
Golden monkey ranging in relation to spatial and temporal variation in food availability

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Abstract

Understanding the determinants of a species' range use aids in understanding their ecological requirements, which in turn facilitates designing effective conservation strategies. The ranging behaviour of golden monkeys (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda was studied from January 2003 to February 2004 to establish habitat preferences. In each 0.25 ha grid cell in the group's home range we quantified the basal area of food trees (n = 12,133 trees), measured bamboo (*Arundinaria alpina*) stems (n = 103,548), and estimated vine and shrub coverage. The evaluation of habitat preferences was facilitated by the fact that only five plant species, plus invertebrates (7.5%) constituted 96.4% of the group's foraging effort; this included bamboo (59.9%), *Maesa lanceolata* (18.7%), *Hypericum revolutum* (6.8%), *Galiniera saxifraga* (2.1%) and *Ilex mitis* (1.4%). Phenology data were collected for all five food tree species, three vines, and two shrubs. Range use generally followed food tree basal area distribution and not the distribution of bamboo, with the abundance of *M. lanceolata* being more closely associated with home range use than any other food plant. Bamboo was ubiquitous in distribution and a vital year-round resource for golden monkeys, which they combined with other food items to meet their nutritional requirements. Illegal bamboo or tree extraction both pose a serious threat to the conservation of the golden monkey, but activities that affect food tree abundance will likely have the most influence on monkey persistence.

Key words: *Cercopithecus mitis kandti*, golden monkey, Mgahinga Gorilla National Park, range use

Résumé

Bien comprendre les éléments déterminant le domaine vital d'une espèce aide à comprendre ses exigences écologiques, ce qui facilite la conception de stratégies de conservation efficaces. Le comportement territorial des singes dorés (*Cercopithecus mitis kandti*) dans le Parc National de Mgahinga Gorilla, en Ouganda, a été étudié de janvier 2003 à février 2004, pour établir leurs préférences en matière d'habitat. Dans chaque quadrat de 0,25 ha du domaine vital du groupe, nous avons quantifié la surface de la base des arbres (n = 12.133 arbres), mesuré les jets de bambous (*Arundinaria alpina*) (n = 103.548) et estimé la couverture par les vignes et les buissons. L'évaluation des préférences en matière d'habitat fut facilitée par le fait que cinq espèces végétales seulement, plus des invertébrés (7,5%) constituent 96,4% des efforts alimentaires du groupe; elles incluent le bambou (59,9%), *Maesa lanceolata* (18,7%), *Hypericum revolutum* (6,8%), *Galiniera saxifraga* (2,1%) et *Ilex mitis* (1,4%). Des données phénologiques ont été récoltées pour les cinq espèces d'arbres consommées, trois vignes et deux buissons. La fréquentation du domaine vital suivait en général la distribution de la superficie de la base des arbres et non la distribution du bambou, l'abondance de *M. lanceolata* étant plus étroitement associée au domaine vital que toute autre plante consommée. Le bambou est omniprésent et c'est une ressource vitale tout au long de l'année pour les singes dorés qui le combinent avec d'autres aliments pour répondre à leurs besoins nutritionnels. Les coupes illégales de bambous ou d'arbres sont une sérieuse menace pour la conservation du singe doré, mais les activités qui affectent l'abondance des arbres consommés sont celles qui risquent d'avoir la plus grande influence sur la persistance des singes.

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Introduction

A fundamental issue in ecology concerns determination of the factors affecting the density of animal populations. The importance of this issue has increased with the need to develop informed management plans for endangered and threatened species (Chapman & Peres, 2001). With respect to primates, these theoretical issues are critical because the tropical forests they occupy are undergoing rapid anthropogenic transformation (National Research Council, 1992) and many populations have been reduced by hunting (Peres, 1990; Oates, 1996). However, the determinants of the abundance of particular primate species have often proven extremely difficult to identify (Oates *et al.*, 1990).

There are many methods of investigating the determinants of primate abundance. One approach is to evaluate a species' nutritional requirements and whether their habitat is providing those needs (Davies, 1994; Ganzhorn, 1995; Balcomb, Chapman & Wrangham, 2000; Chapman *et al.*, 2004; Rode *et al.*, 2006; Twinomugisha *et al.*, 2006). Alternatively, if long-term data are available on changes in both population size and habitat structure, one can evaluate if regeneration or degradation of the habitat corresponds with predictable changes in population size (Struhsaker, 1976, 1997; Plumptre & Reynolds, 1994; Chapman *et al.*, 2000). Another valuable approach is to use an animal's behaviour to demonstrate its resource needs, and subsequently evaluate changes to the habitat providing for those needs. For example, it is assumed that animals move about their home ranges in ways that maximize the intake of nutrients (Pyke, 1984; Rode *et al.*, 2006). By examining a species' ranging patterns and the food available in parts of the home range, the most critical resources can be identified. How anthropogenic habitat change has, or could in the future alter the availability of critical resources can then be evaluated.

In this study, we examined the ranging behavior of the endangered golden monkey (*Cercopithecus mitis kandti* Matschie) in Mgahinga Gorilla National Park, Uganda to determine how their home range use varied with spatial and temporal variation in resource availability. We identified critical food resources by quantifying food items available in each 0.25-ha grid cell throughout the group's home range.

Materials and methods

Mgahinga Gorilla National Park (MGNP), Uganda (33.7 km²) became a National Park in 1991; however,

between the time it was first gazetted as a protected area in 1930 and 1991, it underwent a number of changes of name, status, and management (Uganda National Parks, 1996). During these transitions, there was vegetation clearance for cultivation and bamboo harvesting, grazing, and poaching of animals. The study group ranged in the montane forest belt and this area contained many degraded areas where bamboo had been harvested.

To quantify patterns of habitat use, a habituated golden monkey group was observed all-day (07.00–19.00 hours) for 105 days between January 2003 and February 2004. These systematic observations followed 12 months of habituation of the study group (January 2002–December 2002). Habituation took this long because the illegal bamboo harvesters and hunters associated the presence of the researchers with loss of opportunities to conduct illegal activities, and they disrupted habituation. To systematically follow monkeys and to place feeding observations and food availability data in a spatial context, a grid system with 0.25 ha cells, with corners marked with flagging tape, was laid over an area perceived to be their entire home range, following habituation. The group was typically spread across an area smaller than a single grid cell. (Twinomugisha, Basuta & Chapman, 2003). During each of the all-day follows (an average of 7.5 days a month), the grid cell in which the centre of the group was located was recorded every 15 min. Group members rarely fed in more than one grid cell at a time, thus the centre of the group is an accurate reflection of where most animals were obtaining their food items. During all-day follows, systematic instantaneous scan sampling of diet and other activities were made during 5-min sampling periods separated by 10 min.

To quantify habitat characteristics potentially relevant to habitat selection, we examined density of food trees, abundance of shrub and vine food plants, bamboo culm density, and phenology of food plants. This enabled the quantification of the distribution of the main food sources in the group's home range at any given time and allowed us to relate the pattern of grid cell use to food availability. In each grid cell, the following data were collected on food trees ≥ 5 cm dbh (diameter at breast height): species identity, number, and size (dbh). The dbh ≥ 5 cm lower limit was selected because *Galiniera saxifraga* (A.Rich. Bridson) and *Hypericum revolutum* (R.Keller) provide food items at this size. The dbh of trees has been found to be a good indicator of fruit and leaf abundance (Harrington, 1979; Catchpole & Wheeler, 1992; Chapman *et al.*, 1992).

In total, 12,133 trees were measured. There were seven other tree species that the monkeys did not feed on (*Agauria salicifolia* Hook.f. ex Oliv., 12.1 trees per ha; *Xymalos monospora* Baill., 5.7 trees per ha; *Dovyalis macrocalyx* Warb, 2.2 trees per ha is a food plant; *Pittosporum spathicalyx* De Wild., 1.0 tree per ha; *Dombeya* sp., 0.27 trees per ha; *Erica arborea* Brot., 0.07 trees per ha, *Bersama abyssinica* Fresen., 0.05 tree per ha; golden monkeys do eat *Dovyalis macrocalyx* fruits, but it did not bear fruit during this study period.

Monthly phenological observations determined the temporal availability of the plant parts eaten by the monkeys. For each plant species, five to twenty apparently healthy individuals that were ≥ 10 cm dbh (for *G. saxifraga* and *H. revolutum* ≥ 5 cm dbh) were monitored. Monthly phenophase data were also collected on three vine species and two shrubs known to be golden monkey food plants. The selected individuals of each plant species were distributed throughout the group's home range. The following were monitored: mature leaves, young leaves, flower buds, flowers, and fruits. Phenophase abundance was scored on a scale of 0–8 (i.e. 0 = 0%, 1 = 1–12.5%, 2 = 12.5–25%, 3 = 25–37.5, 4 = 37.5–50, 5 = 50–62.5, 6 = 62.5–75, 7 = 75–87.5 and 8 = 87.5–100% (National Research Council, 1981; Lawes & Piper, 1992; Kaplan, Munyaligoga & Moermond, 1998).

In some areas bamboo was very dense, thus to quantify bamboo culm density, dbh, height, and broad age classes, measurements were made in six 0.5×50 m strip subplots laid at regular intervals in each 0.25 ha grid cell. In total 103,548 bamboo stems were measured. Percentage vine and shrub coverage were also determined for 12 species that bear food items (estimated in 10% intervals).

We first graphically contrasted range use with spatial and temporal variation in resources using Surfer (version 7.0, Golden, CO, USA) then statistically investigated the same patterns using correlation and multiple regressions analysis SPSS (version 14.0, Chicago, IL, USA). Temporal variation in food item use and the number of grid cells used was represented as the coefficient of variation (CV).

Results

Ranging and diet

The group ranged over 67.5 ha (272 cells), and fed in 241 cells ($n = 11,423$ feeding records made in 3435 scans, during 14 months covering 105 days). The number of

feeding events varied substantially among cells (range = 1–505, Fig. 1a). The day path-length of the monkeys varied from 250 to 1670 m, and averaged 898 m (CV = 29.78%).

The golden monkey fed primarily on four food items: young bamboo (*Arundinaria alpina* K.Schum.) leaves (33.4% of feeding observations), *Maesa lanceolata* (G.Don) fruits (20.8%), bamboo shoots (15.3%), and bamboo branchlets (11.6%). Diet selection was strongly influenced by the availability of *M. lanceolata* fruit (Fig. 2). This species fruited primarily in the last month of the dry season (August and during the first 2 months of the rainy season (September and October); mean total fruit phenophase score August (3.64 ± 3.34 SD with a ripe fruit component of 0.86 ± 0.86 SD, $n = 14$ trees; note that the CV among months for total fruit was very high, at 91.75%), September (3.14 ± 2.93 SD total fruit and 1.86 ± 1.92 SD ripe fruit component), October (3.00 ± 2.86 SD total fruit, 2.29 ± 2.58 SD ripe) and November total fruit (1.54 ± 1.97 SD, ripe = 1.21 ± 2.12). There was little feeding on *M. lanceolata* from April through July, when there was less ripe fruit. *Maesa lanceolata* fruit availability coincided closely with bamboo shooting. At this time, the monkeys switched between areas with *M. lanceolata* and areas of bamboo. Bamboo shooting occurs when the rainy season begins. Bamboo shoot availability influenced range use with the monkeys foraging on bamboo shoots in May following the short rains of March–May, but hardly at all on bamboo leaves.

Bamboo shoots, as well as young bamboo leaves, were eaten extensively in October and November and later included bamboo branchlets in December as the shoots grew into young bamboo culms. *Hypericum revolutum* flowers were abundant during January, February, and March 2004 and were an important food at this time and in February 2004 when this tree flowered again (Fig. 2). *Hypericum revolutum* flowered mostly from January through March 2003 (January phenophase score 3.2 ± 1.62 SD, February 4.6 ± 2.01 SD and March 3.2 ± 1.31 SD) and February 2004 (2.33 ± 1.41 SD), while its abundance was lower during other months with a minimum mean score of 0.22 ± 0.35 SD in April and a maximum of 1.44 ± 0.70 SD in June. The monkeys were observed feeding on two shrub species only: *Rhamnus prinoides* (L'Hér.) fruits (1.2% of feeding records over the entire study and 1.1%, 2.5%, 7.9% and 4.2% per month from March to June respectively) and *Clerodendrum* sp. pith which was eaten only in January 2003 (0.4%).

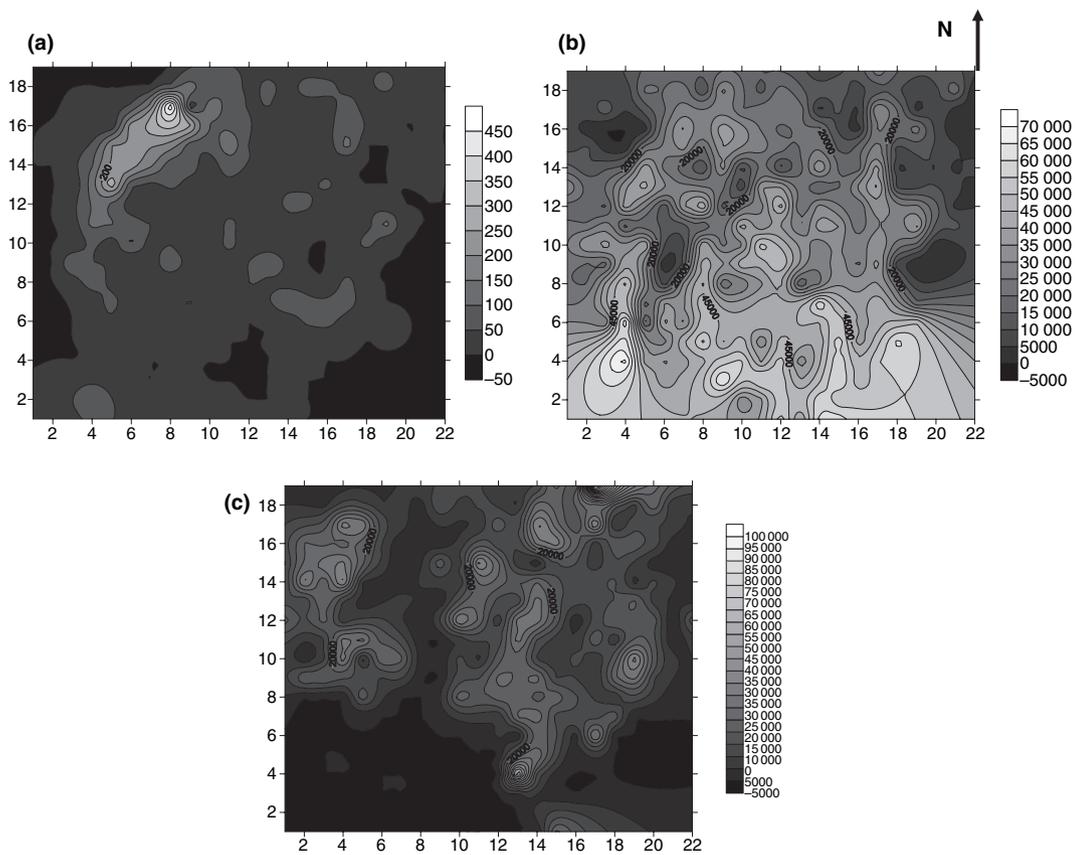


Fig 1 Contour maps of usage of home range by the golden monkey (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda during 14 months covering 105 days between January 2003 and February 2004 showing feeding intensities (number of feeding records in grid cells) in different parts during the study (a), (b) bamboo basal area (*Arundinaria alpina*), (c) the basal area of only three food tree species (*Hypericum revolutum*, *Maesa lanceolata* and *Galiniera saxifraga*) which shows a close pattern between food plant distributions and feeding by the group

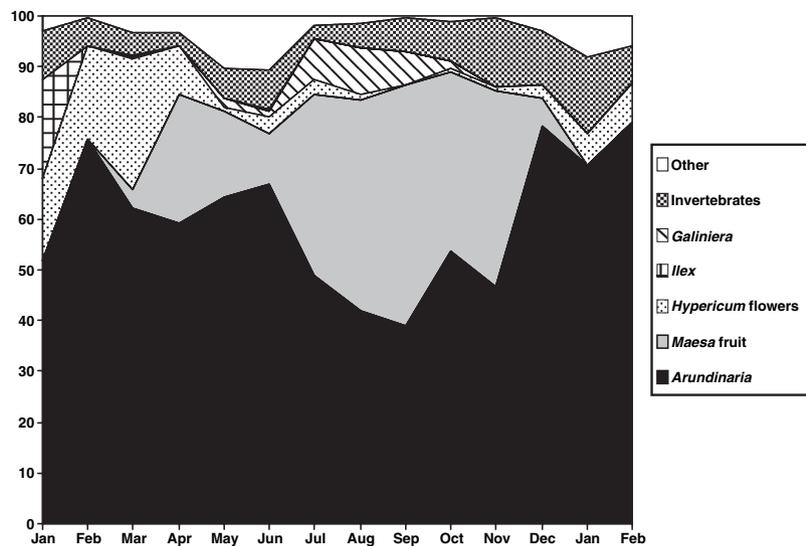


Fig 2 The foraging effort that a group of golden monkeys (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda invested each month on the major food items during 14 months covering 105 days between January 2003 and February 2004

For the purpose of evaluating range use, five plant species were considered: bamboo $59.9 \pm 13.3\%$ SD (CV = 22.1% among months), *M. lanceolata* $18.7 \pm 18.0\%$ SD (CV = 96.4%), *H. revolutum* $6.8 \pm 7.9\%$ SD (CV = 115.9%), *G. saxifraga* $2.1 \pm 3.3\%$ SD (CV = 157.6%), and *Ilex mitis* (Radlk.) $1.4\% \pm 5.2$ (CV = 367.1%). Together with invertebrates $7.5 \pm 3.8\%$ SD (CV = 50.4%), these plant items made up 96.4% of the foraging efforts of the monkeys over 14 months.

Spatial and temporal variation in home range use: a graphical analysis

The study group concentrated much of its activity in the northwestern part of its range, which comprises mixed tree and bamboo and the regenerating zone (Fig. 1a,b). The group used the southern part of its home range less frequently because it consisted almost entirely of bamboo. The monkeys never used this regenerating wooded grassland, which were previously harvest bamboo areas (Lejju, Orygem-Origa & Kasenene, 2001). Excluding bamboo basal area from the graphical presentation reveals that the pattern of range use generally follows the distribution of food tree basal area and range use was most closely depicted by the basal area of only three food tree species (*H. revolutum*, *M. lanceolata* and *G. saxifraga*; Fig. 1c). There was a higher food tree basal area in the north compared to the south of the home range, which corresponds to the group's range use (Fig. 1a,c). The distribution of fruiting *M. lanceolata* alone is more closely associated with patterns of home range use than any other food plant. Overall and individual food vine and shrub species abundance was greater in the lower altitude northern part of the home range than in the higher altitude southern section.

The question remains, whether range use is determined by foraging on *M. lanceolata* or if the vicinity of *M. lanceolata* individuals were selected to allow the golden monkeys to feed both on bamboo, *M. lanceolata*, and other food tree species for a balanced diet? The mean monthly proportion of the group's foraging time spent eating *M. lanceolata* was 18.6% (range 0–47.4%, 23.7% during months when it was available, 11 months). Only bamboo was more frequently eaten and it was eaten in all 14 months and the proportion of the group's foraging time spent eating bamboo was 59.9% (range 39.0–79.1%). The bamboo distribution pattern in the home range was negatively correlated with that of food tree species (*H. revolutum*, $r = -0.150$, $P < 0.001$, *M. lanceolata*, $r = -0.513$, $P < 0.001$, *G. saxifraga*, $r = -0.268$, $P < 0.001$, in all cases $n = 774$) and it appears that food tree abundance, particularly *M. lanceolata*, determines range use.

The golden monkey frequently returned to a few sleeping sites after a day's foraging. The group foraged in areas close to the sleeping sites and often used the same sleeping sites on consecutive days. In most cases, the monkeys slept in small subgroups of approximately four individuals atop bamboo culms, either as individual culms with dense foliage or a cluster of culms that were intertwined creating a firm base of dense foliage.

Spatial and temporal variation in range use: a statistical analysis

Foraging effort on particular items was generally in proportion to an item's abundance (Table 1), with the exception of *G. saxifraga*. Of the five plants considered most influential on range use (bamboo, *M. lanceolata*, *I. mitis*,

Table 1 Correlations between feeding effort of the golden monkeys of Mgahinga Gorilla National Park, Uganda and the abundance (basal area) of each plant item in different cells of its home range between January 2003 and February 2004 and during the month during which the food plant species was fed on most

Temporal Scale	<i>Arundinaria alpina</i>	<i>Maesa lanceolata</i>	<i>Hypericum revolutum</i>	<i>Galineria saxifraga</i>	<i>Ilex mitis</i>	<i>Rhamnus prinoides</i>
Entire study	$r = 0.259$, $P < 0.001$, $n = 778$	$r = 0.312$, $P < 0.001$, $n = 776$	$r = 0.162$, $P < 0.001$, $n = 778$	$r = -0.025$, $P = 0.494$, $n = 776$	$r = 0.671$, $P = 0.001$, $n = 22$	$r = 0.161$, $P < 0.001$, $n = 778$
Month fed on the most	$r = -0.078$, $P = 0.554$, $n = 60$	$r = 0.317$, $P = 0.034$, $n = 45$	$r = 0.562$, $P = 0.001$, $n = 29$	$r = 0.037$, $P = 0.787$, $n = 55$	$r = 0.671$, $P = 0.001$, $n = 22$	$r = 0.174$, $P = 0.170$, $n = 64$

n = number of cells in which the study group fed. *Arundinaria alpina* was fed on most in February 2004, *M. lanceolata* in September, *H. revolutum* in March, *G. saxifraga* in August, *I. mitis* in January 2003 and *R. prinoides* in May.

H. revolutum and *G. saxifraga*), the basal area of each species was correlated with the number of times a grid was used on 57%, 70%, 100%, 50% and 0% of occasions, respectively. While this percentage was high for *I. mitis*, it should be noted that it was fed on only during one month. *Ilex mitis* was also concentrated in a small area of the home range and is possibly less important than some other foods in determining home range use. The golden monkeys fed on *G. saxifraga* less frequently than other species and >5% of foraging time in 3 months, suggesting that it was not actively sought out. In the months that *H. revolutum* flowers were abundant, there was a correlation between its basal area in a grid and the number of times that monkeys fed on its flowers (Table 1). *Maesa lanceolata* fruits and bamboo items were typically the most frequently eaten food items in any cell. Generally, feeding on bamboo and *M. lanceolata* correlated positively with the two food plant species abundance in cells (Table 1). Of these six foods, only the feeding effort on *M. lanceolata*, *H. revolutum* and *I. mitis* correlated with their abundance during the months in which they were consumed most (Table 1).

Regression analysis consistently showed that feeding on food plant species was related to the abundance of the food plants (Table 2). Here total feeding effort was regressed against the abundance of each food plant species. Food plant species were combined beginning with the species contributing most to per cent feeding time adding on the next most contributing species until all the six plant species considered were included. In all cases *G. saxifraga* and *I. mitis* were the only food plant species whose abundance was not a predictor of feeding effort in grid cells.

Discussion

We used a detailed evaluation of the golden monkeys' range use and foraging effort in relation to a quantification

of the spatial and temporal variation of food resources to understand what underlies their ranging patterns. The distribution of food trees varied widely, with most of the trees being down slope in the northern part of the home range, while the south consisted almost entirely of bamboo. This influenced ranging and the group most frequently used the northern part of their home range. Thus, while abundant bamboo is the leading source of protein for the golden monkey (Twinomugisha *et al.*, 2006) and is frequently used throughout the year, the golden monkey appears to require a combination of resources including food items obtained from trees, vines, and shrubs.

Though significant, the regression analyses explained only 19–32% of the variation in ranging behaviour based on the distribution of the food items. This is in spite of detailed resource quantification (i.e. complete inventory of food tree distribution and extensive sampling of bamboo) of a very simple diet dominated by only five plant species. This relatively low explanatory power may be related to a variety of factors. The logic of the regression analysis is developed from an optimal foraging theory framework within which foraging behavior can be assessed based on the idea that natural selection has produced individuals who make decisions that maximize their fitness (Pyke, 1984; Parker & Maynard Smith, 1990; Krebs & Davies, 1993). This framework has a number of explicit assumptions that may be invalidated in the current situation.

First, this analysis assumes that ranging decisions were governed solely by the availability of food, and that other costs or benefits were not spatially variable. However, animals may trade-off the benefits of improved foraging success in a given area, if other costs, such as predation or parasitism, are also higher (Olupot *et al.*, 1997; Perry & Pianka, 1997; Chapman, Gillespie & Goldberg, 2005). In this case, the location of sleeping and resting sites seems to be a major factor, in addition to food availability, that influences the golden monkey's range use. MGNP

Table 2 The percentage of variation in home range use explained over the study of the golden monkeys of Mgahinga National Park, Uganda that is accounted for by the basal area of the most important food species, the most important and second most important food item combined and so on

Most important	% feeding time	
1) <i>Arundinaria alpina</i>	59.9	$r^2 = 0.319, P < 0.001$
2) <i>A. alpina</i> , <i>Maesa lanceolata</i>	78.6	$r^2 = 0.240, P < 0.001$
3) <i>A. alpina</i> , <i>M. lanceolata</i> , <i>Hypericum revolutum</i>	85.4	$r^2 = 0.191, P < 0.001$
4) <i>A. alpina</i> , <i>M. lanceolata</i> , <i>H. revolutum</i> , <i>Galiniera saxifraga</i>	87.5	$r^2 = 0.216, P < 0.001$
5) <i>A. alpina</i> , <i>M. lanceolata</i> , <i>H. revolutum</i> , <i>G. saxifraga</i> , <i>Ilex mitis</i>	88.9	$r^2 = 0.218, P < 0.001$
6) <i>A. alpina</i> , <i>M. lanceolata</i> , <i>H. revolutum</i> , <i>G. saxifraga</i> , <i>I. mitis</i> , <i>Rhamnus prinoides</i>	90.1	$r^2 = 0.212, P < 0.001$

comprises volcanic mountains and the slopes are exposed to high winds. Areas shielded from wind are used by monkeys as sleeping sites. However, these sites may not coincide with the distribution of particular food plant species. Similarly, Raboy and Deitz (2004) found that the need to search for food resources in a relatively large home range, and reliance on a few sleeping sites were the major factors that shaped golden-headed lion tamarins (*Leontopithecus chrysomelas Coimbra-Filho*) range use. Repeated use of specific sleeping sites has implications. These may include elevated travel costs with monkeys having to travel far to find food and return to the sleeping site. Golden monkeys fed most within the vicinity of their sleeping sites. This may be tenable only if food plant abundance is adequate. Chapman (1989) found that spider monkeys (*Ateles geoffroyi* Kuhl) subgroup size at sleeping sites was positively related to food availability and Chapman, Chapman & Mclaughlin (1989) demonstrated that spider monkey sleeping site selection was related to travel costs to feeding sites. Despite the apparent importance of the location of sleeping sites in influencing range use, it does not appear that sleeping site selection influences range use to the degree that the group often went to areas that did not provide important nutritional resources (Twinomugisha *et al.*, 2006).

Second, most optimal foraging models assume that the animals have perfect knowledge about the spatial and temporal availability of foods within their home range, and that there were no constraints on making ranging decisions to maximize foraging benefits. This assumption may be unrealistic for several reasons; it is unlikely that organisms ever have perfect knowledge of food availability due to variation in resource distribution (Pyke, 1984; Kramer, Ranglely & Chapman, 1997). There may be cognitive constraints on tracking resource availability through space and time (Giraldeau, 1997) and constraints on the ability to sample or monitor food conditions in different areas (Kramer *et al.*, 1997), which may prevent groups from optimizing their ranging strategy.

Third, we assumed that ranging decisions were not constrained by travel distance and that groups could visit any area within their home range without incurring prohibitive travel costs. It is possible that monkeys make trade-offs between the habitat quality of a given area and the travel distance required to reach it, particularly if they must return to one of a limited number of sleeping sites.

Given the plight of primates globally, it is valuable to have a variety of tools/approaches that can provide information useful for the construction of informed man-

agement plans. Our research on golden monkeys has taken a variety of approaches to understand the current status of golden monkeys in MGNP and to guide management efforts. Evaluating what plants could meet the nutritional needs of the golden monkeys revealed that bamboo supplied a significant level of protein, but that tree fruits and flowers were needed to provide sugars (Twinomugisha *et al.*, 2006). Examination of the population trends of the golden monkeys over 14 years revealed a decline in abundance despite an improvement in protection, but a concentration of animals in the bamboo and mixed bamboo-tree habitats (Twinomugisha & Chapman, 2007). The distribution of food trees had a positive influence on home range use by golden monkeys.

Presently, bamboo is the most sought-after item by the local community bordering the national park. The local people claim that bamboo in specific locations is particularly suitable for crafts and other uses, thus the same areas tend to be repeatedly harvested year after year. This harvesting pattern may eventually negatively affect the growth of bamboo leading to poor yield or even a retreat in coverage. In similar bamboo stands on Mt. Elgon, Uganda, Scott (1994) found that bamboo culm dbh decreased with increasing harvest intensity. A recent trend that we have observed is that bamboo shoots are being harvested for human consumption (D. Twinomugisha, pers. obs.). This is a practice that has been brought to the local community by soldiers positioned in the national park to provide security. For some, bamboo shoots are a delicacy and there is a possibility that the local people, who have not traditionally fed on bamboo shoots, will take on the practice.

Illegal activities in the golden monkey habitat, which modify the ecosystem through bamboo and tree extraction, pose a serious threat to the conservation of the golden monkey. The results here suggest that activities that influence tree abundance will likely have a more significant impact than the bamboo harvest. The findings of this research suggest restoration in the regenerating zone of the park would be a profitable conservation strategy to promote golden monkey populations. The restoration efforts should aim for a habitat that is a mixture of bamboo and trees, particularly *M. lanceolata* and *H. revolutum*.

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References

- BALCOMB, S.R., CHAPMAN, C.A. & WRANGHAM, R.W. (2000) Relationship between chimpanzee (*Pan troglodytes*) density and large, fleshy-fruit tree density: conservation implications. *Am. J. Primatol.* **51**, 197–203.
- CATCHPOLE, W. & WHEELER, J. (1992) Estimating plant biomass: a review of techniques. *Aust. J. Ecol.* **17**, 121–131.
- CHAPMAN, C.A. (1989) Spider monkey sleeping sites: use and availability. *Am. J. Primatol.* **18**, 53–60.
- CHAPMAN, C.A. & PERES, C.A. (2001) Primate conservation in the new millennium: the role of scientists. *Evol. Anthropol.* **10**, 16–33.
- CHAPMAN, C.A., CHAPMAN, L.J. & MCLAUGHLIN, R.L. (1989) Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia* **79**, 506–511.
- CHAPMAN, C.A., CHAPMAN, L.J., WRANGHAM, R., HUNT, K., GEBO, D. & GARDNER, L. (1992) Estimators of fruit abundance of tropical trees. *Biotropica* **24**, 527–531.
- CHAPMAN, C.A., BALCOMB, S.R., GILLESPIE, T.R., SKORUPA, J.P. & STRUHSAKER, T.T. (2000) Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* **14**, 207–217.
- CHAPMAN, C.A., CHAPMAN, L.J., NAUGHTON-TREVES, L., LAWES, M.J. & MCDOWELL, L.R. (2004) Predicting folivorous primate abundance: validation of a nutritional model. *Am. J. Primatol.* **62**, 55–69.
- CHAPMAN, C.A., GILLESPIE, T.R. & GOLDBERG, T.L. (2005) Primates and the ecology of their infectious diseases: how will anthropogenic change affect host-parasite interactions? *Evol. Anthropol.* **14**, 134–144.
- DAVIES, A.G. (1994) Colobine populations. In: *Colobine Monkeys. Their Ecology, Behaviour and Evolution* (Eds A. G. DAVIES and J. F. OATES). Cambridge University Press, Cambridge.
- GANZHORN, J.U. (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* **76**, 2048–2096.
- GIRALDEAU, L.A. (1997) The ecology of information use. In: *Behavioural Ecology: An Evolutionary Approach* (Eds J. R. KREBS and A. G. DAVIES). Blackwell Science, Boston.
- HARRINGTON, G. (1979) Estimation of above-ground biomass of trees and shrubs. *Aust. J. Bot.* **27**, 135–143.
- KAPLIN, B.A., MUNYALIGOGA, V. & MOERMOND, T.C. (1998) The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica* **30**, 56–71.
- KRAMER, D.L., RANGLEY, R.W. & CHAPMAN, L.J. (1997) Habitat selection: patterns of spatial distribution from behavioural decisions. In: *Behavioural Ecology of Teleost Fishes* (Ed. J. G. J. GODIN). Oxford University Press, Oxford.
- KREBS, J.R. & DAVIES, N.B. (1993) *An Introduction to Behavioural Ecology*. Blackwell Publishing, Malden.
- LAWES, M.J. & PIPER, S.E. (1992) Activity patterns in free-ranging samango monkeys (*Cercopithecus mitis erythrarchus* Peters, 1852) at the southern range limit. *Folia Primatol. (Basel)* **59**, 186–202.
- LEJU, J.B., ORYGEM-ORIGA, H. & KASENENE, J.M. (2001) Regeneration of indigenous trees in Mgahinga Gorilla National Park, Uganda. *Afr. J. Ecol.* **39**, 65–73.
- NATIONAL RESEARCH COUNCIL (1981) *Techniques for the Study of Primate Population Ecology*. National Academy Press, Washington.
- NATIONAL RESEARCH COUNCIL (1992) *Conserving Biodiversity: A Research Agenda for Development Agencies*. National Academy Press, Washington.
- OATES, J.F. (1996) Habitat alteration, hunting, and the conservation of folivorous primates in African forests. *Aust. J. Ecol.* **21**, 1–9.
- OATES, J.F., WHITESIDES, G.H., DAVIES, A.G., WATERMAN, P.G., GREEN, S.M., DASILVA, G.L. & MOLE, S. (1990) Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology* **71**, 328–343.
- OLUPOT, W., CHAPMAN, C.A., WASER, P.M. & ISABIRYE-BASUTA, G. (1997) Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *Am. J. Primatol.* **43**, 65–78.
- PARKER, G.A. & MAYNARD SMITH, J.M. (1990) Optimality theory in evolutionary biology. *Nature* **348**, 27–33.
- PERES, C.A. (1990) Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* **54**, 47–59.
- PERRY, G. & PIANKA, E.R. (1997) Animal foraging: past, present and future. *Trends Ecol. Evol.* **12**, 360–364.
- PLUMPTRE, A.J. & REYNOLDS, V. (1994) The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *J. Appl. Ecol.* **31**, 631–641.
- PYKE, G.H. (1984) Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* **15**, 525–575.
- RABOY, B.E. & DEITZ, J.M. (2004) Diet, foraging, and use of space in wild golden-headed lion tamarins. *Am. J. Primatol.* **63**, 1–15.
- RODE, K.D., CHAPMAN, C.A., MCDOWELL, L.R. & STICKLER, C. (2006) Nutritional correlates of population density across habitats and logging intensities in redbell monkeys (*Cercopithecus ascanius*). *Biotropica* **38**, 625–634.
- SCOTT, J.P. (1994) *Bamboo: Potential for Utilisation by the Communities Surrounding Mt. Elgon National Park*. Technical report. IUCN Country Office and Ministry of Natural Resources, Kampala.

- STRUHSAKER, T.T. (1976) A further decline in numbers of Amboseli vervet monkeys. *Biotropica* **8**, 211–214.
- STRUHSAKER, T.T. (1997) *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. University of Florida Press, Gainesville.
- TWINOMUGISHA, D. & CHAPMAN, C.A. (2007) Golden monkey populations decline despite improved protection in Mgahinga Gorilla National Park, Uganda. *Afr. J. Ecol.* **46**, 220–224.
- TWINOMUGISHA, D., BASUTA, G.I. & CHAPMAN, C.A. (2003) Status and ecology of the golden monkey (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda. *Afr. J. Ecol.* **41**, 47–55.
- TWINOMUGISHA, D., CHAPMAN, C.A., LAWES, M.J., WORMAN, C. & DANISH, L. (2006) How does the golden monkey of the Virungas cope in a fruit scarce environment. In: *Primates of Western Uganda* (Eds N. NEWTON-FISHER, H. NOTMAN, V. REYNOLDS and J. D. PATTERSON). Springer, New York.
- UGANDA NATIONAL PARKS (1996) *Mgahinga Gorilla National Park Management Plan 1996–2000*. Unpubl. Report. Uganda Government, Kampala.
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