Impacts of Habitat Loss and Fragmentation on the Activity Budget, Ranging Ecology and Habitat Use of Bale Monkeys (Chlorocebus djamdjamensis) in the Southern Ethiopian Highlands

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Running header: Habitat Fragmentation Impact the Ecology of Bale monkey
Abstract: Understanding the extent to which primates in forest fragments can adjust behaviorally and ecologically to changes caused by deforestation is essential to designing conservation management plans. During a 12-month period, we studied the effects of habitat loss and degradation on the Ethiopian endemic, bamboo specialist, Bale monkey (Chlorocebus djamdjamensis) by comparing its habitat quality, activity budget, ranging ecology and habitat use in continuous forest and two fragments. We found that habitat loss and fragmentation resulted in major differences in vegetation composition and structure between forest types. We also found that Bale monkeys in continuous forest spent more time feeding and traveling and less time resting and socializing than monkeys in fragments. Bale monkeys in continuous forest also had higher movement rates (m/hr) than monkeys in fragments. Bale monkeys in continuous forest used exclusively bamboo and mixed bamboo forest habitats while conspecifics in fragments used a greater variety of habitats including human use areas (i.e., matrix). Our findings suggest that Bale monkeys in fragments use an energy minimization strategy to cope with the lower availability of the species’ primary food species, bamboo (Arundinaria alpina). We contend that Bale monkeys may retain some of the ancestral ecological flexibility assumed to be characteristic of the genus Chlorocebus, within which all extant species except Bale monkeys are regarded as ecological generalists. Our results suggest that, like other bamboo eating primates (e.g., the bamboo lemurs of Madagascar), Bale monkeys can cope with a certain threshold of habitat destruction. However, the long-term conservation prospects for Bale monkeys in fragments remain unclear and will require further monitoring to be properly evaluated.

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

Habitat loss and fragmentation are the primary threats to biodiversity in the tropics [Haddad et al., 2015]. Among mammals, nonhuman primates are particularly threatened by tropical deforestation [Cowlishaw and Dunbar, 2000; Irwin, 2016]. Currently, more than half of the world’s primate species are vulnerable to extinction because of anthropogenic habitat modifications [Estrada et al., 2012; Marsh et al., 2013]. Many species are increasingly reliant on human modified landscapes [Arroyo-Rodríguez and Fahrig, 2014].

The persistence of primates in small and isolated forest fragments depends on their behavioral and ecological flexibility [Onderdonk and Chapman, 2000]. Some primates persist in forest fragments by adopting an energy maximizing strategy, spending more time feeding and less time resting (e.g., *Ateles geoffroyi*: [Chaves et al., 2011]), or by traveling longer distances per day (*Propithecus edwardsi*: [Gerber et al., 2012]) than conspecifics in continuous forest. Conversely, many other primates survive in forest fragments by using an energy minimizing strategy, spending less time feeding, more time resting and less time traveling (e.g., *Chiropotes satanas*: [Boyle and Smith, 2010], *Alouatta seniculus*: [Palma et al., 2011], *Colobus vellerosus*: [Wong and Sicotte, 2007], or by traveling shorter distances per day (*Propithecus diadema*: [Irwin, 2008], *Eulemur collaris*: [Campera et al., 2014]) than their counterparts in continuous forest. There are also some primate taxa that have proven largely incapable of persisting in small, isolated fragments, ultimately resulting in widespread local extirpation (e.g., *Ateles geoffroyi*: [Estrada and Coates-Estrada, 1996]; *Trachypithecus pileatus*: [Sharma et al., 2014]). Generally, the smaller the fragment size, the higher the probability of extirpation. Species with specialized habitat and dietary requirements, limited geographic range, larger body size and larger home range needs are also particularly vulnerable to extinction [Harcourt, 2006; Benchimol and Peres,
However, the long-term persistence of primates in forest fragments also depends on several additional factors including the level of anthropogenic disturbance, hunting pressure, patch quality, matrix type and level of protection [Benchimol and Peres, 2013].

Successful conservation of threatened species in forest fragments depends on basic knowledge of the species’ ecology and subsequent implementation of appropriate conservation management strategies [Marsh, 2003]. Research on critically endangered Tana River mangabeys (Cercocebus galeritus) identified a link between fragment size and mangabey abundance [Wieczkowski, 2004] and quantified competition between humans and mangabeys over forest products [Kinnaird, 1992], factors that were subsequently incorporated into management plans for the species and its fragmented habitat [Wieczkowski, 2005]. Unfortunately, similar studies of behavioral and ecological responses to habitat loss and fragmentation are still lacking for many threatened species, including the enigmatic Bale monkey (Chlorocebus djamjamenis). The Bale monkey is endemic to the montane forests of the southern Ethiopian Highlands and is unusual among primates in occupying a bamboo specialist niche, consuming a diet of 77% bamboo in intact forest [Mekonnen et al., 2010a; Mekonnen and Jaffe, 2016]. Until recently, it was among the least studied primates in Africa [Mekonnen et al., 2010a; Mekonnen et al., 2010b] and is currently classified as Vulnerable by the IUCN [Butynski et al., 2008].

As for many other tropical primates [Marsh, 2003], much of the Bale monkey’s historical geographic range has been converted into agricultural land, grazing land and human settlements, leaving many populations in small and isolated forest fragments [Mekonnen et al., 2012]. With its specialized habitat (montane bamboo forest) and dietary (bamboo) requirements and its narrow geographic range (southern Ethiopia) [Butynski et al., 2008; Mekonnen et al., 2010a; Mekonnen et al., 2010b], the Bale monkey may consequently be at high risk of extinction due to
the increasing habitat loss and fragmentation across much of its range [Mekonnen et al., 2012].

The Bale monkey’s high degree of specialization is unique among its sister species, including the vervet (Chlorocebus pygerythrus) and grivet (C. aethiops) monkeys, which are able to exploit many different habitat types and consume a variety of diets [Isbell et al., 1998; Enstam and Isbell, 2007]. The recent discovery of Bale monkey populations in several heavily-disturbed forest fragments lacking bamboo suggests that the species may be capable of greater habitat flexibility [Mekonnen et al., 2012] than previously thought [Carpaneto and Gippoliti, 1994; Butynski et al., 2008; Mekonnen et al., 2010a]. Thus, despite their tendency towards specialization in continuous forest, the possibility that Bale monkeys retain some of the ecological flexibility characteristic of other members of the Chlorocebus genus warrants more detailed evaluation.

The main purpose of this study was to examine how bamboo habitat loss and fragmentation influence habitat quality, activity budget, home range use, movement rates and habitat use of Bale monkeys in continuous forest and forest fragments. In particular, we (1) tested the hypothesis that fragmentation would reduce habitat quality for Bale monkeys; (2) evaluated whether Bale monkeys adopt an energy minimizing or maximizing strategy in forest fragments; and (3) assessed how flexible Bale monkeys are behaviorally and ecologically in forest fragments. Our results suggest that forest fragments are indeed of lower quality than intact habitat, and that Bale monkeys manage to persist in fragments by using a wider variety of habitat types (including matrix) and by adopting an energy minimizing strategy. Based on this study, we recommend continued monitoring of Bale monkeys in forest fragments to evaluate their long-term viability in these suboptimal habitats [cf., Chapman et al., 2013] as well as the development
of conservation and management programs that protect not only the fragments but the access of
Bale monkeys to the surrounding matrix as well.

METHODS

Study Site and Habitat Characteristics

Based on the availability and disturbance status of bamboo (*Arundinaria alpina*), the species
which dominates the diet of Bale monkeys in continuous forest [Mekonnen et al., 2010a], we
selected three study sites: a continuous forest with intact bamboo (Odobullu Forest), a forest
fragment with degraded bamboo (Kokosa Forest) and a forest fragment with nearly eradicated
bamboo (Afursa Forest; Fig. 1). Odobullu Forest (hereafter Continuous forest) is a large forest
(14,100 ha) with a high density of bamboo that lies east of Bale Mountains National Park
[Mekonnen et al., 2010a]. Odobullu consists of four habitat types including bamboo forest, tree-
dominated forest, shrubland and grassland [Mekonnen et al., 2010b]. It is partially protected by
the privately owned hunting company, Ethiopian Rift Valley Safari, though legal bamboo harvest
is practiced by the local community in some sections of the forest [Mekonnen et al., 2010a].
However, disturbance is uncommon within the home ranges of our two study groups at Odobullu
because of the difficult terrain and inaccessibility of the area.

Kokosa forest fragment (hereafter Patchy fragment) consists of several “islands” of degraded
bamboo and large trees amidst a matrix of human settlements, cultivated land, shrubland and
grazing land. Only a portion of the 162 ha fragment is owned by the community while most of
the fragment is owned by private individuals. Selective cutting of bamboo is common in the
fragment. This forest fragment was dominated by bamboo forest as recently as three decades ago
[Mekonnen et al., 2012].
Afursa forest fragment (hereafter Hilltop fragment) consists of 34 ha of secondary forest, shrubland/bushland and *Eucalyptus* on a hilltop where bamboo has been nearly eradicated. Hilltop fragment is surrounded by an anthropogenic matrix consisting of cultivated land, pastures and human settlements. Currently, tree cutting and grazing in this fragment are forbidden by the district government. However, the edge of the fragment, especially a portion consisting of a *Eucalyptus* plantation with an understory of graminoids and forbs, is used for grazing of livestock. Hilltop fragment was also dominated by bamboo forest three decades ago [Mekonnen et al., 2012]. The distance between Hilltop and Patchy fragments is 9 km and they have been separated from each other by human settlement, grazing land and agriculture for many decades [Mekonnen et al., 2012]. The distance between the continuous forest and forest fragments is ~160 km (Fig. 1).

**Study Groups**

We selected four Bale monkey groups in the three forests for detailed study: two adjacent groups in the continuous forest at Odobullu (Continuous A and Continuous B), one group in Patchy fragment and one group in Hilltop fragment. We habituated each group to human observers for four months (from March-June 2013) by following them from dawn to dusk on a near daily basis. Group sizes varied among the study groups: Continuous A: 65 individuals, Continuous B: 38 individuals, Patchy fragment: 28 individuals and Hilltop fragment: 23 individuals. We determined the sizes of our study groups by opportunistically counting them when they crossed gaps in the forest canopy or, in the case of fragment groups, descended to the ground. During these counts, we were unable consistently to determine the age-sex category of each individual and did not recognize animals individually.
Vegetation Description and Food Availability

We examined vegetation composition and structure along 2-4 randomly selected transects 200-750 m long and 5 m wide within the home range of each study group. We sampled large trees in 50 m x 10 m vegetation quadrats (24 in Continuous forest, 27 in Patchy fragment and 24 quadrats in Hilltop fragment). We sampled only 12 quadrats for each of the continuous forest groups because of the high homogeneity of bamboo forest habitats [Mekonnen et al., 2010a; Eppley et al., 2015]. In each vegetation quadrat, AM, with the help of two research assistants, measured and recorded the following variables for all large trees with a diameter at breast height (DBH) ≥ 10 cm: species name, growth form, DBH (cm) (using caliper or tape measure), height (m) (Nikon 550 range finder) and canopy size/diameter (m) (tape measure). We randomly selected 50% of the vegetation quadrats for each group within which we counted and identified to species level all plants ≥ 2 m tall. We felt this was necessary because the monkeys depend not only on large trees but also on bamboo, shrubs and forbs. We classified plant growth forms into six categories: bamboo, large trees (≥ 10 cm DBH), small trees (≥ 2 m tall and < 10 cm DBH), shrubs, lianas (including climbers and epiphytes), and forbs. We collected unidentified plant species and pressed them for later identification by professional botanists at the National Herbarium, Addis Ababa University.

In each group’s home range, we quantified species richness, stem density, and species diversity for all plants ≥ 2 m tall and trees ≥ 10 cm DBH. We quantified plant species diversity using the Shannon-Wiener index of diversity, $H'$, dominance index, $D$ and evenness index, $J$ [Krebs, 1999]. We also assessed plant species richness and similarity. Plant species similarity was calculated by the Sorensen’s ($S$) index of similarity coefficient using EstimateS [Colwell,
To estimate the biomass of each large tree species, we calculated the basal area (BA) of each tree from the DBH recorded using the following formula (BA = \(0.5 \times DBH^2 \times \pi\)) [Fashing, 2001b].

To evaluate temporal changes in the availability of potential food resources over an annual cycle, we carried out monthly phenological assessments of 8 plant species we anticipated would be important in the diets of Bale monkeys based on preliminary observations of the four groups in this study as well as the results from an earlier 8-month study of the species in continuous forest [Mekonnen et al., 2010a]. We marked and identified 10-15 individuals of each species within or near the vegetation transects for monthly monitoring, including trees (≥ 10 cm DBH), bamboo (Arundinaria alpina) and shrubs. After visual inspection (using binoculars when necessary), we assigned each individual plant a relative abundance score for each of its potential food items (young leaves, mature leaves, flowers, ripe fruits and shoots). Relative abundance score ranged from 0 (item absent from plant) to 8 (plant fully laden with item, though keeping in mind that different species may have different densities of an item, especially fruits, when fully laden) at intervals of 1.

We analysed phenological data from five tree species (Canthium oligocarpum, Dombeya torrida, Galiniera saxifraga, Hagenia abyssinica, and Ilex mitis), two shrubs (Rubus apetalus and Bothriocline schimperi) and bamboo (A. alpina). These species accounted for 92.6% of the overall diet for Continuous A; 93.4% for Continuous B, 50.9% for Patchy fragment and 44.5% for Hilltop fragment. The lower contribution of monitored plants to the diets of fragment groups resulted from them consuming much less bamboo as well as a greater variety of food species, including difficult to monitor grasses and herbs [cf., Fashing et al., 2014], than continuous forest groups [Mekonnen et al., in prep]. We calculated the monthly mean phenological scores for
young leaves, fruits, flowers, and shoots for each individual plant species. We calculated a monthly food availability index (FAI) for each plant part by multiplying the mean phenology scores of species $i$ with the mean basal area of species $i$ and density of the corresponding species $i$ per ha [Fashing, 2001b].

**Activity Budget**

After two months of practice data collection, AM collected activity data with the help of two well-trained research assistants from July 2013 through June 2014. From ca 0700 to 1730, these data were collected via instantaneous scans [Altmann, 1974] of up to 5 minutes length every 15 minutes. The activity recorded for each individual was the first activity that lasted for $\geq 3$ seconds once it came into view. During scans, we collected data for up to the first 5 adults or juveniles but not from infants. We scanned the group each time from left to right to avoid possible biases towards eye-catching activities like grooming, agonism and mating. During scans, we recorded individuals as performing one of the following behaviors: feeding (foraging for or masticating food items), moving (any locomotor behavior), resting (inactive), socializing (playing, grooming, engaging in agonistic or sexual activity) or vocalizing. We obtained a total of 28,583 individual behavioral scan records during 2085 h of observation (Continuous A = 441; Continuous B = 432; Patchy fragment = 601; Hilltop fragment = 611) over 234 group follow days (Continuous A = 52; Continuous B = 54; Patchy fragment = 61; Hilltop fragment = 67) lasting 6.0 (incomplete but usable day) – 10.5 h (complete day).

We calculated the proportions of time spent on different activities by dividing the number of behavioral records for each activity category with the total number of activity records. We used the behavioral records of the group to calculate the activity budgets per day and averaged within
each month to construct monthly activity budgets for each study group (mean ± SD records; Continuous A = 453.5 ± 81.7; Continuous B = 458.3 ± 139.0; Patchy fragment = 854.5 ± 135.2; Hilltop fragment = 615.7 ± 113.6). The grand mean proportions of the monthly budgets provided the annual activity budgets for the entire study period. We combined social behaviors (agonism, grooming, playing and sexual activity) in our data analyses because some of these behaviors accounted for <1% of the total activity budget.

Spatial Analysis: Home Range and Movement Rate

We also recorded the location of the estimated geographic center of the group [Fashing, 2001a] and elevation using a handheld Garmin GPSMap 62s Geographic Positioning System (GPS) at 15-minute intervals. We recorded GPS locations even if activity data were not recorded owing to poor visibility as long as we confirmed the group’s location via cues such as distinctive tree movements or vocalizations.

For spatial analysis, we used a combination of ArcGIS 10.3 [ESRI, 2011], Home Range Tools (HRT) version 2.0 [Rodgers et al., 2015], Geospatial Modeling Environment (GME) Version 0.7.3 [Beyer, 2015] and R [R Development Core Team, 2015]. We modelled home range using Home Range Tools (HRT) in ArcGIS 10.3 using all GPS locations recorded. We used fixed Kernel Density Estimations (KDEs) which measure utilization distribution [Worton, 1989; Seaman and Powell, 1996]. We used an ad hoc bandwidth estimator, which minimizes over-smoothing of the reference bandwidth (h_{ref}), that performs better for large sample sizes and clumped GPS locations [Kie et al., 2010]. In this study, we defined home range as ad hoc fixed KDE with 95% isopleths (contour lines) and core areas with 50% isopleths. In addition, we modelled home range using the Minimum Convex Polygon (MCP) method to enable comparison.
with earlier studies [Harris et al., 1990]. We calculated MCP (90%, 95% and 100% MCPs) using fixed mean points [Rodgers et al., 2015]. To estimate home range and core area overlap between adjacent groups, we used ArcGIS analysis tools to intersect the corresponding home ranges and core areas of adjacent groups. We defined home range overlap as the percentage of the area shared by adjacent groups relative to the total home range used by each group. To assess the influence of patch effect in each group’s home range, we calculated a shape index (perimeter-to-area ratio) of 95% KDE by dividing its perimeter (m) by the square root of home range size (m²) multiplied by π. Shape index values usually vary from 1 (more circular) to >5 (more elongated and irregular) [Forman and Godron, 1986]. A shape index value indicates the patch area exposed to the edge [Helzer and Jelinski, 1999].

To estimate hourly movement rates (MVRs, m/h), we used complete days as well as incomplete days with group follows of ≥ 7 hrs. We first converted the consecutive GPS locations of each study group to point shapefile in ArcGIS 10.3 and measured daily path length using two commands in GME (convert.pointstolines and addlength). We calculated hourly movement rate (m/hr) by dividing the daily path length (m) by the total time traveled (hr) per day. The mean of the 12 monthly MVRs provided the mean annual MVR for each group.

Habitat Use

During the scan sampling at 15-minute intervals, we also recorded the habitat type occupied by the majority of the group. We categorized habitats as bamboo forest, mixed-bamboo forest, tree-dominated forest, shrubland, cultivated land, grazing land, or Eucalyptus plantation. In bamboo forest, bamboo accounts for ≥50% of the stem density and large trees are scarce. Mixed-bamboo forest is a habitat consisting of 10-49% bamboo as well as many large trees. In tree-
dominated forest, large trees account for >50% the canopy cover and bamboo accounts for <10% of the stem density. Shrubland consists of ≥50% of shrubs, predominantly *Rubus apetalus*, *Bothriocline schimperi* and *Jasminum abyssinicum*, and relatively few trees. Cultivated land is used for cultivation, especially enset (*Ensete ventricosum*) and home gardens. Grazing land is covered by graminoids and forbs and exploited by livestock. *Eucalyptus* plantation consists primarily of *Eucalyptus* sp. with or without a graminoid and forb understory. To examine matrix use patterns, we also categorized the locations occupied by most of the group members during scans as matrix (human use areas used for cultivation, plantation, and grazing) or forest (all other areas).

Within each group’s 95% KDE home range, we calculated habitat selection ratios by dividing the frequency of observed use (% of scans in each habitat type) by the frequency of expected use (% of home range area accounted for by each habitat type) [Manly et al., 2002]. To obtain the frequency of expected use, the habitat types within each home range were classified using high resolution Google Earth images (continuous forest: 18 January 2014; forest fragments: 24 January 2014) of the study area in ArcGIS 10.3 [Pebsworth et al., 2012; Kelley, 2013] and ground-truthed with the GPS and habitat type data collected during group follows. A habitat selection ratio close to 1 indicates no selectivity for that habitat, <1 indicates a habitat is avoided and >1 indicates a habitat is selected.

**Statistical Analyses**

All statistical tests were carried out using the statistical software R version 3.2.3 [R Development Core Team, 2015] with significance level $P \leq 0.05$ unless otherwise stated. We tested all data for normality using the Shapiro-Wilk test and homogeneity of variances using the
Levene test ($P > 0.05$). We initially calculated and compared all the variables for each Bale monkey study group individually and examined the differences using a one-way ANOVA model followed by Tukey’s HSD post hoc test. When the results for the two continuous forest or the two forest fragment groups showed the same general patterns, we then combined them into a single continuous forest or forest fragment category unless otherwise stated. To examine differences across groups in general habitat characteristics and monthly movement rates, we used a one-way ANOVA after we log transformed the data to fit the assumption of normality. We also used a one-way ANOVA test for differences in monthly activity budgets among groups in continuous forest and forest fragments. We performed logit transformations of proportion data prior to statistical analysis to normalize the data as recommended by Warton and Hui [2011].

Permission to conduct this research was granted by the Ethiopian Wildlife Conservation Authority. This study complied with the American Society of Primatologists’s Principles for the Ethical Treatment of Nonhuman Primates and adhered to the legal requirements of Ethiopia.

RESULTS

Habitat Description and Resource Availability

Plant species richness was higher in the fragments (Patchy: 35 species; Hilltop: 47 species) than in the continuous forest (Continuous A: 23 species; Continuous B: 19 species). The ranges of the two continuous groups had a higher plant species similarity index (19 shared species; Sorensen’s $S = 0.91$) than the ranges of the two fragment groups (28 shared species; Sorensen’s $S = 0.68$). Plant species diversity and evenness were much higher and dominance much lower in fragmented forest than continuous forest (Table I). Bamboo dominated (85.9% of stems $\geq 2$ m tall, $n = 6217$) in continuous forest, but accounted for only 39.6% of stems ($n = 1341$) in Patchy...
fragment and 1.6% of stems (n = 37) in Hilltop fragment. The density of bamboo was nearly 5-
times greater in Continuous forest than in Patchy fragment and 170-times greater in Continuous
Forest than in Hilltop fragment (Table I). Large trees (≥ 10 cm DBH) were also more abundant
in Continuous forest (mean = 198.3 stems/ha) than in the fragments (mean = 138.1 stems/ha).
However, shrubs were far more abundant in fragments (mean = 979.2 stems/ha) than in
continuous forest (mean = 65.0 stems/ha) (Table I).

The basal area of large (≥ 10 cm DBH) food trees was nearly 3-times higher in continuous
forest (mean = 2292.0 cm^2/ha) than in fragments (mean = 780.2 cm^2/ha) (Table I). Further, Bale
monkeys had significantly higher monthly food availability indices of bamboo young leaves
(ANOVA: F = 544.00, df = 1, P < 0.001), non-bamboo young leaves (ANOVA: F = 17.17, df =
1, P < 0.001), and fruits (ANOVA: F = 4.19, df = 1, P = 0.05) in continuous forest than in forest
fragments.

**Activity Budget**

Bale monkeys in all study groups spent most of their time feeding (51.5-56.2%), followed by
moving (17.5-25.3%), resting (12.0-18.1%), socializing (2.8-12.7%) and vocalizing (0.3-4.8%)
(Fig. 2). Groups in continuous forest spent significantly more time feeding (55.5% vs. 52.3%;
ANOVA: F = 4.9, df = 1, P < 0.001), moving (24.7% vs. 18.6%; ANOVA: F = 34.1, df = 1, P <
0.001) and vocalizing (4.6% vs 0.6%; ANOVA: F = 181.3, df = 1, P < 0.001) and significantly
less time resting (12.2% vs. 17.6%; ANOVA: F = 30.4, df = 1, P < 0.001) and socializing (2.9%
vs. 10.9%; ANOVA: F = 57.4, df = 1, P < 0.001) than groups in forest fragments.

**Spatial Analysis**
The 95% KDE home ranges were 39.9 ha for Patchy fragment group, 26.1 ha for Continuous group A, 15.9 ha for Continuous group B and 15.8 ha for the Hilltop fragment group (Fig. 3; Table II). Home range overlap between the continuous forest groups was 7.5 ha (Fig. 3). The Patchy and Hilltop fragment groups each overlapped with one adjacent group, although we did not carry out a systematic study to determine the amount of overlap. The Patchy fragment group had a larger annual core area than groups at the other sites (Fig. 3; Table II). The two adjacent continuous forest groups had only 0.1 ha overlap of their core areas. We found that the Patchy fragment group had a higher perimeter-to-area ratio (5.8) than the other groups (Continuous A: 4.1; Continuous B: 2.6; Hilltop: 2.2) because of its extremely elongated and irregularly shaped home range. Bale monkeys in continuous forest had a significantly higher movement rate (Mean = 121.2 ± 6.4 m/hr) than monkeys in forest fragments (Mean = 94.5 ± 5.1 m/hr) (ANOVA: F = 16.77, df = 1, P < 0.001) (Table III).

Habitat Use

The home ranges of continuous forest groups consisted solely of bamboo and mixed-bamboo forest habitats while Patchy fragment group used five and Hilltop fragment group four habitat types (Fig. 4; Table IV). Continuous A used both bamboo and mixed bamboo forest in accordance with their respective availabilities in its home range. However, Continuous B used the bamboo forest significantly more than expected based on its percentage representation in the home range. Patchy fragment group used mixed-bamboo forest and shrubland more than expected while using grassland, tree-dominated forest and cultivated land less than expected. Hilltop fragment group used shrubland and tree-dominated forest more than expected, and Eucalyptus plantation and grazing land habitats less than expected (Table IV). Overall, Patchy
fragment group spent far more time in matrix habitat than the other groups (Patchy: 73.5%; Hilltop: 26.9%; Continuous A: 0% and Continuous B: 0%).

**DISCUSSION**

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

Habitat loss and fragmentation resulted in major differences in habitat characteristics, vegetation composition and structure in our montane forest study sites in southern Ethiopia. Our results are consistent with those from studies of tropical forests elsewhere which have shown that fragmentation leads to reduction in the availability of large food trees, changes in tree composition and diversity, and reduction in overall habitat quality [Laurance et al., 2000; Arroyo-Rodríguez et al., 2007]. In our study, although fragments had higher plant species richness, Bale monkey groups in continuous forest had access to a greater abundance of both bamboo and large food trees, suggesting that the continuous forest was of much higher habitat quality than the forest fragments. In Malagasy forests, which also contain primate bamboo specialists (bamboo lemurs: *Hapalemur* spp.), habitat destruction has also been demonstrated to increase plant species richness, but lower the density of food plants, leading to reduced overall habitat quality for lemurs in forest fragments [Tan, 1999; Grassi, 2006]. Furthermore, fragmentation-induced reduction in habitat quality may lower carrying capacity and group size, adversely affecting the long-term viability of primates occupying fragments [Arroyo-Rodríguez and Mandujano, 2006]. In our study, group size was indeed much lower in forest fragments (mean=25.5 individuals, n=2 groups) than in continuous forest (51.5 individuals, n=2 groups), though we lack the population density data necessary to evaluate the possibility of differences in Bale monkey carrying capacity between forest types [cf., Butynski, 1990].
Are Bale Monkeys in Forest Fragments Energy Minimizers?

Our study suggests that Bale monkeys in fragments adopt an energy minimization strategy. Specifically, they spent more time resting, less time feeding and moving, and traveled at a slower rate than conspecifics in continuous forest. They also socialized more in fragmented forests, though most Bale monkey social behavior consists of grooming, which is not believed to be a very energetically demanding activity [Russell and Phelps, 2013]. The apparent energy conservation strategy of Bale monkeys in fragments may be a response to the lower overall food availability at these sites. A number of primates adopt a similar strategy to cope with the limited abundance, density and quality of food resources in fragments, including several other folivores, Colobus vellerosus [Wong and Sicotte, 2007], Alouatta palliata [Dunn et al., 2009], and Alouatta seniculus [Palma et al., 2011], and at least one granivore, Chiropotes satanas [Boyle and Smith, 2010]. Another proximate factor that may contribute to primates adopting an energy conservation strategy in fragments is that ambient temperatures are often higher there than in nearby continuous forests [Silva and Ferrari, 2009; Korstjens et al., 2010]. Indeed, mean daily temperature averaged a full two degrees higher in forest fragments (16.7 °C SE ± 0.4) than in continuous forest (14.7 °C SE ± 0.2) during our study [Mekonnen et al. in prep.], perhaps contributing to the greater time spent resting and slower rates of movement among Bale monkeys inhabiting fragments. However, we cannot rule out the possibility that the monkeys in the hotter forest fragments are more active during what are presumably the coolest times of day, earlier in the morning and later in the evening than our observation hours (typically 0700-1730). Lastly, it is often the case, including in our study, that primates in continuous forest live in considerably larger groups than conspecifics in fragments [Marsh, 2003], raising the possibility that increased
scramble competition [Isbell, 1991] might also contribute to increases in the proportion of time spent foraging and moving by Bale monkeys and other primates in continuous forest.

How Ecologically Flexible are Bale Monkeys?

Habitat loss and degradation affect plant species richness, diversity and structure in forest fragments consequently modifying the natural habitat and availability of food resources for species [Marsh, 2003]. Forest fragments generally consist of islands of disturbed vegetation surrounded by areas of intensive human use [Benchimol and Peres, 2013]. Bale monkeys in forest fragments proved able to use the surrounding human matrix, with the group in Patchy fragment, in particular, spending nearly ¾ of its time in matrix habitat. Groups in fragments also supplemented their diets with alternative food resources to bamboo including shrubs, forbs, graminoids, and even cultivated foods; most of these items were never consumed by groups in continuous forest [Mekonnen et al., in prep]. These findings suggest that Bale monkeys in forest fragments are capable of much greater ecological flexibility than was previously believed [Carpaneto and Gippoliti, 1994; Butynski et al., 2008; Mekonnen et al., 2010a].

Intriguingly, the sister taxa to Bale monkeys, the five other species of Chlorocebus (two of whom - C. aethiops and C. pygerythrus - also occur in Ethiopia), are renowned for their ecological flexibility, inhabiting a variety of habitats including shrublands, grasslands, woodlands and riverine forests as well as human matrix areas [Isbell et al., 1998; Zinner et al., 2002; Enstam and Isbell, 2007]. While Bale monkeys do not match the other Chlorocebus taxa in degree of plasticity of diet or habitat use [Enstam and Isbell, 2007], our study suggests that they retain at least some of the ancestral ecological flexibility we assume to be characteristic of the genus Chlorocebus. However, given recent morphological [some individuals in fragments
exhibit intermediate physical characteristics between Bale monkeys and grivets: Mekonnen et al., 2012] and genetic [mitochondrial DNA haplotypes suggest continuous and fragment populations form two different clades: Mekonnen et al., in prep.] evidence, it is also possible that a recent history of hybridization with other Chlorocebus taxa has contributed to the ecological plasticity of Bale monkeys in fragments that we documented.

Our results show that Bale monkeys can cope with a certain threshold of habitat destruction. This flexibility stands in stark contrast to the case of the giant panda (Ailuropoda melanoleuca) of China, another bamboo specialist, which shows few signs of being able to cope with intensive disturbance of its habitat. Indeed, 99% of the diet of the giant panda consists of bamboo and it has never been observed to occur outside of thick bamboo forest [Schaller, 1985; Reid and Jinchu, 1991]. Conversely, the other major primate bamboo specialists, the bamboo lemurs (Hapalemur aureus, H. griseus, and H. simus) of Madagascar, are able to exploit modified habitats and subsist on a mix of bamboo and other food resources, including human crops, in logged and degraded forests [Tan, 1999; Grassi, 2006; Tan, 2006]. These patterns suggest that bamboo-eating primates are more flexible than carnivora (i.e., pandas) that subsist on bamboo for whom the bamboo eating adaptation may be a more ancient adaptation. Nevertheless, it remains unclear whether even the more ecologically versatile bamboo lemurs and Bale monkeys, can persist over the long-term in such small and isolated forest fragments particularly if their exploitation of human crops within the nearby matrix results in conflict with local communities [Tan, 2006; Mekonnen et al., 2012].

Implications for Conservation and Management
Bale monkeys in fragments have smaller group sizes, experience lower bamboo availability, and appear to adopt a strategy of energy minimization. Long-term monitoring of Bale monkeys in fragments will be essential to determining if life in fragments is an evolutionarily viable strategy for the species or if these adjustments are having negative fitness consequences [cf., Chapman et al., 2013]. If population declines are occurring in fragments, the possibility of connecting isolated patches to ensure metapopulation connectivity should be explored [Foster et al., 2016]. In light of recent genetic evidence that fragmented populations form a separate clade from continuous populations [Mekonnen et al., in prep.], as many remaining fragments as possible containing Bale monkeys should be protected. We recommend that Bale monkey habitat restoration programs should focus first on increasing fragment sizes, minimizing edge effects and incorporating matrix habitats into management plans [cf., Anderson et al., 2007] now that our study has demonstrated that Bale monkeys in fragments can and do exploit adjacent areas of matrix. In sum, the conservation actions we recommend would help to conserve the important remaining tropical montane forest habitats of southern Ethiopia and minimize the future extinction risk of isolated populations of Bale monkeys and other wildlife in the human dominated landscapes of the region.

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

<table>
<thead>
<tr>
<th>Characteristics of study sites and groups</th>
<th>Continuous A</th>
<th>Continuous B</th>
<th>Patchy fragment</th>
<th>Hilltop fragment</th>
<th>df, F, P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest/fragment size (ha)</td>
<td>14100</td>
<td>14100</td>
<td>162</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>Group size</td>
<td>65</td>
<td>38</td>
<td>28</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Mean elevation (m asl) (Range)</td>
<td>2758 (2617-2893)</td>
<td>2751 (2628-2842)</td>
<td>2650 (2544-2780)</td>
<td>2706 (2582-2790)</td>
<td></td>
</tr>
<tr>
<td>Distance to the nearest village (m)</td>
<td>6000</td>
<td>6000</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Habitat quality</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total species richness ≥ 2 m tall</td>
<td>23</td>
<td>19</td>
<td>35</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td>All plant species diversity index, Shannon-Weaver H'</td>
<td>0.78</td>
<td>0.68</td>
<td>2.17</td>
<td>3.13</td>
<td></td>
</tr>
<tr>
<td>All plant species evenness index, J</td>
<td>0.09</td>
<td>0.10</td>
<td>0.25</td>
<td>0.48</td>
<td></td>
</tr>
<tr>
<td>All plant species dominance index, D</td>
<td>0.72</td>
<td>0.76</td>
<td>0.21</td>
<td>0.08</td>
<td></td>
</tr>
<tr>
<td>Large tree species richness ≥ 10 cm DBH</td>
<td>9.00</td>
<td>7.00</td>
<td>14.00</td>
<td>12.00</td>
<td></td>
</tr>
<tr>
<td>Large tree species diversity index,</td>
<td>1.17</td>
<td>1.10</td>
<td>1.58</td>
<td>1.61</td>
<td></td>
</tr>
<tr>
<td>Shannon-Weaver H'</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large tree species evenness index, J</td>
<td>0.36</td>
<td>0.43</td>
<td>0.35</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>Large tree species dominance index, D</td>
<td>0.48</td>
<td>0.50</td>
<td>0.32</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>Bamboo stem density per ha</td>
<td>7720.00</td>
<td>4713.33</td>
<td>1332.74</td>
<td>37.22</td>
<td></td>
</tr>
<tr>
<td>Large tree stem density per ha</td>
<td>236.67</td>
<td>160.00</td>
<td>137.04</td>
<td>139.18</td>
<td></td>
</tr>
<tr>
<td>Shrub stem density per ha</td>
<td>93.33</td>
<td>36.67</td>
<td>878.49</td>
<td>1079.94</td>
<td></td>
</tr>
<tr>
<td>Small tree density per ha</td>
<td>340.00</td>
<td>140.00</td>
<td>831.36</td>
<td>529.91</td>
<td></td>
</tr>
</tbody>
</table>
Lianas density per ha | 693.33 | 266.67 | 208.55 | 368.54  
Forbs density per ha  | 26.67  | 93.33  | 0.00   | 157.22 
Total stem density per ha (N) | 9110.00 | 5410.00 | 3388.47 | 2312.00 

**Characteristics of home ranges** (large trees ≥10 cm DBH and bamboo, mean ± SE)

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of large trees measured (N)</td>
<td>142</td>
<td>96</td>
<td>185</td>
<td>167</td>
</tr>
<tr>
<td>DBH of large trees (cm)</td>
<td>33.20 ± 2.03</td>
<td>31.88 ± 2.40</td>
<td>23.68 ± 1.20</td>
<td>38.27 ± 1.06</td>
</tr>
<tr>
<td>Height of large trees (m)</td>
<td>18.49 ± 0.53</td>
<td>19.04 ± 0.63</td>
<td>11.11 ± 0.42</td>
<td>22.13 ± 0.94</td>
</tr>
<tr>
<td>Canopy size of large trees (m)</td>
<td>6.07 ± 0.32</td>
<td>7.10 ± 0.39</td>
<td>3.93 ± 0.12</td>
<td>4.78 ± 0.17</td>
</tr>
<tr>
<td>Basal area of large trees (cm²/ha)</td>
<td>2208.83 ± 392.38</td>
<td>2046.29 ± 424.08</td>
<td>480.91 ± 59.54</td>
<td>1079.52 ± 63.19</td>
</tr>
<tr>
<td>DBH of food trees (cm)</td>
<td>33.64 ± 2.12</td>
<td>34.90 ± 2.74</td>
<td>22.64 ± 1.16</td>
<td>41.37 ± 1.46</td>
</tr>
<tr>
<td>Height of food trees (m)</td>
<td>18.62 ± 0.59</td>
<td>19.41 ± 0.71</td>
<td>11.01 ± 0.45</td>
<td>15.72 ± 0.70</td>
</tr>
<tr>
<td>Canopy size of food trees (m)</td>
<td>6.12 ± 0.35</td>
<td>7.34 ± 0.46</td>
<td>3.88 ± 0.11</td>
<td>5.46 ± 0.22</td>
</tr>
<tr>
<td>Basal area of food trees (cm²/ha)</td>
<td>2213.29 ± 412.84</td>
<td>2370.68 ± 501.11</td>
<td>433.99 ± 60.22</td>
<td>1263.51 ± 91.57</td>
</tr>
<tr>
<td>DBH of bamboo stems (cm)</td>
<td>4.23 ± 0.04</td>
<td>4.05 ± 0.05</td>
<td>2.14 ± 0.04</td>
<td>-</td>
</tr>
<tr>
<td>Height of bamboo stems (m)</td>
<td>7.64 ± 0.08</td>
<td>6.78 ± 0.13</td>
<td>4.37 ± 0.08</td>
<td>-</td>
</tr>
</tbody>
</table>

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

(***

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

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Group</th>
<th>No of days</th>
<th>*No. GPS points</th>
<th>95% KDE*</th>
<th>100% MCP</th>
<th>95% MCP</th>
<th>90% MCP</th>
<th>50% KDE*</th>
<th>Group size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continuous forest</td>
<td>Continuous A</td>
<td>56</td>
<td>1488</td>
<td>26.1</td>
<td>37.6</td>
<td>26.9</td>
<td>22.6</td>
<td>5.9</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>Continuous B</td>
<td>57</td>
<td>1496</td>
<td>15.9</td>
<td>22.2</td>
<td>17.0</td>
<td>15.3</td>
<td>4.0</td>
<td>38</td>
</tr>
<tr>
<td>Fragment</td>
<td>Patchy fragment</td>
<td>61</td>
<td>2296</td>
<td>39.9</td>
<td>78.8</td>
<td>71.7</td>
<td>70.2</td>
<td>8.8</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Hilltop fragment</td>
<td>67</td>
<td>2241</td>
<td>15.8</td>
<td>18.7</td>
<td>15.0</td>
<td>13.4</td>
<td>5.2</td>
<td>23</td>
</tr>
</tbody>
</table>

*Results were similar when the analysis was done using only 1488 randomly selected GPS points for each group, with little variation within repeated randomly selected samples.
Table III. Mean movement rates (m/hr) of the four Bale monkey study groups.

<table>
<thead>
<tr>
<th>Forest</th>
<th>Group</th>
<th>No. of days</th>
<th>Mean No. GPS points per day</th>
<th>Movement rate (m/hr)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>Continuous</td>
<td>Continuous A</td>
<td>44</td>
<td>29.0</td>
<td>128.5</td>
</tr>
<tr>
<td></td>
<td>Continuous B</td>
<td>41</td>
<td>29.0</td>
<td>113.8</td>
</tr>
<tr>
<td>Fragment</td>
<td>Patchy fragment</td>
<td>58</td>
<td>38.4</td>
<td>102.7</td>
</tr>
<tr>
<td></td>
<td>Hilltop fragment</td>
<td>61</td>
<td>34.4</td>
<td>86.3</td>
</tr>
</tbody>
</table>
TABLE IV. Differences in the total area of available habitat types (ha) and their percentage representations, observed use (observed number of habitat records), expected use (expected number of habitat records) and selection ratio of each habitat calculated within the 95% KDE home ranges of each study group.

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

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

Fig. 2. The proportion of time members of the four Bale monkey study groups spent engaging in different activities (N=12 months, mean±SE; Continuous A 5442 scans on 52 days; Continuous B 5499 scans on 54 days; Patchy fragment 10254 scans on 61 days, and Hilltop fragment 7388 scans on 67 days).

Fig. 3. Annual home ranges (ha) and core areas (ha) of Bale monkey groups in continuous and fragmented forests: open line (95% MCP), orange (95 % KDE home range), light green (50% KDE core area), red crossbars (95% KDE overlap between Continuous A and Continuous B), and dark green (50% core area overlap between Continuous A and Continuous B).

Fig. 4. Map of available habitats in the home ranges of the Bale monkey study groups.
Fig. 1. Map of the study sites showing continuous and fragmented forests in southern Ethiopian Highlands.
Fig. 2. The proportion of time members of the four Bale monkey study groups spent engaging in different activities (N=12 months, mean±SE; Continuous A 5442 scans on 52 days; Continuous B 5499 scans on 54 days; Patchy fragment 10254 scans on 61 days, and Hilltop fragment 7388 scans on 67 days).
Fig. 3. Annual home ranges (ha) and core areas (ha) of Bale monkey groups in continuous and fragmented forests: open line (95% MCP), orange (95% KDE home range), light green (50% KDE core area), red crossbars (95% KDE overlap between Continuous A and Continuous B), and dark green (50% core area overlap between Continuous A and Continuous B).
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