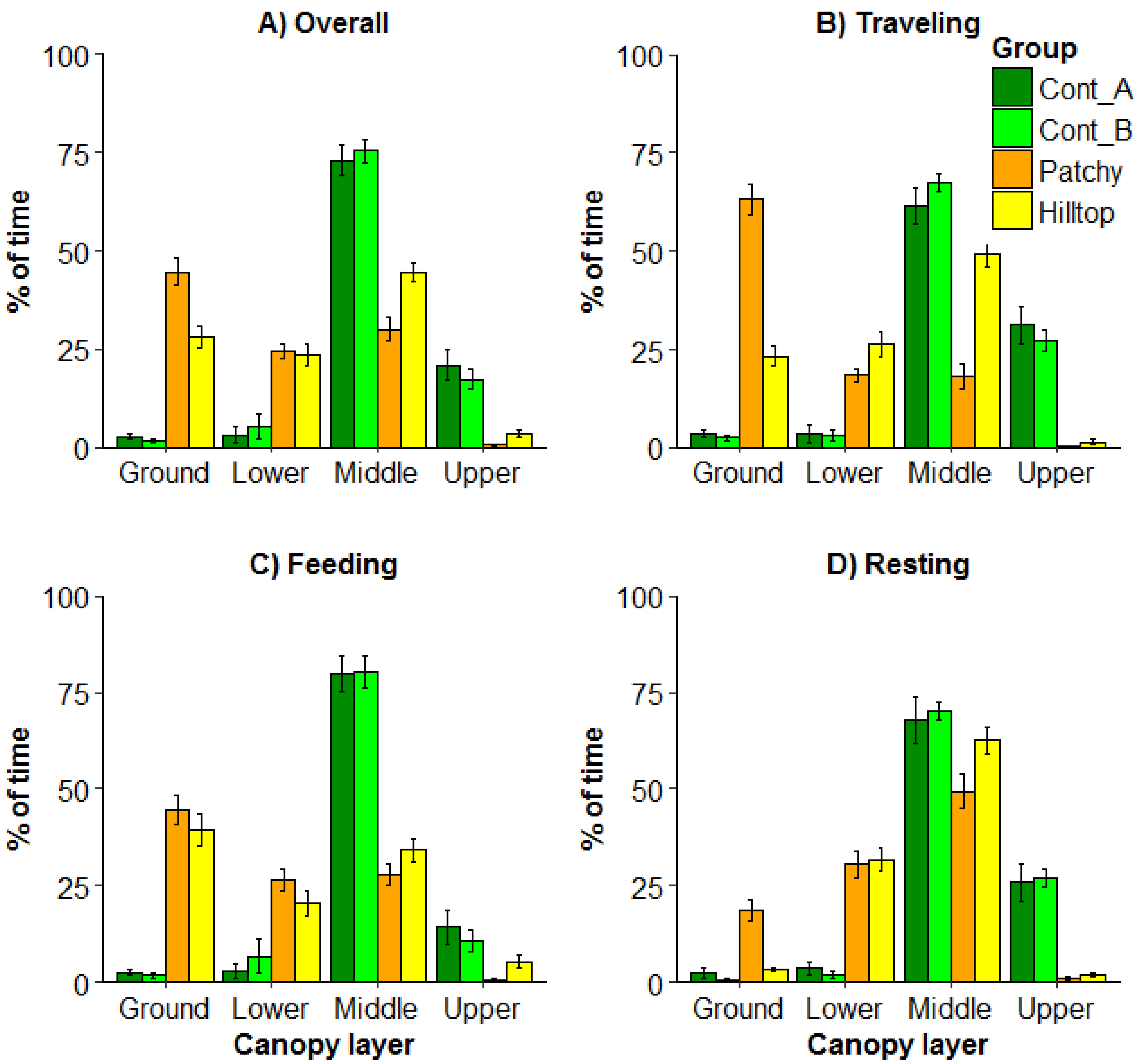

A) Traveling
D) Traveling
Group
Cont_A
Cont_B
Patchy
Hilltop
B) Feeding
E) Feeding
C) Resting
F) Resting
% of time
100
75
50
25
0
Trunk
Bough
Branch
Twig
Liana
Small
Medium
Large
Very large
Substrate type
Substrate size


A) Overall
Group
Cont_A
Cont_B
Patchy
Hilltop
% of time
100
75
50
25
0
Sit
Stand
Lie
B) Feeding
% of time
100
75
50
25
0
Sit
Stand
Lie
C) Resting
% of time
100
75
50
25
0
Sit
Stand
Lie
Posture

819


60
40
20
0
% of time
Group
Cont_A
Cont_B
Patchy
Hilltop
Climbing
Leaping
Walking
Running
Galloping
Bridging
Locomotor modes

820


A) Overall
B) Traveling
C) Feeding
D) Resting
% of time
100
75
50
25
0
Ground
Lower
Middle
Upper
Canopy layer
Group
Cont_A
Cont_B
Patchy
Hilltop

821

822