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journal homepage: www.elsevier.com/locate/forecoIs *Markhamia lutea*'s abundance determined by animal foraging?Colin A. Chapman^{a,b,*}, Tyler R. Bonnell^c, Raja Sengupta^c, Tony L. Goldberg^d, Jessica M. Rothman^e^a McGill School of Environment and Department of Anthropology, McGill University, Montreal, Quebec H3A 2T7, Canada^b Wildlife Conservation Society, Bronx, NY, USA^c Department of Geography, McGill University, Montreal, Quebec, Canada^d Department of Pathobiological Sciences, University of Wisconsin-Madison, Madison, WI, USA^e Department of Anthropology, Hunter College of the City University of New York, and New York Consortium in Evolutionary Primatology, 695 Park Avenue, New York, NY 10065, USA

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ABSTRACT

Understanding the determinants of tropical forest tree richness and spatial distribution is a central goal of forest ecology; however, the role of herbivorous mammals has received little attention. Here we explore the potential for red colobus monkeys (*Procolobus rufomitratus*) to influence the abundance of *Markhamia lutea* trees in a tropical forest by feeding extensively on the tree's flowers, such that this tree population is not able to regularly set fruit. Using 14 years of data from Kibale National Park, Uganda, we quantify *M. lutea* flower and fruit production. Similarly, using 21 years of data, we quantify temporal changes in the abundance of stems in size classes from 1 m tall and above. Our analyses demonstrate that *M. lutea* is rarely able to produce fruit and that this corresponds to a general decline in its abundance across all size classes. Moreover, using 7 years of feeding records, we demonstrate that red colobus feed on *M. lutea*, consuming large amounts of leaf and flower buds whenever they were available, suggesting that this behavior limits fruit production. Therefore, we suggest that red colobus are presently important for structuring the distribution and abundance of *M. lutea* in Kibale. This dynamic raises the intriguing question of how a large *M. lutea* population was able to originally establish. There is no evidence of a change in red colobus population size; however, if this old-growth forest is in a non-equilibrium state, *M. lutea* may have become established when red colobus ate a different diet.

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1. Introduction

Tropical rain forests are renowned for their extraordinary tree species richness (Connell, 1978; Phillips et al., 1994; Wright, 2002), with many forests containing more than 100 tree species per ha and as many as 283 species per ha (Phillips et al., 1994). Understanding the factors that explain this richness and determine the causes of the spatial distribution of trees has been a central goal of forest ecology for decades (Connell, 1971; Grubb, 1977; Hubbell, 1979; Grubb, 1996; Terborgh et al., 2002; Lawes et al., 2008; Condit et al., 2012; Dalling et al., 2012). Variation in the abiotic environment has been shown by some studies to be important in predicting tree diversity and distribution (Hubbell et al., 1999; Harms et al., 2001; Valencia et al., 2004; John et al., 2007). Topography in particular is often implicated (Grubb, 1996; Valencia et al., 2004), suggesting that soil moisture or nutrient availability play an important role in influencing tree distribution. For example, on Barro Colorado Island, Panama 52 of 171 shrub and tree species

show distributional biases with respect to swamps and 44 species show distributional biases with respect to slopes (Harms et al., 2001; Dalling et al., 2012). Similarly, John et al. (2007) demonstrated that 104 of 258 tree species on BCI had biased distributions based on soil chemistry.

Tree diversity patterns and distributional biases can be affected by the actions of animals through seed dispersal (Wright, 2002; Balcomb and Chapman, 2003; Condit et al., 2012) and herbivory (Janzen, 1970; Zanne and Chapman, 2005; Zanne et al., 2005; McCall and Irwin, 2006). Insects and small rodents are typically the focus of herbivory studies and there is usually an emphasis on the seed and seedling life history stages (Howe, 1990; Terborgh and Wright, 1994; Sagers and Coley, 1995; Wright and Duber, 2001; McCall and Irwin, 2006). By contrast, the importance of non-rodent mammalian herbivores and their impact on other tree life stages has received comparatively little attention, with the exception of very large scale impacts. Perhaps the best known large scale example of animals influencing tree distribution involves elephants (*Loxodonta africana*), which play an important role in maintaining open wooded grasslands (Laws, 1970; Dublin et al., 1990) and converting forest to grassland (Stuart et al., 1985). Animals that modify the environment and change, maintain, and/or create new habitats in ways that affect resource availability for other

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species are called “ecosystem engineers” (Jones et al., 1994; Jones et al., 1997; Power, 1997; Wilby, 2002; Crain and Bertness, 2006; Wright and Jones, 2006; Chapman et al., 2013).

Here, we investigate how herbivore could influence tree distribution patterns and explore the potential for red colobus monkeys (*Procolobus rufomitratus*) to systematically influence the abundance of *Markhamia lutea* (Bignoniaceae) trees by feeding on the tree's flowers to the extent that the population is not able to regularly set fruit. Struhsaker (1978) documented that red colobus frequently eat all or the majority of the flowers of *M. lutea* and hypothesized that this limited fruit set. He quantified red colobus feeding over 130 months and document that *M. lutea* constituted 8.66% of the overall red colobus diet, with floral buds consumed on 59 occasions, flowers on 34 occasions, and fruit on no occasions (Struhsaker, 2010). To further evaluate this potential we first describe the number of occasions that individual trees monitored over 176 months were able to successfully flower, and did not have their developing flowers eaten by red colobus. Second, we quantified feeding of a single group of red colobus on *M. lutea* flowers over 81 months. Third, we quantify fruit set of individual trees in the area used by a red colobus focal group over almost 15 years. Finally, we describe the recruitment and stand structure of *M. lutea* on permanent plots over 24 years and examine whether the number of trees, their cumulative size, and the number of individuals recruiting into the smaller size classes decline over time.

2. Materials and methods

2.1. Study site

This study was conducted in Kibale National Park, a mid-altitude, moist-evergreen forest in western Uganda (0°13' – 0°41'N and 30°19' – 30°32'E) (Chapman and Lambert, 2000). The area has been protected since it became a forest reserve in 1932, eventually being designated a national park in 1993. During the time it was a forest reserve, several areas of the forest were logged (Chapman et al., 2000; Chapman and Lambert, 2000), but the K-30 area (282 ha) was not commercially harvested, though some stems were removed selectively before 1970 (Struhsaker, 1997). Rainfall is heterogeneous across the park (Stampono et al., 2011), but the area of the study receives an average of 1696 mm annually (1990–2011; Chapman and Chapman unpublished data collected at Makerere University Biological Field Station).

2.2. Flower production

From 1998 to the present, we conducted phenological monitoring of 10 individuals of 36 tree species including *M. lutea*. Here, we compile phenological data from June 1998 to March 2013 ($n = 176$ months). We only monitored trees greater than the smallest DBH known to be capable of reproduction. *M. lutea* is a common edge species and also occurs in the forest in tree fall gaps (Hamilton, 1991). The flowers of *M. lutea* are bright yellow, occur in showy terminal clusters, and each trumpet shaped flower is up to 6 cm long, with 5 frilly lobes (Hamilton, 1991); thus it is very unlikely that the observer missed recording an incident when a tree had mature flowers. The red colobus often eat developing flowers. In these cases we did not score the tree as flowering since flowers never got the chance to develop to the stage where they opened and could receive pollen.

2.3. Consumption

We observed a single social group of red colobus for 88 months (May 2006 to March 2013). From May 2006 to May 2010 we

conducted 30-min scan samples. By June 2010 we had learned to easily recognize individuals and we conducted 15-min scan samples. In total, we collected 52,700 scan samples, which represents approximately 4140 h of observations. During these scans we recorded the individual's identity, age and sex class, behavior (e.g., feeding, traveling, being social [i.e., grooming, playing]), and the species and plant part being consumed if the animal was feeding. Data were collected by CAC and five trained field assistants who have worked with the project for up to 24 years. We conducted an intensive training period to standardize all data collection techniques and minimize interobserver error prior to beginning data collection.

2.4. Fruit set

The presence of fruit was evaluated from June 1998 to March 2013 ($n = 176$ months) using the same 10 *M. lutea* individuals for which flowering was monitored. The fruits of *M. lutea* are 75 cm long, thin, brown capsules, that hang in clusters and split open to release seeds approximately 2.5 cm long with transparent wings (Hamilton, 1991). The conspicuous nature of the *M. lutea* fruit makes it unlikely that any fruiting events were overlooked.

2.5. Stand structure

We used data from permanent plots to test the hypotheses that the number of trees, their cumulative size, and the number of individuals recruiting into the smaller size classes were declining over time. In December 1989 we established 11 permanent tree plots (200 × 10 m; total area = 2.2 ha) in the relatively undisturbed section of the forest. These plots were resurveyed in May 2000, September–November 2006 (Chapman et al., 2010a), and January 2013. In these plots, each tree with a DBH > 10 cm was identified to species-level, marked with an aluminum tag, and measured. When plots were resurveyed, all tagged trees were located again and measured. In addition, all new trees recruiting into the >10 cm DBH size class were located, identified, tagged, and measured. Changes in the distribution of tree size, across years, were tested using an Anderson–Darling k-sample test.

In 1991, we identified and measured the DBH of all plants that were greater than 1.2 m in height and less than 10 cm DBH. This sampling was done in 4 m wide × 200 m long plots that were 2 m from trails and within the larger vegetation plots ($n = 26$ transects). We resampled the same areas using the same methods approximately 20 years later (between July 2011 and Jan 2012). We used paired *t*-tests to compare stems in different size classes up to 6 cm DBH between times (stems greater than 6 cm DBH and <10 cm were rare and thus were not considered). In total, 131 *M. lutea* individuals were identified and measured in 1991 and 95 in 2011. An analysis using only the plots in the old-growth forest reveals the same trends (i.e., significant or not) as the analysis which uses plots in all areas; here we only report results for all areas since the sample is more robust.

3. Results

3.1. Flower production

All of the 10 individual *M. lutea* trees that were monitored over the 176 months produced fruit or flowered at least once, with the exception of the largest tree which did not fruit or flower (88 cm DBH). Thus, ninety percent of the trees flowered over the 176 months. However, mature flowers were only recorded in 10 of the 176 months and in only 1 month did two individuals have

flowers, thus most of the monitored individuals flowered only once in 14.7 years.

3.2. Consumption

The red colobus regularly eat young leaves, flowers, and leaf petioles. In months that the red colobus ate from *M. lutea* trees they spent 1.26% of their feeding time eating from this species. Over a home range that averaged 45 ha (range 23–66 ha; Snaith and Chapman, 2008), they ate leaf and flower buds in 62 of the 80 months that observations were made. *M. lutea* flower consumption represents 30.7% of all flower consumption. They were only observed to eat mature flowers on one occasion. Furthermore, in every month that one of the ten monitored trees had flowers, the red colobus ate the flowers or buds.

3.3. Fruit set

Only on 3 occasions did one of the ten trees that were monitored for 176 months bear ripe fruit. Fruiting occurred in April 2010, April 2011, and August 2011; each event was a different tree. On four occasions trees produced unripe fruit, but these fruit did not develop to ripeness. Assuming that a tree could potentially fruit for 1 month a year, the 10 monitored trees each had at least 14 chances to fruit, for a cumulative of 140 potential events. Observed fruiting was therefore only 2.1% of potential fruiting. Among individual trees, 1 tree did not fruit or flower, 4 trees produced reproductive part on 1 occasion, 2 produced them on 3 occasions, 1 produced them on 4 occasions, and 1 produced them on 5 occasions.

3.4. Stand structure

Both the number of *M. lutea* trees and their cumulative size (DBH) declined over time in the old-growth forest (Fig. 1a and b).

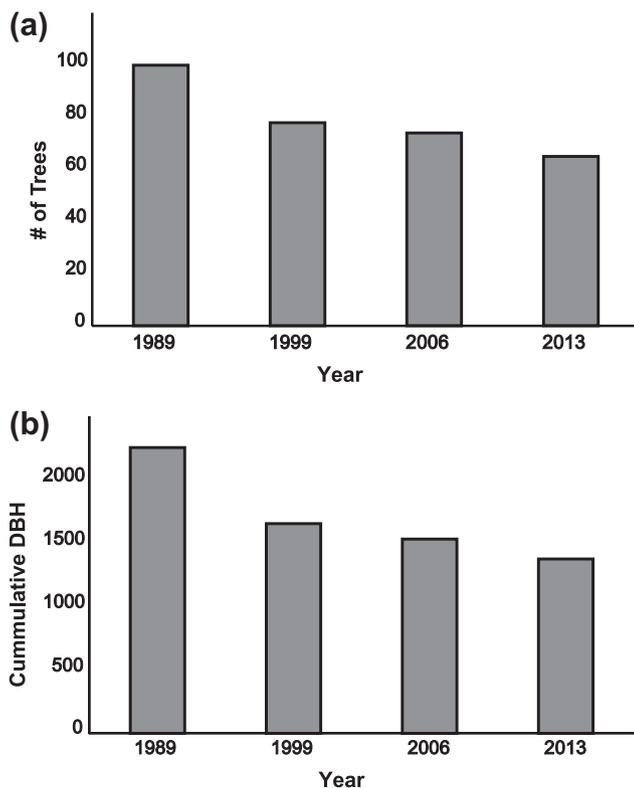


Fig. 1. The number and cumulative DBH (cm) of *Markhamia lutea* trees found in permanent plots during 4 time periods.

An examination of the stand structure in progressively larger 10 cm size bins in the four time periods (1989, 1999, 2006, and 2013), reveals a progressive decline in the number of trees in each size class, with the exception of the 50–59.9 size class where sample sizes were very low (Fig. 2). The distribution of tree sizes was not significantly different over the 24 years (Anderson–Darling k-sample test $P = 0.77$), suggesting an even loss of trees across size classes.

By sampling subplots within the larger vegetation plots for stems from 1 m in height to 10 cm DBH, we were able to locate 131 stems in 1991 and 95 in 2013 in all forestry compartments. The classes (<1 cm DBH, <2 cm DBH... to <6 cm DBH) were fewer in 2011 than in 1991 ($P < 0.001$ in all cases).

4. Discussion

Using data spanning 14 years on *M. lutea* flower and fruit production and spanning 21 years on the abundance of stems in size classes from 1 m tall to the largest trees, we documented that this species is rarely able to produce fruit in Kibale National Park, Uganda, which corresponds with a general decline in this species abundance. Moreover, we show that red colobus feed in these trees and often concentrate their feeding on immature flowers and buds when they are available. Thus, this herbivore is likely playing an important role in structuring the distribution pattern of *M. lutea*. Although we cannot rule out other factors affecting flower production (e.g., temperature or soil chemistry), observation by Struhsaker in the early 1970 came to similar conclusions (Struhsaker, 1978). Furthermore, both Tom Struhsaker and Colin Chapman who together have conducted research in Kibale for over 43 years have frequently seen *M. lutea* trees fruiting and flowering in the farmlands neighboring the national park where red colobus are absent, suggesting that the presence of red colobus in the national park is limiting flower production and thereby tree recruitment.

This raises the intriguing question: How was a large *M. lutea* population able to establish in the National Park to begin with? Over the last few 100 years the forest outside of what is now Kibale National Park was converted from forest to agricultural and grazing lands. With this conversion, the red colobus in the forests being converted likely moved into what is now the national park. This would have resulted in an artificially high population density in

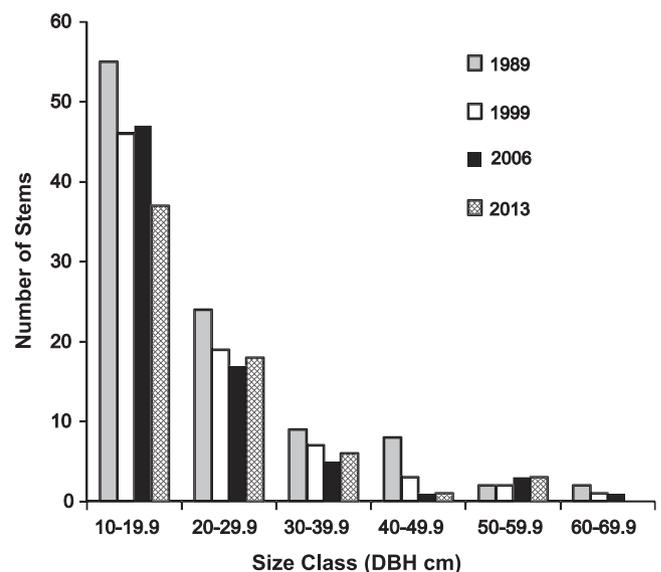


Fig. 2. Number of *Markhamia lutea* trees found in four DBH size classes in Kibale National Park, Uganda at four time periods.

the park and could have led to the overexploitation of *M. lutea*'s floral buds and flowers. However, by the 1950s the majority of the forest that could be cleared was felled (Chapman and Lambert, 2000), so the population within the park has had approximately 60 years to adjust to an appropriate carrying capacity. Census data (groups per km²) and detailed group counts suggest that the red colobus population has been stable since the 1970s (Chapman et al., 2010b; Gogarten et al., Submitted for publication). Population genetic analyses of red colobus also suggest long-term population stability (Allen et al., 2012). Thus, recent demographic expansion of red colobus does not explain current trends of low *M. lutea* fruit set success. Rather, we suggest that changes in red colobus foraging behavior, independent of demographic changes, may be impacting the *M. lutea* population that became established long ago. We have previously documented a gradual change in forest composition in the old-growth area of Kibale (Chapman et al., 2010a). Species that frequently recruit into areas of disturbance (e.g., *Celtis durandii* a favored red colobus food) have a more strongly negative annualized rate of population change than trees recruiting into the understory or canopy gaps, and these species are declining in their average cumulative diameter at breast height, but not as rapidly as *M. lutea* which recruit along edges and canopy gaps (Chapman et al., 2010a). These changes suggest that the forest is currently in a non-equilibrium state. If these changes have led to the decline in the abundance of preferred foods, the red colobus may have shifted to eating foods of lower preference, and one such food could be *M. lutea* flowers.

Other primate species have been described to feed extensively on certain species' flowers and may similarly be impacting their distribution and abundance. For example, spider monkeys (*Ateles geoffroyi*) limit the fruit set of *Symphonia globulifera* by eating its flowers (Riba-Hernandez and Stoner, 2005). For 3 months *S. globulifera* flowers represented between 86% and 100% of a study groups monthly foraging time, resulting in the complete detachment of flowers in 80% of their feeding episodes. In the subsequent fruiting season, none of these trees set fruit. In contrast 70% of trees outside of the home range of the spider monkey group fruited. Similarly, giraffes (*Giraffa camelopardalis*) consumed approximately 85% of *Acacia nigrescens* flowers within the height range they can reach, which significantly reduced flower set (Fleming et al., 2006). While insect florivory has been described in a number of studies (McCall and Irwin, 2006), the impact of mammals has received little attention (but see Marell et al., 2009; Pearson et al., 2012). The mammal examples that do exist and the data presented here suggest that more attention should be placed on understanding the long-term effects of mammalian foraging patterns on the population structure of tropical trees.

The distribution of *M. lutea* trees over its range could be influenced by the abundance of red colobus. The five recognized species of red colobus (Grubb, 1990) have a very patchy distribution and are absent from large areas of equatorial Africa (e.g., Gabon, mainland Equatorial Guinea, and much of Cameroon) (Kingdon, 1971; Struhsaker, 1975; Oates, 1994; Struhsaker, 2010). Similarly, the Uganda red colobus (*Procolobus rufomitratu tephrosceles*) occurs in a few isolated forests along the western side of Tanzania and in Kibale (Struhsaker, 2005). This patchy distribution of an important herbivore offers a means to test the hypothesis that mammalian herbivores can be playing significant roles in structuring forest plant communities.

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