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Diet, Activity Patterns, and Ranging Ecology of the Bale Monkey (*Chlorocebus djamdjamensis*) in Odobullu Forest, Ethiopia

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Abstract Bale monkeys (*Chlorocebus djamdjamensis*) are little-known primates endemic to the forests of the Bale Massif and Hagere Selam regions of Ethiopia. From August 2007 to May 2008, we conducted the first ever study of the species' behavior and ecology, focusing in particular on its diet, activity patterns, and ranging ecology in the Odobullu Forest. We studied 2 neighboring groups (group A: 55–60 members; group B: 46–50 members) and conducted behavioral scan samples on the first 2–5 individuals sighted at 15-min intervals. Feeding accounted for 65.7% of the activity budget, followed by moving (14.4%), resting (10.7%), social (7.1%), and other behaviors (2.4%). Overall diet during the study was dominated by young leaves (80.2%), though subjects also ate fruits (9.6%), flowers (3.1%), animal prey (2.3%), shoots (1.5%), stems (1.4%), mature leaves (1.1%), and roots (0.9%). Bale monkeys consumed only 11 plant species; of these, the top 5 species accounted for 94.3% of their diet. The top food item, bamboo (*Arundinaria alpina*), was responsible for a remarkable 76.7% of their diet, with most (95.2%) of the bamboo consumption consisting of young leaves. Mean daily path length for the study

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groups was 928 m and mean (100% minimum convex polygon) home range size was 15.2 ha. Though we are cautious in drawing conclusions from only 2 groups, the larger group traveled further per day and occupied a larger home range, patterns suggesting scramble competition may be occurring in Bale monkey groups at Odobullu. The dietary specialization of Bale monkeys on bamboo makes them unique among *Chlorocebus* spp. and suggests an intriguing ecological convergence with the golden monkeys (*Cercopithecus mitis kandti*) of Uganda and bamboo lemurs (*Hapalemur* spp.) of Madagascar. Their narrow ecological niche, limited geographic distribution, and bamboo harvesting by local people for commercial purposes place Bale monkeys at risk of extinction. To ensure the long-term survival of Bale monkeys, appropriate management action should be taken to conserve the species and the bamboo forests upon which it depends.

Keywords activity budget · bamboo · feeding ecology · home range · quantitative natural history · scramble competition

Introduction

An understanding of the basic quantitative natural history of primate species is vital to their conservation (Caro 1998, 2007; Fashing 2007b). For instance, data on feeding ecology provide not only information on the individual food species necessary to a primate's survival but also insight into its level of dietary specialization (Caro 1998). The more specialized a primate's diet, the greater is its risk of extinction (Harcourt *et al*. 2002). Further, data on activity patterns can help guide monitoring strategies for threatened and elusive primates (Caro 1998). Once the periods during which a primate is most active have been identified, researchers can focus their censusing efforts on the species during these times (Struhsaker 1981). Lastly, data on primate ranging behavior are also critical to conservation planning. In particular, home range size and shape can contribute to decisions relating to reserve design, while degree of territoriality influences the extent to which multiple groups can be distributed within a given patch of habitat (Caro 1998).

Despite the importance of quantitative natural history data to conserving primates, there are many primate species whose basic behavior and ecology today remain completely unknown. Bale monkeys (*Chlorocebus djamdjamensis*), enigmatic primates endemic to Ethiopia and currently restricted only to the forests of the Bale Massif and Hagere Selam regions, are one such species. First described by Neumann in 1902, the species was named after the Djam-Djam Mountains, a region *ca*. 30 km west of Harenna Forest and east of Lake Abaya (Carpaneto and Gippoliti 1990). Today, Groves (2005) classifies Bale monkeys as 1 of 6 species of *Chlorocebus*, a genus commonly known as the vervets or green monkeys.

Most members of *Chlorocebus* are generalists inhabiting a variety of savannah/woodland habitat types and feeding on a wide array of food sources (Enstam and Isbell 2007). They are opportunistic omnivores with gum, flowers, fruits, leaves, seeds, and insects, all making substantial contributions to their diets (Enstam and Isbell 2007). Most *Chlorocebus* are active monkeys and have rather small home ranges that they defend against other groups to varying degrees (Chapman and Chapman 1984; Cheney 1981; Harrison 1983b; Kavanagh 1981).

Preliminary surveys that we conducted recently across the Bale Massif raised the possibility that Bale monkeys may not fit the ecological generalist category to which other *Chlorocebus* spp. belong. Mostly notably, we found that Bale monkeys appear to occur exclusively in bamboo forests (Mekonnen *et al.* in press). The goals of the present study were thus to investigate the natural history of Bale monkeys to 1) identify behavioral or ecological adaptations to life in bamboo forests; 2) evaluate the extent to which they differ from other more generalized *Chlorocebus* and forest guenons (*Cercopithecus* spp.) in terms of their diet, activity patterns, and ranging ecology; and 3) explore their ecological convergence with other bamboo forest-dwelling primates including bamboo lemurs (*Hapalemur* spp.) and golden monkeys (*Cercopithecus mitis kandti*). In addition to permitting ecological comparisons to other *Chlorocebus*, guenons, and bamboo forest-living primates, these data will also help inform conservation strategies for one of the world's least known primates.

Methods

Study Site

The Bale Mountains region is part of the eastern Afromontane global biodiversity hotspot which harbors a diverse range of endemic fauna and flora (Myers *et al.* 2000). We conducted the study from August 2007 to May 2008 in the Odobullu Forest, southeastern Ethiopia, a 71-km^2 montane rain forest located 460 km southeast of Addis Ababa (06°50′–6°56′N and 40°07′–40°12′E). Odobullu Forest lies to the east of Bale Mountains National Park (BMNP) and is owned and managed by a private organization, Rift Valley Hunting Safaris, which provides partial protection to the area and does not permit hunting of Bale monkeys. The study area is mountainous and consists of forested cliffs and valleys bisected by streams. The altitude ranges from 2250 m to 3022 m asl.

The Bale Mountains region experiences a long wet season from March to October and a relatively short dry season from November to February. During much of the wet season, the area is blanketed by thick white fog and clouds. We obtained average monthly rainfall and temperature for the area over 6 yr from the Ethiopian Meteorology Agency's Robe Field Station, *ca.* 30 km northwest of Odobullu Forest (Fig. 1). The average annual rainfall at Robe for the period from 1999 to 2004 was 796 mm. Rainfall at Robe is probably a considerable underestimate for Odobullu, however, because forested areas such as Odobullu typically receive much more rain than nonforested areas such as Robe. Rainfall at Robe varied between a mean monthly minimum of 10 mm in February to a mean monthly maximum of 143 mm in August. The temperature ranged from a lowest mean monthly minimum of 6.4°C in January to a highest mean monthly maximum of 24.0°C in February.

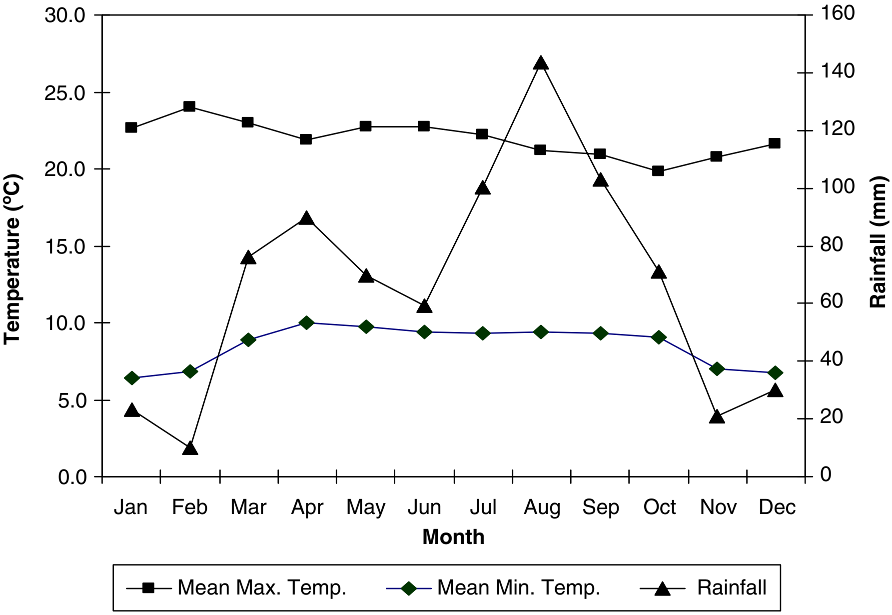

Fig. 1 Monthly changes in mean minimum and maximum temperatures, and rainfall at Robe Field Station, *ca*. 30 km northwest of the study area at Odobullu.

Study Species and Groups

We conducted behavioral research on 2 groups habituated to 7–30 m of observers. We undertook group counts opportunistically when the monkeys crossed a narrow forest gap or existing animal tracks in the bamboo forest. Based on repeated counts, the total size of group A was 55–60 individuals and group B was 46–50 individuals. We identified the focal groups by the natural markings, sizes, coat color, and facial features of distinctive members of each group. The focal groups occupied mountainous terrain that varied from 2695 to 2900 m asl.

Data Collection and Analysis

Vegetation To describe the vegetation in our study area, we established 2 50 × 10 m quadrats in the home ranges of each of the 2 focal groups. We counted all individual plants including lianas >2 m tall within the plots and identified them to species. We used these quadrats to quantify the overall vegetation composition of the study area as well as to identify differences in forest composition between the home ranges of the study groups. We calculated the density of each plant species as the total number of individuals of a species divided by the total number of all plant species sampled per hectare in the home range. In addition, we calculated plant species diversity via the Shannon-Wiener index, H', and plant species evenness using the evenness index, J (Krebs 1989). After examining these vegetation variables for each group separately, we found no substantial differences in the vegetation between the ranges of our 2 focal groups, i.e., species composition and relative abundance were similar, and have therefore presented the combined data from the 2 groups' ranges in our results.

Activity Budget

A. Mekonnen and a field assistant collected data on the activity patterns of the members of the 2 neighboring focal groups on an average of 5–6 d/mo from September 2007 to May 2008 (with the exception of March 2008, when no data were collected), covering both the wet and dry seasons. In particular, we used scan sampling (Altmann 1974) at 15-min intervals from 0700 h to 1730 h to determine the activities of the first two to five adults, subadults, or juveniles sighted during scans of ≤5 min duration. During each sample, we scanned the group from left to right to avoid possible bias toward eye-catching activities such as grooming, fighting, and mating (Fashing 2001a). The activity recorded for each individual was the first activity that lasted 5 s.

We recorded individuals as performing one of the following behaviors: feeding, moving, resting, playing, aggression, grooming, sexual activity, or other. We recorded feeding when monkeys manipulated, masticated, or ingested a particular food item. We recorded moving when monkeys changed spatial position, including walking, jumping, or running. We recorded resting when monkeys were inactive, either sitting or lying down. Playing included chasing, hitting, and other vigorous activities involving exaggerated movements and gestures by a monkey interacting with others in a nonaggressive manner. We recorded aggression when a monkey chased, bit, grabbed, displaced, threatened another monkey, or vocalized in an aggressive context. We recorded grooming when a monkey used its hands to explore or to clean its body or the body of another monkey. We recorded sexual activity when an individual engaged in copulatory behaviors. We recorded other when a monkey performed activities such as vocalizating, defecating, or drinking that did not fit into the main categories.

We initially calculated the activity budgets of the 2 neighboring study groups, A and B, individually. Because the results for each group showed the same general pattern; i.e. proportion of time spent engaging in different behaviors was similar, however, we then calculated the activity budget for the combined focal groups. To calculate the proportion of time engaged in each activity, we divided the number of behavioral records for each activity category by the total number of activity records. We then used the behavioral records of the combined groups to calculate the activity budgets for each day and averaged within each month to construct monthly activity budgets. The grand mean proportions of the monthly budgets provided activity budgets for the wet and dry seasons, and also the overall activity budgets for the entire study period. We merged social activities such as playing, aggression, grooming, and sexual activities for analyses. We compared the percentage of time the combined focal groups engaged in major activities between seasons using Mann-Whitney *U* tests and across months using Kruskal-Wallis *H* tests.

Feeding Ecology

At the time of each activity scan sample, we collected dietary data on individuals scored as feeding. In particular, we recorded the type of food item (young leaves, mature leaves, roots, stems, flowers, fruits, shoots, or animal prey) and the species. We collected unidentified species for later taxonomic identification at the National Herbarium, Addis Ababa University, Ethiopia. We recorded animal prey as the food item when we observed a monkey scratching tree bark, exposing curled leaves, or masticating and ingesting invertebrates. Our direct observations revealed that whenever it was possible to determine what the monkeys were foraging for when scratching tree bark and exposing curled leaves, the food item proved to be invertebrates.

We determined dietary composition by calculating the proportion of different food items and species consumed by the monkeys. The dietary composition of groups A and B were initially calculated individually. After the results showed the same general pattern, i.e., proportion of time spent feeding on different food items/species was similar between groups, however, we calculated the dietary composition for the combined focal groups. We summed the daily food items consumed by the combined focal groups within each month to determine the monthly proportion of the diet devoted to each food item. We calculated the monthly proportion of each food item in the diet as the total number of monthly individual scans for each food item divided by the total number of monthly scan records for all food items. We used the grand means of the monthly proportion of food items and food species consumed to calculate the overall wet and dry season diets as well as the overall diet for the entire study period.

To assess dietary diversity over the study period, we calculated the Shannon-Wiener index of diversity, H', for each month of the study (Krebs 1989). High values of H' (in biological communities, H' seems to peak around 5.0) indicate greater levels of diversity (Krebs 1989). We calculated dietary evenness on a monthly basis as well using the evenness index, J (Krebs 1989). Values for J can range from 0.0 to 1.0, with 1.0 indicating that an equal number of feeding records exist for each species in the diet (Krebs 1989). We measured relative dietary preferences for different food species in the study groups' diet, i.e., food selection ratio, by dividing the annual percentage of time spent feeding on species i by the percentage of the stem density that species i contributes to the total stem density in the study groups' home ranges (Fashing 2001b).

Ranging Patterns

At the time of each activity scan sample, we also recorded the location of the geographic center of the group via a handheld Garmin GPS 12 unit. We recorded these data even if activity data were not obtainable owing to poor visibility as long as the group's location could be confirmed via cues such as distinctive tree movements or vocalizations. We determined day range length for each group based on the shortest point-to-point movements of the group between consecutive GPS locations during full-day follows from 0700 h to 1730 h (group A: 25 d, mean = 28.3 points/d, range = 23–37 points; group B: 23 d, mean = 27.6 points/d, range 24–35 points).

We plotted each day range on a GIS-system generated map (ArcMap version 9.1) by connecting the consecutive GPS location records and the total distances traveled per day. We calculated these values from the map by using measuring tools in the GIS software ArcGIS 9.1. Because sample sizes of all-day follows were small for some months, we calculated seasonal rather than monthly mean day range lengths. We then compared the wet and dry season day range lengths via Mann-Whitney *U* tests.

We used the minimum convex polygon method (MCP) in ArcMap version 9.1 to determine the home range sizes (100% MCPs) of our focal groups for each season and for the entire study period (Fashing *et al*. 2007b; Wong and Sicotte 2007). We used data from both full- and partial-day follows (group A: 42 d, 1175 points; group B: 44 d, 1114 points) in these home range estimations. We calculated the home ranges for both focal groups by constructing a polygon around the outermost GPS locations used by each group. The use of the MCP technique has the disadvantage of overestimating home range size by including areas contained within the polygon not actually entered by the individuals being studied (Fashing *et al*. 2007b; Worton 1987). Conversely, in mountainous environments like Odobullu, home range calculations in 2 dimensions tend to underestimate actual range size given their failure to account for the undulating topography of the range (Sprague 2000). We anticipate that these 2 types of error canceled each other out, leaving us with relatively accurate home range estimates for our focal groups. We then compared wet and dry season home range areas via Mann-Whitney *U* tests.

Results

Vegetation

The vegetation in the home ranges of our Bale monkey focal groups was species poor and dominated by bamboo (*Arundinaria alpina*). We found a total of only 13 tree species, 1 shrub, 5 lianas, 1 epiphyte, and 2 herbs within the vegetation quadrats in the combined home ranges of the focal groups (Table I).

The vegetation quadrats contained 15,645 stems/ha, with bamboo (*Arundinaria alpina*) accounting for 91% of the total stem density. The plant species diversity and evenness in the combined home ranges of the focal groups were 0.54 and 0.19, respectively. Thus, plant species that occurred in the home ranges of the Bale monkeys were neither very diverse nor evenly distributed.

Activity Budget

We recorded a total of 11,393 individual scan records during 2830 group scans on 86 days (group A: 42 d; group B: 44 d). Bale monkeys spent 65.7% (monthly mean range 58.9–72.0%, SD ± 4.1%, $n=8$ mo) of their time feeding, 14.1% (monthly mean range 10.9–16.3%, SD ± 1.8%) moving, 10.7% (monthly mean range 7.9–13.9%, SD ± 1.8%) resting, 7.1% (monthly mean range 5.2–9.1%; SD ± 1.1%) engaging in social activities (2.7% grooming, 1.8% playing, 1.7% aggression, 0.9% sexual activity), and 2.4% (monthly mean range 1.2–4.0%, SD ± 1.0%) engaging in other activities. Further, they spent significantly more time feeding and significantly

Table I Stem density of all plant species (including lianas) >2 m tall within the home ranges of the 2 Bale monkey focal groups at Odobullu

Local name	Species name	Family	Type	No. of stems/ha	% of stem density
Leemman	*Arundinaria alpine*	Poaceae	Tree (S)	14,165	90.5
Haliilaa	*Urera hypselodenron*	Urticaceae	Shrub (M)	220	1.4
Tullaa	*Manilkara butugi*	Sapotaceae	Tree (S, M)	220	1.4
Korraallaa	*Psychotria orohila*	Rubiaceae	Tree (M)	190	1.2
Lallacaa	*Cypostemma adenocaule*	Vitaceae	Liana	150	1.0
Allaafitree	*Thlophora lugardae*	Asclepiadaceae	Liana	150	1.0
Ciroontaa	*Brucea antidysenterica*	Simarubaceae	Tree (S)	130	0.8
Goraa	*Rubus apetalus*	Rosaceae	Liana	100	0.6
Qrqooraa	*Mikaniopsis clematoides*	Asteraceae	Liana	70	0.4
Anshaa	*Schifflera volcensii*	Araliaceae	Tree (M)	65	0.4
Daannisa	*Dombeya torrida*	Sterculiaceae	Tree (L)	50	0.3
Kombolcha	*Maytenus obscura*	Celastraceae	Tree (S, M)	40	0.3
Horoqa	*Bersama abyssinica*	Melianthaceae	Tree (S)	30	0.2
Heexoo	*Hagenia abyssinica*	Rosaceae	Tree (L)	20	0.1
Garambaa	*Hypericum revoltum*	Hypericeae	Tree (S, M)	20	0.1
Xorsoo	*Jasminum abyssinicum*	Oleaceae	Liana	10	0.1
Taruuraa	*Leggera sp.*	Asteraceae	Tree (M)	5	0.0
Abaaraa	*Allophylus macrobothys*	Sapindaceae	Tree (M)	5	0.0
Maraaroo	*Datura strrammonium*	Solanaceae	Tree (M)	5	0.0
Herayyee	*Acanthopale pubescens*	Acanthaceae	Herb	0	0.0
Garaabaa	*Bothrichloa radicans*	Poaceae	Herb	0	0.0
Aanquu	*Embelia schimperi*	Embenaceae	Epiphyte	0	0.0

Trees are classified based on their size as small (S), medium (M), and large (L)

less time moving, resting, and socializing in the wet season than during the dry season (Mann-Whitney *U* tests: $p<0.05$; Fig. 2).

Feeding Ecology

Dietary Composition Young leaves accounted for 80.2% (SD ± 4.1%) of the overall diet ($n=7223$ feeding records) of Bale monkeys at Odobullu. Fruits and flowers made the second and third largest contributions to the diet at 9.6% (SD ± 6.9%) and 3.1% (SD ± 4.8%), respectively. Animal foods, primarily insects, accounted for 2.3% (SD ± 1.0%) of the diet. The Bale monkeys consumed other items only rarely: shoots, 1.5% (SD ± 2.9%); stems, 1.4% (SD ± 1.8%); mature leaves, 1.1% (SD ± 0.9%); and roots, 0.9% (SD ± 2.1%).

Monthly feeding time devoted to different food items is shown in Table II. Young leaves dominated the diet during all months (72.9–86.7%), while fruit (0.0–20.0%) and flower (0.0–13.1%) consumption varied widely across months. Kruskal-Wallis *H* tests revealed no significant differences in time spent feeding on different food

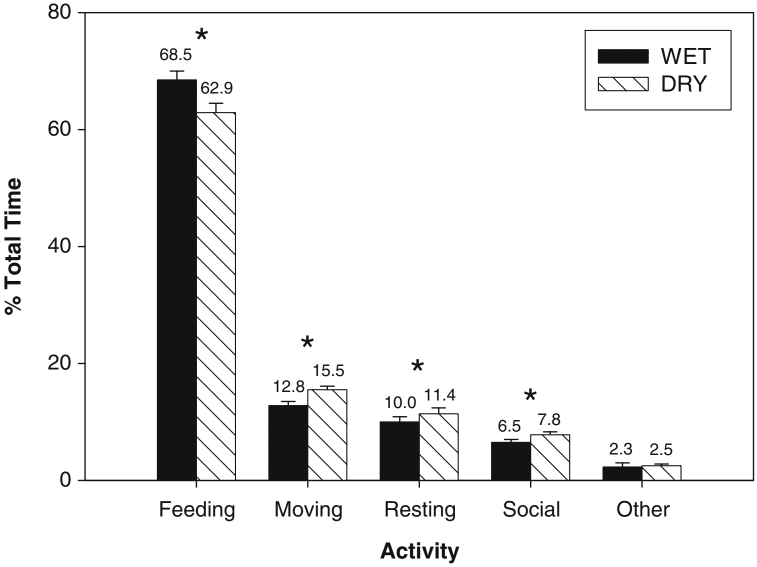

Fig. 2 Wet and dry season activity budgets of Bale monkeys in the Odobullu Forest. An *asterisk* (*) above an activity denotes that there were significant seasonal differences in time spent engaged in the activity (Mann-Whitney *U*-test; $p<0.05$).

items across months ($p>0.05$). Across seasons, however, 2 food items, fruits and shoots, exhibited significant differences, with more fruit consumption in the dry season and more shoot consumption in the wet season (Fig. 3).

During the study period, 11 plant species combined to account for 97.7% of the Bale monkeys' diet. The percentage contribution, type of plant species, and food items consumed from each plant species are presented in Table III. The most consumed plant species was bamboo (*Arundinaria alpina*) which accounted for 76.7% (monthly range 68.1–84.2%, SD ± 5.8%) of the diet. *Psychotria orohila*

Table II Monthly variation in percentage contribution of food items to the diet of Bale monkeys at Odobullu

Month	Percentage of diet							
	Young leaves	Mature leaves	Root	Stem	Flower	Fruit	Shoot	Animal prey
September	82.1	2.6	1.2	5.4	2.5	–	2.6	3.8
October	80.6	0.7	–	0.7	13.1	2.3	0.8	1.8
November	80.0	–	–	–	7.7	10.5	–	1.8
December	83.2	–	–	1.2	1.4	12.8	–	1.5
January	78.9	1.4	–	2.2	–	16.3	–	1.2
February	72.9	1.9	–	1.4	–	20.0	–	3.7
April	86.7	0.7	–	0.4	–	10.1	–	2.1
May	77.5	1.3	6.0	–	–	4.8	8.3	2.1
Mean	80.2	1.1	0.9	1.4	3.1	9.6	1.5	2.3

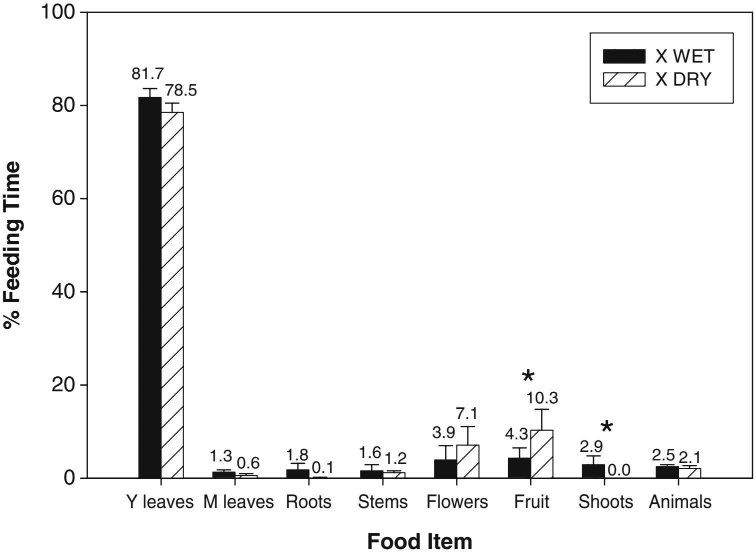

Fig. 3 Seasonal variability in food item consumption by Bale monkeys in Odobullu Forest. An *asterisk* (*) above a food item denotes that there were significant seasonal differences in time spent consuming the item (Mann-Whitney *U*-test; $p<0.05$).

ranked second and *Dombeya torrida* ranked third, accounting for 10.6% (monthly range 2.8–20.7%; SD ± 6.6%) and 3.1% (monthly range 0–13.1%; SD ± 4.8%) of the diet, respectively.

The main food item consumed during the study period was the young leaves of *Arundinaria alpina*, which comprised 73.0% (SD ± 4.9%) of the diet, while mature leaves, roots, stems, and shoots of this species together accounted for an additional 3.7% (SD ± 5.5%) of the overall diet. *Psychotria orohila* contributed fruits (8.9%) and young leaves (2.0%), and *Dombeya torrida* contributed flowers (3.0%) to the diet (Table III).

Bale monkeys did not exhibit significant seasonal differences in consumption of most food species including their primary food species, *Arundinaria alpina* (Table IV). However, consumption of *Psychotria orohila* provided a notable exception to this pattern among the major food items in that it was consumed significantly more often during the dry season. In addition, though never consumed regularly at any time of year, *Bothrichloa radicans* was the only species that Bale monkeys consumed significantly more often during the wet season.

Arundinaria alpina was the primary component of the Bale monkey diet in all months, ranging from a low of 68.1% in February to a high of 84.2% in May (Table V). In most months, young leaves accounted for nearly all of the feeding records on *Arundinaria alpina*. During the early wet season (particularly in May), however, *Arundinaria alpina* shoots became available (Mekonnen, *pers. obs.*) and Bale monkeys began to complement *A. alpina* young leaf consumption with newly emerging *A. alpina* shoot and root consumption. *Psychotria orohila*, the next largest contributor to the overall diet, was also consumed in all months ranging from a minimum of 2.8% in September to a maximum of 20.7% in February.

Table III Overall percentage of time spent feeding on specific food items in each plant species during the study period

Local name	Species	Family	Type	Percentage of diet								
				Young leaves	Mature leaves	Root	Stem	Flower	Fruit	Shoot	Animal prey	Total
Leemman	*Arundinaria alpina*	Poaceae	Tree	73.0	1.1	0.9	0.2	–	–	1.5	–	76.7
Korraallaa	*Psychotria orohila*	Rubiaceae	Tree	2.0	–	–	–	–	8.6	–	–	10.6
Daannisa	*Dombeya torrida*	Sterculiaceae	Tree	–	–	–	–	3.1	–	–	–	3.1
Qrqooraa	*Mikaniopsis clematoides*	Asteraceae	Liana	2.6	–	–	–	–	–	–	–	2.6
Haliilaa	*Urera hypselodenron*	Urticaceae	Shrub	1.3	–	–	0.1	–	–	–	–	1.4
Herayyee	*Acanthopale pubescens*	Acanthaceae	Herb		–	–	1.2	–	–	–	–	1.2
Garaabaa	*Bothrichloa radicans*	Poaceae	Herb	0.9	–	–	–	–	–	–	–	0.9
Aanquu	*Embelia schimperi*	Embenaceae	Epiphyte	–	–	–	–	–	0.6	–	–	0.6
Lallacaa	*Cypostemma adenocaule*	Vitaceae	Liana	–	–	–	–	–	0.3	–	–	0.3
Alafitre	*Thlophora lugardae*	Asclepiadaceae	Liana	0.3	–	–	–	–	–	–	–	0.3
Goraa	*Rubus apetalus*	Rosaceae	Liana	–	–	–	–	–	0.1	–	–	0.1
	Animal prey			–	–	–	–	–	–	–	2.3	2.3
Total				80.2	1.1	0.9	1.4	3.1	9.6	1.5	2.3	100.0

Table IV Seasonal percentage contribution of plant species to the diet of Bale monkeys

Species consumed	Wet season (%) Mean ± SE	Dry season (%) Mean ± SE
Arundinaria alpina	80.3±2.7	73.2±2.0
Psychotria orohila	4.9±1.0[a]	16.3±1.5[a]
Dombeya torrida	3.9±3.1	2.3±1.8
Mikaniopsis clematoides	2.1±0.3	3.0±0.5
Urera hypselodenron	1.7±0.3	1.0±0.2
Acanthopale pubescens	1.2±0.5	1.2±0.5
Bothrichloa radicans	1.7±0.1[a]	0.1±0.1[a]
Embelia schimperi	0.6±0.6	0.6±0.5
Cypostemma adenocaule	0.7±0.7	0.0±0.0
Thlophora lugardae	0.4±0.4	0.1±0.1
Rubus apetalus	0.1±0.2	0.0±0.0
	97.5	97.9

[a] Denotes that a Mann-Whitney *U*-test revealed significant differences ($p<0.05$) between the seasons in the consumption of an item

Dietary Diversity The mean monthly Shannon-Wiener index (*H*′) for food species diversity was 0.74 (range 0.58–0.94; SD ± 0.14; Table VI). Dietary diversity was highest in October and lowest in September. In general, the diet of Bale monkeys was not very diverse and showed little variation over the study period. The mean monthly dietary evenness index, *J*, was also relatively low at 0.40 (SD ± 0.07), ranging from 0.31 in September to 0.52 in November (Table VI).

Food Choice *Dombeya torrida* had the highest selection ratio (9.7) of any plant species in the diet of Bale monkeys at Odobullu (Table VII). *Psychotria orohila* (8.7) and *Mikaniopsis clematoides* (5.8) had the second and third highest selection ratios,

Table V Monthly percentage contribution of plant species to the diet of Bale monkeys ($n=7223$ feeding records)

Species consumed	September	October	November	December	January	February	April	May	Mean
Arundinaria alpina	84.1	72.7	73.0	77.9	73.9	68.1	80.0	84.2	76.7
Psychotria orohila	2.8	4.5	13.9	15.5	15.4	20.7	7.5	4.7	10.6
Dombeya torrida	2.5	13.1	7.7	1.4	–	–	–	–	3.1
Mikaniopsis clematoides	1.8	3.0	2.3	2.1	3.7	4.1	2.0	1.6	2.6
Urera hypselodenron	1.2	2.4	1.3	0.5	0.9	1.1	1.8	1.6	1.4
Acanthopale pubescens	2.5	0.7	–	1.2	2.2	1.4	0.4	1.5	1.2
Bothrichloa radicans	1.5	1.8	–	–	0.3	0.2	1.5	1.7	0.9
Embelia schimperi	–	–	–	–	2.2	0.4	2.5	–	0.6
Cypostemma adenocaule	–	–	–	–	–	–	–	2.7	0.3
Thlophora lugardae	–	–	–	–	0.3	0.3	1.5	–	0.3
Rubus apetalus	–	–	–	–	–	–	0.6	–	0.1

Table VI Food species diversity and evenness indices for each month during the study period

Month	Shannon-Wiener diversity index, H'	Evenness index, J
September	0.60	0.31
October	0.94	0.48
November	0.58	0.52
December	0.65	0.39
January	0.87	0.42
February	0.88	0.42
April	0.79	0.36
May	0.64	0.33
Mean	0.74	0.40

respectively. Even though it was by far the top species in percentage contribution to the diet, *Arundinaria alpina* had a relatively low selection ratio of 0.9. The low selection ratio for *Arundinaria alpina* resulted from the species' extremely high density in the study area. We found several plant species, including *Manilkara butugi*, *Schifflera volcansii*, *Maytenus obscura*, and *Hagenia abyssinica*, in the vegetation plots in the focal groups' home ranges but the monkeys did not consume them (Tables I and VII).

Ranging Patterns

The 100% minimum convex polygon home range areas of groups A and B over the study period were 18.1 and 12.3 ha, respectively (Fig. 4). The home range areas of the study groups were significantly larger during the dry season than during the wet season (Table VIII; Mann-Whitney *U* test, $p<0.05$). Though their ranges were

Table VII Food selection ratios of Bale monkeys based on stem densities for plant species consumed

Rank	Species name	Family	Habit	Stem density (%)	% of diet	Selection ratio
1	*Arundinaria alpina*	Poaceae	Tree	90.5	76.7	0.9
2	*Psychotria orohila*	Rubiaceae	Tree	1.2	10.6	8.7
3	*Dombeya torrida*	Sterculiaceae	Tree	0.3	3.1	9.7
4	*Mikaniopsis clematoides*	Asteraceae	Liana	0.4	2.6	5.8
5	*Urera hypselodenron*	Urticaceae	Shrub	1.4	1.4	1.0
6	*Acanthopale pubescens*	Acanthaceae	Herb	–	1.2	–
7	*Bothrichloa radicans*	Poaceae	Herb	–	0.9	–
8	*Embelia schimperi*	Embenaceae	Epiphyte	–	0.6	–
9	*Cypostemma adenocaule*	Vitaceae	Liana	1.0	0.3	0.3
10	*Thlophora lugardae*	Asclepiadaceae	Liana	1.0	0.3	0.3
11	*Rubus apetalus*	Rosaceae	Liana	0.6	0.1	0.2

Rank is presented in the order of percentage contribution to the overall diet. We did not calculate dietary preference for herbs and epiphytes

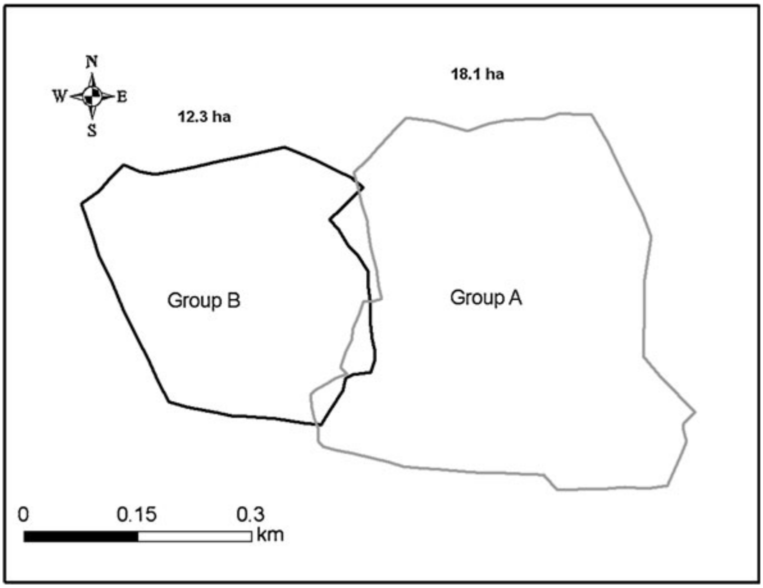

Fig. 4 Depiction of the 100% minimum convex polygon (MCP) home ranges of the 2 study groups of Bale monkeys at Odobullu.

adjacent to one another, there was only slight home range overlap between the 2 groups. Specifically, only 2.8% of group A's range was ever entered by group B and only 4.1% of group B's range was ever entered by group A.

The mean daily path lengths for groups A and B during the 8-month study period were 956 m (range 759–1288 m, SE ± 29.9) and 898 m (range 724–1207 m, SE ± 22.7), respectively (Table VIII). Both groups traveled significantly further per day during the dry season than during the wet season (Mann-Whitney *U* test, $p<0.05$).

Discussion

We report the first published information on the diet, activity patterns, and ranging ecology of Bale monkeys (*Chlorocebus djamdjamensis*). We found that Bale

Table VIII Mean daily travel distance and home range size of groups A and B during the wet and dry seasons

Season	Group	Mean daily travel distance (m)		Home range area (ha)
		Mean (*n*)	SE	
Wet	A	897 (13)	35.8	8.8
	B	853 (11)	23.6	7.3
Dry	A	1021 (12)	42.6	17.3
	B	939 (12)	34.6	11.3

monkeys are highly specialized primates, relying entirely on bamboo forest to meet their needs. They are also active monkeys that spend most of their time feeding on bamboo parts, especially the young leaves. Further, they travel relatively short distances per day and occupy rather small home ranges (Table IX). Their limited geographic distribution and degree of habitat specialization appear to put the species at considerable risk of extinction (Mekonnen *et al.* in press; this study).

Feeding Ecology

Bale monkeys at Odobullu exhibited an extreme degree of folivory more typical of many colobines, howlers, or lemurs (Di Fiore and Campbell 2007; Fashing 2007a; Gould and Sauther 2007) than of their close relatives in *Chlorocebus* and *Cercopithecus* (Table X). For example, *Chlorocebus* spp. have traditionally been known as generalists consuming mostly fruit, gum, and invertebrates, and only occasionally resorting to leaves (Harrison 1983a; Isbell *et al.* 1998; Lee and Hauser 1998; Whitten 1983). Further, *Cercopithecus* spp. typically consume mostly a combination of fruit and invertebrates (Brugiere *et al.* 2002; Cords 1986; Struhsaker 1978), eating diets rich in leaves at only a few locations (Plumptre 2006; Twinomugisha *et al.* 2006). Thus, our finding that Bale monkeys appear to be specialist folivores is both striking and surprising.

Further evidence of the Bale monkey's unusual degree of dietary specialization comes from the remarkably species-poor nature of its diet which consisted of only 11 plant species during the study period. Indeed, the top 5 plant species alone accounted for 94.3% of the overall diet. Of these, a single species, bamboo (*Arundinaria alpina*), stood out as by far the most important, contributing 76.7% of the overall diet, the vast majority of it in the form of young leaves. Intriguingly, there appears to be at least 1 additional guenon, the golden monkey (*Cercopithecus mitis kandti*), that shares Bale monkeys' specialization on bamboo as a food source though to a somewhat lesser degree. In particular, bamboo (*Arundinaria alpina*), primarily young leaves, accounted for 52.4–59.9% of the overall diet of golden monkeys at Mgahinga, Uganda (Twinomugisha *et al.* 2006; Twinomugisha and Chapman 2008). Like Bale monkeys at Odobullu, golden monkeys at Mgahinga also consumed an unusually species-poor diet (16 species) (Twinomugisha *et al.* 2006). Aside from the golden monkey and possibly the heretofore unstudied owl-faced guenon (*Cercopithecus hamlyni*; Plumptre *et al.* 2002), however, Bale monkeys remain unique among the guenons and their allies in their dietary specialization on bamboo.

Indeed, the only primates known to rely more heavily on bamboo than Bale monkeys are the bamboo lemurs endemic to the rain forests of Madagascar (Table X; Grassi 2006; Mutschler *et al.* 1998; Overdorff *et al.* 1997; Tan 1999). The 3 species of bamboo lemurs, *Hapalemur aureus*, *H. griseus*, and *H. simus*, are considered obligate bamboo eaters, obtaining nearly 90% or more of their diets from bamboo, especially the giant bamboo, *Cathariostachys madagascariensis* (Tan 1999). One problem raised for Malagasy bamboo lemurs that almost certainly applies to Bale monkeys and golden monkeys as well is the cyanide contained within bamboo (Tan 1999). Lacking the specialized stomachs of the colobines (Chivers 1994), these taxa probably require behavioral strategies to avoid consuming overly toxic food sources. Tan (1999: 560) found preliminary evidence that *Hapalemur griseus* select the

Table IX Activity budgets and ranging patterns of *Chlorocebus* spp. and *Cercopithecus* spp. in Africa and *Hapalemur* spp. bamboo specialists in Madagascar

Species	% of time contribution					Mean day range length (m)	Total home range (ha)	Site, country	Reference
	F	M	R	S	O				
Chlorocebus aethiops (vervet)	39	15	17	26	3	865	77	Blydeberg Conservancy, South Africa	Barrett (2005)
C. aethiops (vervet)	–	–	–	–	–	1188	42	Amboseli, Kenya	Struhsaker (1967)
C. aethiops (vervet)	–	–	–	–	–	1329	25	Segera Ranch, Kenya	Enstam and Isbell (2007)
C. aethiops (vervet)	–	–	–	–	–	–	14	Bakossi, Cameroon	Kavanagh (1981)
C. aethiops (vervet)	–	–	–	–	–	–	56	Kalamaloue, Cameroon	Kavanagh (1981)
C. aethiops (vervet)	–	–	–	–	–	–	103	Bufflenoir, Cameroon	Kavanagh (1981)
Chlorocebus djamdjamensis (Bale)	65.7	14.1	10.7	7.1	2.4	928	15	Odobullu Forest, Ethiopia	This study
Chlorocebus sabaeus (green)	–	–	–	–	–	–	178	Mt. Assirik, Senegal	Harrison (1983a)
Cercopithecus ascanius	38.2	38.7	20.8	1.0	1.3	1543	60	Kakamega Forest, Kenya	Cords (1987)
C. campbelli	48.5	28.0	18.0	5.2	0.3	1155	60	Taï, Ivony Coast	Buzzard (2004), (2006b)
C. diana	40.6	27.7	24.4	7.3	0.0	1152	59	Taï, Ivony Coast	Buzzard (2004), (2006b)
C. lhoesti	47.6	22.7	13.6	10.4	5.8	2092	117	Nyungwe Forest Reserve, Rwanda	Kaplin and Moermond (2000); Kaplin (2001)

Cercopithecus mitis doggetti	49.2	20.4	15.5	11.4	3.5	1307	88	Nyungwe Forest Reserve, Rwanda	Kaplin and Moermond (2000); Kaplin (2001)
C. m. kandti	–	–	–	–	–	898	68	Mgahinga Gorilla National Park, Uganda	Twinomugisha and Chapman (2008)
C. m. stuhlmanni	46.6	14.4	35.9	1.4	1.6	1136	38	Kakamega Forest, Kenya	Cords (1987)
C. m. stuhlmanni	60.3	19.7	9.9	8.3	1.8	1216	36	Kibale Forest (Kanyawara), Uganda	Butynski (1990)
C. m. stuhlmanni	54.7	24.7	11.7	7.0	1.7	1406	335	Kibale Forest (Ngogo), Uganda	Butynski (1990)
C. petaurista	45.2	25.6	23.8	5.4	0.0	1051	69	Taï, Ivony Coast	Buzzard (2004), (2006b)
Hapalemur aureus	–	–	–	–	–	–	26	Ranomafana National Park, Madagascar	Tan (1999)
H. griseus	–	–	–	–	–	–	15	Ranomafana National Park, Madagascar	Tan (1999)
H. griseus	29.8	26	44.1	–	–	–	20	Ranomafana National Park, Madagascar	Overdorff *et al.* (1997)
H. simus	–	–	–	–	–	–	62	Ranomafana National Park, Madagascar	Tan (1999)

F = feeding and foraging; M = moving; R = resting; S = socializing; O = other

Table X Percentage of feeding time devoted to different plant parts by *Chlorocebus* spp. and *Cercopithecus* spp. in Africa and *Hapalemur* spp. bamboo specialists in Madagascar

Species	YL	ML	SH	TL	ST	RO	FL	FR	SD	TF	GU	AP	OT	No. species	Site, country	Reference
Chlorocebus aethiops	–	–	–	0.8	8.0	–	7.6	7.0	10.2	17.2	47.9	0.7	17.8	–	Laikipia (*Acacia xanthophloea* woodland), Kenya	Isbell *et al.* (1998)
C. aethiops	–	–	–	3.2	–	–	2.3	1.7	6.6	8.3	39.5	7.5	39.2	–	Laikipia (*A. drepanolobium* woodland), Kenya	Isbell *et al.* (1998)
C. djamdjamensis	80.2	1.1	1.5	82.8	1.4	0.9	3.1	9.6	–	9.6	0.0	2.3	0.0	11	Odobullu Forest, Ethiopia	This study
C. sabaeus	–	–	–	–	–	–	13.0	50.2	12.8	63.0	–	13.1	10.9	–	Mt. Assirik, Senegal	Harrison (1983a)
Cercopithecus ascanius	8.9	0.3	–	9.2	–		1.4	55.0	–	55.0	–	29.5	4.9	–	Kakamega (Buyangu), Kenya	Gathua (2000)
C. ascanius	6.8	0.4	0.7	7.9	–	–	2.0	61.3	0.4	61.7	2.8	25.1	0.5	98	Kakamega (Isecheno), Kenya	Cords (1986)
C. ascanius	11.4	4.5		15.9			15.3	43.7	0.1	43.8	–	24.7	0.4	–	Kibale (Kanyawara), Uganda	Struhsaker (1978)
C. ascanius	–	–	–	34.7	–	–	2.7	44.6	–	44.6	–	17.6	0.4	–	Kibale (Sebatoli), Uganda	Chapman *et al.* (2002a)
C. ascanius	–	–	–	28.2	–	–	3.7	35.7	–	35.7	–	31.2	1.2	–	Kibale (Kanyawara), Uganda	Chapman *et al.* (2002a)
C. ascanius	–	–	–	15.4	–	–	8.2	55.6	–	55.6	–	20.6	0.2	–	Kibale (Dura River), Uganda	Chapman *et al.* (2002a)
C. ascanius	–	–	–	12.8	–	–	11.6	59.7	–	59.7	–	14.5	1.4	–	Kibale (Mainaro), Uganda	Chapman *et al.* (2002a)
C. campbelli	–	–	–	8	–	–	1	46	–	46	–	33	12	75	Taï, Ivony Coast	Buzzard (2006a)
C. diana	–	–	–	16	–	–	3	59	–	59	–	16	6	84	Taï, Ivony Coast	Buzzard (2006a)
C. lhoesti	–	–		35.2	–	–	4.0	24.5	17.7	42.2	–	8.8	9.8	83	Nyungwe Forest Reserve, Rwanda	Kaplin and Moermond (2000)

Cercopithecus mitis doggetti	–	–		6.7	–	–	6.2	47.4	9.3	56.7	–	24.9	6.1	59	Nyungwe Forest Reserve, Rwanda	Kaplin *et al.* (1998)
C. m. kandti[a]	44.0	0.1	–	44.1	3.4	–	14.8	22.5	–	22.5	–	14.3	1.1	16	Mgahinga, Uganda	Twinomugisha *et al.* (2006)
C. m. stuhlmanni	16.6	2.3	1.1	20.0	–	–	3.7	54.6	2.5	57.1	1.9	16.8	0.5	104	Kakamega, Kenya	Cords (1986)
C. m. stuhlmanni	13.7	6.8	–	20.5	–	–	12.5	45.1	2.4	47.5	–	19.8	2.1	–	Kibale (Kanyawara), Uganda	Struhsaker (1978)
C. m. stuhlmanni	–	–	–	31.4	–	–	6.4	22.1	–	22.1	–	39.4	0.8	–	Kibale (Kanyawara), Uganda	Butynski (1990)
C. m. stuhlmanni	–	–	–	22.8	–	–	9.8	30.1	–	30.1	–	35.9	1.3	–	Kibale (Ngogo), Uganda	Butynski (1990)
C. m. stuhlmanni	22.4	10.8	–	33.2	–	–	4.9	39.5	16.5	56.0	–	2.9	3.0	–	Budongo (logged), Uganda	Plumptre (2006)
C. m. stuhlmanni	33.8	13.1	–	46.9	–	–	7.4	23.2	14.8	38.0	–	5.9	1.8	–	Budongo (unlogged), Uganda	Plumptre (2006)
C. nictitans	10.2	0.1	–	10.3	–	–	4.1	35.5	50.2	85.7	–	–	0.0	31 (Families)	Makand´e Forest, Gabon	Brugiere *et al.* (2002)
C. petaurista	–	–	–	40	–	–	6	34	–	34	–	12	7	76	Taï, Ivony Coast	Buzzard (2006a)
C. pogonias	12.5	0.1	–	12.6	–	–	4.7	26.9	49.8	76.7	–	–	0.0	30 (Families)	Makand´e Forest, Gabon	Brugiere *et al.* (2002)
Hapalemur aureus	–	–	–	91	–	–	–	4	–	4	–	–	5	≥21	Ranomafana, Madagascar	Tan (1999)
H. griseus	0.3	6.3	89.1	95.7	–	–	0.4	1.2	–	1.2	–	–	2.7	12	Ranomafana, Madagascar	Overdorff *et al.* (1997)
H. griseus	–	–	–	92	–	–	–	5	–	5	–	–	3	≥24	Ranomafana, Madagascar	Tan (1999)
H. simus	–	–	–	98	–	–	–	0.5	–	0.5	–	–	1.5	7	Ranomafana, Madagascar	Tan (1999)

YL = young leaves; ML = mature leaves; SH = shoots; TL = total leaves; ST = stems; RO = roots; FL = flowers; FR = fruits; SD = seeds; TF = total fruits; GU = gum; AP = animal prey; OT = other

[a] From Table I in Twinomugisha *et al.* (2006), we took the average of the values for groups G and N during time 1 and then averaged that value with the value for time 2

'young growths' of giant bamboo, which appear to be lower in cyanide than more mature growths. Perhaps the preference for young bamboo leaves by Bale monkeys and golden monkeys achieves a similar end of limiting cyanide intake. Another potential advantage of focusing primarily on young leaves is that numerous studies have shown that young leaves contain more protein, have lower fiber content, and are more digestible than mature leaves (Chapman *et al*. 2002b; Fashing *et al*. 2007a; Milton 1979). Nutritional analyses focusing on the macronutrients, micronutrients, and secondary compounds contained in the items eaten and avoided by Bale monkeys are clearly the next step in achieving a better understanding of the species' extreme dietary specialization. In the meantime, there seems little question that bamboo must be considered a keystone resource for Bale monkeys, and that the loss of this resource would have a profoundly adverse effect on the long-term survival of this species.

Activity Budget

Unlike most folivorous primates (Di Fiore and Campbell 2007; Fashing 2007a), Bale monkeys at Odobullu were extremely active, devoting more than three-quarters of their time to feeding and moving. This level of activity is relatively typical of other *Chlorocebus* and *Cercopithecus* spp., though Bale monkeys spent somewhat more time feeding and less time moving than other related taxa (Table IX). Their need to feed more may stem from their presumably lower-quality, leafier diet than those of other *Chlorocebus* and *Cercopithecus* spp. Further, the extreme abundance of their primary food species, bamboo, in their habitat probably explains why Bale monkeys had to spend less time moving between food sources than related taxa. Thus, while generally about equally active as other *Chlorocebus* and *Cercopithecus* spp., Bale monkeys partition their time in a considerably different manner, presumably owing to their unusual ecological circumstances.

Though we did not collect systematic data on substrate use, it is also noteworthy that Bale monkeys confined their activities primarily to the trees, only rarely venturing to the ground (Mekonnen, *pers. obs.*). This arboreal lifestyle is more akin to those of *Cercopithecus* spp. rather than to other *Chlorocebus* spp. which are far more terrestrial (Anapol *et al*. 2005).

Ranging Patterns

Compared to other *Chlorocebus* and *Cercopithecus* spp. (Table IX), the mean daily travel distances and overall home range areas used by the 2 Bale monkey groups in our study were relatively small. The more limited ranging patterns characteristic of Bale monkeys are probably due to their ability to rely on the abundant leaf resources provided by bamboo. Indeed, across the primate order, it is typical for folivores to have smaller home ranges than frugivores and omnivores (Clutton-Brock and Harvey 1977).

Another general trend among primates is that in populations experiencing intragroup scramble competition, larger groups have longer day range lengths and use larger home range areas than smaller groups (Isbell 1991). Though we are cautious in drawing conclusions from only 2 study groups, the larger group in our study (A) traveled further per day and occupied a larger home range than the smaller group (B), a pattern suggesting that scramble competition may be occurring within Bale monkey groups at Odobullu despite their abundant and seemingly evenly dispersed food resources. Another result suggestive of scramble competition among Bale monkeys at Odobullu is the increase in day journey length and home range size experienced by both focal groups during the dry season.

Conservation Requirements

The primary threat facing primates today is habitat destruction (Chapman *et al.* 2006; Wieczkowski 2004). By reducing forest size and quality, habitat destruction leads to the reduction of food sources for forest-dwelling primates and in some cases threatens them with local extinction (Lee and Hauser 1998; Muoria *et al.* 2003). Indeed, the destruction of bamboo forests for local consumption and commercial purposes is the main threat to remaining populations of Bale monkeys. Unfortunately, bamboo harvesting remains legal in Odobullu Forest and is almost certainly having a negative effect on the Bale monkeys, which exhibit a narrow and extreme specialization to life in the bamboo forests at this site. Therefore, based on the results of the present study, we recommend that management action be taken to outlaw bamboo harvesting in Odobullu Forest and the several other forests in the Bale Massif and Hagere Selam regions where Bale monkeys still exist. These urgent conservation measures must be implemented if the long-term survival of Bale monkeys and their bamboo forest habitats are to be ensured.

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