

## CHAPTER 5.

# A 12-YEAR PHENOLOGICAL RECORD OF FRUITING: IMPLICATIONS FOR FRUGIVORE POPULATIONS AND INDICATORS OF CLIMATE CHANGE

COLIN A. CHAPMAN, LAUREN J. CHAPMAN, AMY E. ZANNE,  
JOHN R. POULSEN, AND CONNIE J. CLARK

### Abstract

Answering the fundamental ecological question of what determines animal abundance has become critical with the accelerating need for informed management plans for endangered species. A major difficulty in testing general hypotheses to account for variation in abundance is that periods of food scarcity, which may be responsible for limiting population size, occur on a superannual basis. Research on folivorous primates suggests that periods of food scarcity are critical in determining regional biomass; however, studies of frugivores have found no single fallback food generally used by all species. In this study we quantify fruit availability during a 12-year period in Kibale National Park, Uganda to determine patterns of fruit scarcity. Over these 12 years, temporal variability in fruit availability was high; the proportion of trees per month with ripe fruit varied from 0.14 to 15.93%. In addition, there was dramatic interannual variation in fruit availability: in 1990, on average only 1.09% of trees bore ripe fruit each month, while in 1999 an average of 6.67% of trees bore fruit each month. Over the past 12 years, fruit has become more available, fruit-scarce months have declined in frequency, and the duration of periods of fruit scarcity has decreased. If figs (*Ficus* spp.) served as a fallback food resource over these 12 years, they would have had to be available during months when few trees were fruiting. Over this 149-month period, there were 34 months when less than 1% of monitored trees fruited. Figs were not fruiting in 17 of these months, and, in only 11 of the 34 months were more than 1% of the fig trees fruiting. Rainfall data collected since 1903 indicates that the region is becoming moister, and droughts are less frequent. There has also been a significant increase in the maximum mean monthly temperature and a decrease in the minimum mean monthly temperature since we started recording these data in 1990.

**Key words:** Bottlenecks, conservation, fruit, frugivore, global climate change, keystone species, phenology, Uganda

## INTRODUCTION

A fundamental issue in ecology is determining factors that regulate the density of animal populations. A variety of potential factors have been proposed to influence population size and density, including external factors, such as food resources, weather, predation, and disease and internal conditions, such as territoriality and aggressive behaviors (Nicholson, 1934; Andrewartha & Birch, 1954; Krebs, 1978; Boutin, 1990; Milton, 1996). The importance of understanding determinants of animal abundance has increased with the need to develop informed management plans for endangered or threatened species. With respect to primates, these theoretical issues are critical because tropical forests occupied by primates are undergoing rapid anthropogenic transformation and modification (National Research Council, 1992). Cumulatively, countries with primate populations are losing 125,140 km<sup>2</sup> of forest annually; based on global estimates of primate densities, this results in the loss of 32 million primates per year (Chapman & Peres, 2001). Other populations are being affected by forest degradation (logging and fire) and hunting.

Unfortunately, understanding and predicting factors that determine the primate abundance has proven extremely difficult. A fundamental difficulty in testing general hypotheses to account for variation in primate abundance is that periods of food scarcity, which may be responsible for limiting population size, may occur on a superannual basis. For folivorous primates, evidence suggests that bottleneck periods of food scarcity are critical in determining regional biomass. Milton (1979) and McKey (1978) proposed that year-round availability of digestible mature leaves, which are used by folivorous primates when more preferred foods are unavailable, limits their population size (see Milton et al., 1980, and Milton, 1982, 1998 for a full description of this model). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality (Waterman et al., 1988, Oates et al., 1990; Davies, 1994; Chapman et al., 2002a). By collecting all previously published data on colobine biomass and protein to fiber ratio of mature leaves and combining it with new data from a series of forest fragments, Chapman et al. (submitted) demonstrated that Milton's protein to fiber model accounted for 87% of the variance in folivore biomass.

Unfortunately, for frugivores there is no single fallback food generally used by all species in an area. For example, in Kibale National Park, Uganda, during periods of food scarcity mangabeys (*Lophocebus albigena*) eat foods more resistant to crushing; the smaller redbellied monkeys (*Cercopithecus ascanius*) rely on young leaves and insects (Lambert et al., submitted); and chimpanzees feed on terrestrial vegetation (Wrangham et al., 1993). In general, an accumulation of data on the diets of frugivorous primates over the last three decades has also led to a growing appreciation of dietary variation within species, including differences among populations, among groups in a single population, and within a single group over time (Chapman, 1987; Gautier-Hion, 1988; Chapman & Chapman, 1990; Gautier-Hion et al., 1993; Poulsen et al., 2001; Chapman et al., 2002b). As a result of this

dietary flexibility, long-term studies are needed to evaluate the importance of superannual periods of fruit scarcity to frugivores.

The objective of this study was to quantify fruit availability over a 12-year period in Kibale National Park, Uganda. This provides a means to evaluate the frequency and duration of periods of fruit scarcity, interannual variation in fruit production, the ability to infer fruit patterns from a single year study, and the potential importance of fruit scarcity periods in determining frugivore population dynamics. In addition, we consider if and when figs (*Ficus* spp.) serve as a fallback food resource over the 12 years. Figs have been frequently presented as examples of keystone plant resources in tropical forests (Terborgh, 1986; Power et al. 1996), and recently textbooks have presented figs as a clear case of the keystone species concept (Bush, 2000). The widespread acceptance of figs as keystone species has come in the absence of detailed data demonstrating their importance (Gautier-Hion & Michaloud, 1989; Peres 2000). Finally, we quantify changes in patterns of fruiting (over 12 years) and rainfall and temperature (over the last century) to examine regional patterns of global climate change and consider how such changes might influence phenology patterns.

## METHODS

### *Study sites*

Kibale National Park (766 km<sup>2</sup>) is located in western Uganda (0 13' - 0 41' N and 30 19' - 30 32' E) near the foothills of the Ruwenzori Mountains (Struhsaker, 1975, 1997; Skorupa, 1988; Chapman et al., 1997). The park consists of mature, mid-altitude, moist semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; primarily *Cupressus lusitanica*, *Pinus patula*, *P. caribaea*, and *Eucalyptus* spp.; Chapman & Lambert, 2000). Mean annual rainfall in the region is 1749 mm (1990-2001, or 1547 mm from 1903-2001); the mean daily minimum temperature is 14.87 C°; and the mean daily maximum temperature is 20.18 C° (1990-2001). There are distinct wet and dry seasons that are bimodal in distribution. May to August and December to February tend to be drier than other months (Chapman et al., 1999a).

Kibale forest received the protected status of a National Park in 1993. Prior to this date, it was a Forest Reserve, gazetted in 1932 with the stated goal of providing a sustained production of hardwood timber (Osmaston, 1959). A polycyclic felling cycle of 70 years was initiated, and it was recommended that logging open the canopy by approximately 50% through the harvest of trees over 1.52 m in girth (Kingston, 1967). We have been monitoring the phenology of trees in the Kanyawara area of Kibale, which has three different forestry compartments, since 1990. K-15 is a 360-ha section of forest that experienced heavy selective felling in 1968 and 1969. Total harvest averaged 21 m<sup>3</sup>/ha or approximately 7.4 stems / ha (Skorupa, 1988); however, incidental damage was much higher and it is estimated

that approximately 50% of all trees were destroyed by logging and incidental damage (Skorupa, 1988; Chapman & Chapman, 1997). A total of 18 tree species were harvested, with nine species contributing more than 95% of the harvest volume (Skorupa, 1988). Just to the south, is the K-14 forestry compartment, a 405-ha forest block that experienced low intensity selective felling from May through December 1969 (averaging 14m<sup>3</sup>/ha or 5.1 stems/ha). Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa, 1988; Struhsaker, 1997). K-30 is a 300-ha area that has not been commercially harvested; however, prior to 1970, a few large stems (0.03 - 0.04 trees ha<sup>-1</sup>) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988; Struhsaker, 1997).

### *Phenological Monitoring*

Over 12-years three different phenological monitoring systems were used. Twenty-six 200 m x 10-m transects were established at random locations along the existing trail system at Kanyawara in January 1990 producing a sampling area of 5.2 ha (Chapman et al., 1999b). At both sites, all trees with a diameter at breast height (DBH)  $\geq$  10 cm and within 5 m of the trail were tagged and the DBH recorded. A total of 2096 trees (67 species) were tagged. Phenological data for all trees in these plots were recorded monthly between January 1990 and April 1996. During that time 72% of the trees flowered. The majority of those individuals that did not flower were small individuals and were probably immature. Subsequently, from May 1996 to May 1998 we randomly selected 6 of these 26 plots to continue monitoring. And, 591 trees were monitored each month in an area of 1.2 ha. Finally, since May 1998 (until May 2002 analyzed here) we evaluated phenological patterns using a phenology trail system that monitored 300 individuals from 33 species (average number of individuals / species = 8.8, range = 2-12).

For each monitored tree we determined the presence of different leaf stages (i.e., leaf buds, young leaves, and mature leaves), flowers, and ripe and unripe fruit. Data were collected by Ugandan field assistants, the first and second author, and North American volunteers. Inter-observer precision in evaluating phenological status was repeatedly assessed throughout the study.

We analyzed overall patterns of fruit availability, considering (a) all species that produce fruits and (b) the 10 most abundant species. The 10 most abundant species and their densities are the following: *Uvariopsis congensis* (60.4 tree/ha), *Markhamia platycalyx* (50.0 tree/ha), *Bosqueia phoberos* (50.0 tree/ha), *Celtis durandii* (47.1 tree/ha), *Diospyros abyssinica* (40.0 tree/ha), *Funtumia latifolia* (33.8 tree/ha), *Chaetacme aristata* (17.1 tree/ha), *Strombosia scheffleri* (12.5 tree/ha), *Pancovia turbinata* (10.8 tree/ha), and *Dombeya mukole* (9.2 tree/ha). To consider if and when figs (*Ficus* spp.) could serve as a fallback food resource over the 12 years, we monitored 37 fig trees from January 1990 to April 1996, 12 from May 1996 to May 1998, and 24 since May 1998.

Rainfall data were available between 1903 to 1971 from the Government of Uganda meteorological records for the town of Fort Portal (approximately 20 km east of Kanyawara, supplied by T.T. Struhsaker), between 1972 to 1989 from T.T. Struhsaker (Kanyawara), and from 1990 to present from our data (Kanyawara). Temperature data were available from NASA ([http://www.giss.nasa.gov/cgi-bin/update/name\\_or\\_map.py](http://www.giss.nasa.gov/cgi-bin/update/name_or_map.py)) from 1905 - 1948 for Fort Portal, from 1976 - 1989 from T.T. Struhsaker (Kanyawara), and from 1990 to present from our data (Kanyawara).

Ideally, to evaluate whether fruit scarcity can regulate frugivore populations, only those fruits suitable for a particular frugivore species would be considered. Unfortunately, identifying suitable fruits is extremely difficult. Many fruits eaten during periods of fruit scarcity are likely not preferred by the animals. Thus, fallback foods capable of sustaining a population may not be eaten during typical years, and their importance can only be determined through long-term observations (Chapman et al., 2002c). As a result of these difficulties, we report the fruiting patterns of all species, whether frugivores are known to eat them or not. We consider all types of fruits, since even wind-dispersed fruits are often consumed by frugivores. In Kibale approximately 80% of the tree species produce fleshy fruits that are eaten and presumably dispersed by frugivores (Chapman et al., unpublished data).

When there are appreciable differences in mean values, variation can be evaluated using the coefficient of variation (CV; Sokal & Rohlf, 1981). We use the CV to evaluate interannual variation in monthly fruit production. The CV was calculated as the standard deviation of the proportion of monitored trees bearing ripe fruit each month divided by the mean.

## RESULTS

### *Phenology*

On average, 3.97% of monitored trees bore ripe fruit each month. However, temporal variability in fruit availability was high; the proportion of trees with ripe fruit varied from 0.14 to 15.93% per month (Fig. 1). Interannual variation in fruit availability was also high (Table 1). In 1990, an average of 1.09% of trees bore ripe fruit each month; while in 1999, an average of 6.67% trees bore fruit each month. If a month of fruit scarcity is considered as one with less than 1% of monitored trees bearing ripe fruit, there is considerable interannual variation in how often frugivores experienced food shortages (Table 1). For example, 9 of the 12 months in 1990 had <1% of the trees with fruit; while in 2000, no month had less than 1% of trees fruiting.

*Table 1. Interannual variation in fruit production (proportion of trees monitored each month bearing ripe fruit) in Kibale National Park, Uganda. #<1% and #<2% are the number of months in a year where there are less than 1% and 2% of the trees monitored with ripe fruit. Months with the lowest (Lowest) and highest (Highest) proportion of trees with ripe fruit are also presented.*

Year	Mean	CV	#<1	#<2	Lowest	Highest
1990	1.17	1.49	9	10	1.14	6.11
1991	1.09	1.16	9	11	0.29	4.87
1992	2.06	1.03	6	9	0.44	6.62
1993	2.35	0.89	4	7	0.54	6.3
1994	4.35	0.82	0	4	1.17	10.55
1995	3.93	0.65	1	3	0.98	8.92
1996	4.49	0.91	0	2	1.1	15.93
1997	5.13	0.7	1	3	0.18	11.36
1998	2.22	0.73	4	5	0.37	5.5
1999	6.67	0.48	0	1	1.4	12.28
2000	6.14	0.51	0	1	1.17	13.06
2001	5.93	0.33	0	0	3.47	9.34

Fig. 1 suggests that in general fruit has become more available to the frugivores of Kibale over the past 12+ years; year and the proportion of trees that with ripe fruit are positively correlated ( $r=0.557$ ,  $P<0.001$ ). This relationship holds for two of the three phenological methods (Jan 1990 to April 1996:  $r=0.506$ ,  $P<0.001$ , May 1996 to May 1998:  $r=-0.133$ ,  $P=0.526$ , June 1998 to May 2002:  $r=0.398$ ,  $P=0.005$ ). There was also a decline in the number of fruit scarce months each year over the 12 years ( $r=-0.820$ ,  $P<0.001$ ).

Consistency in fruit production may be important for frugivore populations since a less variable fruiting schedule would have fewer periods of fruit scarcity and fewer periods of superabundance of fruit that cannot be utilized. Over the 12 years, there is a consistent decline in the annual coefficient of variability (Table 1;  $r=-0.921$ ,  $P<0.001$ ).

There was no difference in the proportion of fruiting trees ( $t=0.192$ ,  $P=0.848$ ) or the proportion of figs with ripe fruit ( $t=0.418$ ,  $P=0.677$ ) between wet and dry season months.

Frugivores, particularly the larger ones, may be able to cope with short periods of food scarcity by using stores or by losing weight. Thus, it may be long periods of fruit scarcity that are critical. There were 13 periods of fruit scarcity (<1% of monitored trees bearing ripe fruit) over the 12 years. The average period of fruit scarcity was 2.4 months, but fruit-scarce periods lasted as long as 9 months. If we define a fruit scarce month as one in which less than 2% of the trees bore ripe fruit, then there were 17 periods of fruit scarcity that had an average duration of 3.4 months, and the longest period was 16 months. Using either criteria the average

duration of the longest period of fruit scarcity in a year decreased over the 12 years (1%  $r = -0.820$ ,  $P < 0.001$ , 2%  $r = -0.920$ ,  $P < 0.001$ ).

It seems reasonable to speculate that certain fruiting tree species may be particularly important to specific frugivores. For example, with the fruiting of an abundant species with nutritious fruits, females may build up reserves necessary for reproduction, possibly synchronizing births among females (Lee 1987, Butynski 1988). To have a robust sample to consider fruiting patterns, we consider the 10 most abundant species. These species show a diversity of fruiting patterns over the 12 years (Fig. 2a,b). *Uvariopsis congensis* exhibited a fairly regular pattern of fruiting, where approximately 60% of the entire community fruited synchronously typically in June or July (although over 50% of the population did fruit in December 1991). Despite this synchronized pattern, there were often a number of years between fruiting events. For example, *U. congensis* fruited in June 1996, but did not fruit again until July 2000. While *Celtis durandii* had very poor fruiting seasons in 1990 and 1991, subsequently greater than 30% of the trees fruited each year, typically in the October to December period, although it did not fruit in the fall of 2000. A significant proportion of the *Strombosia scheffleri* population only fruited once during the entire 12 years. *Funtumia latifolia*, *Chaetacme aristata*, and *Dombeya mukole* had irregular fruiting patterns; however, they all seemed fruit poorly in the first 3 years of the study. *Diospyros abyssinica* similarly had an irregular fruiting pattern, and never more than 12% of the population fruited in a given month. As a group, *Ficus* spp. had an irregular fruiting schedule (the sample size was not adequate to evaluate each species separately). Less than 4% of the population of *Markhamia platycalyx*, *Bosqueia phoberos*, and *Pancovia turbinata* fruited in any year. While there were many trees of these species monitored, only a few ever fruited, and these fruiting events tended to be in the first few years of the study.

### *Figs as Fallback Foods*

On average the density of figs trees bearing fruits was 0.29 trees/ha each month. In Kibale, redtail monkeys have a home range of 24 ha, while blue monkeys and mangabeys have home ranges of 50 ha and 410 ha, respectively (Cords, 1987; Melnick & Pearl, 1987). If figs (*Ficus* spp.) served as a fallback food resource over these 12 years, they would have had to be available during months when few trees were fruiting. Over this 149-month period, there were 34 months when less than 1% of the monitored trees fruited. The average density of fruiting fig trees during these months was 0.21/ha. Thus, redtails would have had on average five fruiting trees available, and blue monkeys would have 10 fruiting fig trees in their home range. However, fallback foods should always be available when the preferred resource is lacking, so it may not be appropriate to consider the average. In the 34 months when fruit was scarce, figs were not fruiting in 17 of these months, and in only 11 of the 34 months were more than 1 % of the fig trees fruiting.

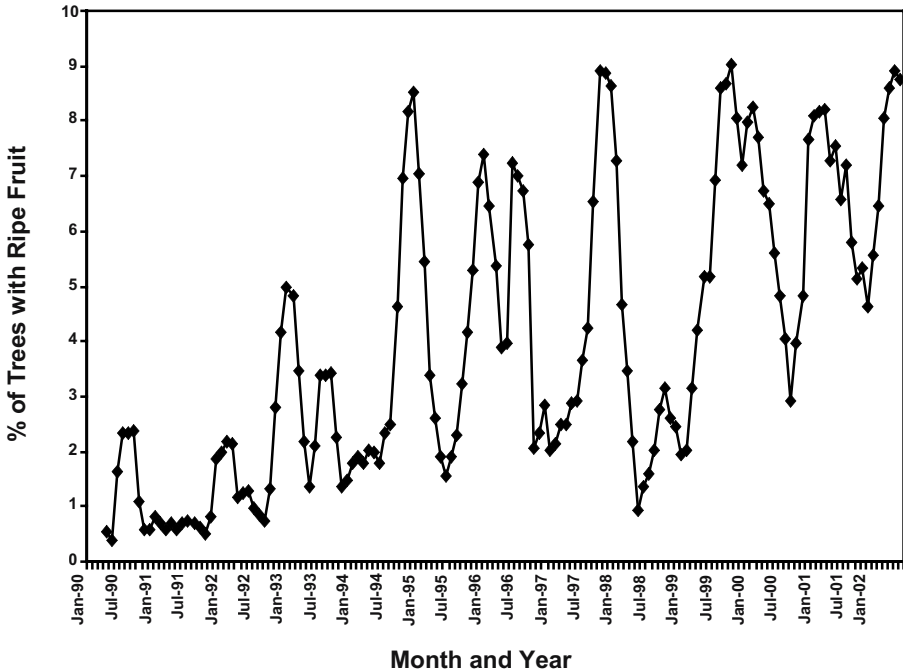


Figure 1. The 4-month running average of the percentage of trees bearing ripe fruit in Kibale National Park, Uganda over a 12-year period.

### Climate Change

Rainfall data collected since 1903 indicates that the region is becoming moister (Fig. 3); year and annual rainfall are positively correlated ( $r=0.415$ ,  $P<0.001$ ; see also Struhsaker, 1997). If a drought year is considered one with less than 1300 mm of rain a year, then there has also been a decline in the number of drought years per decade over the last century ( $r_{sp}=0.850$ ,  $P=0.002$ ). There has also been an increase in the maximum mean monthly temperature since we started recording it in 1990 at the field station at Kanyawara ( $r=0.767$ ,  $P<0.001$ ; Fig. 4). This trend is supported by data collected since 1975 by T.T. Struhsaker and ourselves ( $r=0.767$ ,  $P<0.001$ ; Fig. 5). In contrast, the average monthly minimum temperature has decreased over that same period ( $r=-0.652$ ,  $P<0.001$ ; 1990 to 2002  $r=-0.784$ ,  $P=0.003$ ; Fig. 5). Examining temperature data available from 1905 to the present (the average of the minimum and maximum daily temperatures) suggests an increase in temperature; however, the trend was not significant ( $r=0.161$ ,  $P=0.204$ ; Fig. 6). This analysis averaged maximum and minimum temperatures, and if these parameters are changing in opposite directions as is indicated in Fig. 5, it is not surprising that this relationship is not significant. Fig. 6 does, however, suggest that there may be some long-term cycles in temperature.



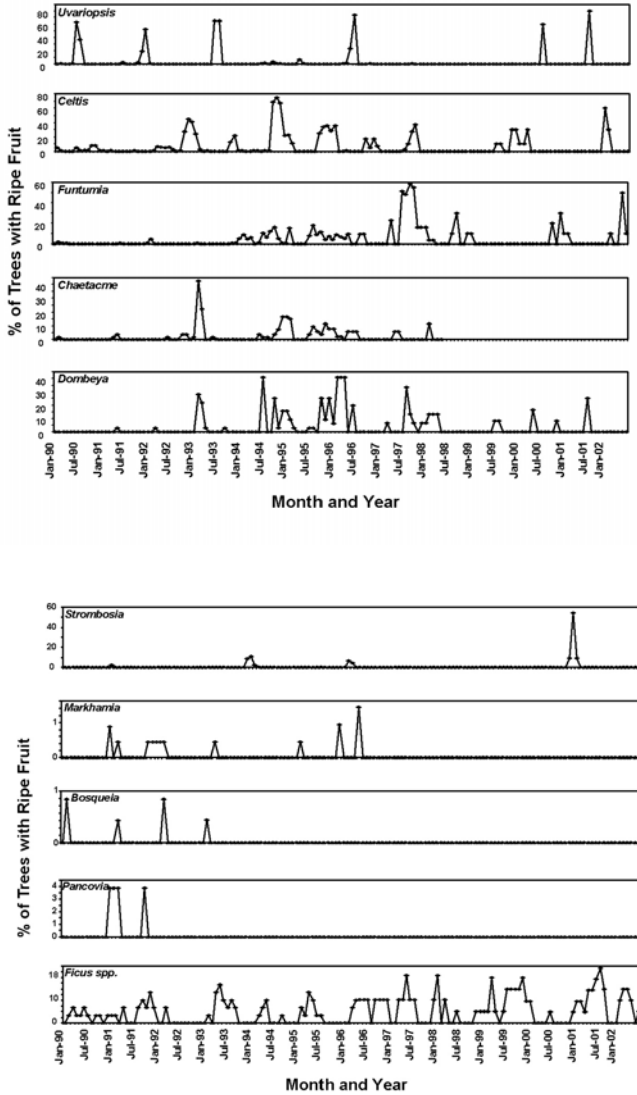


Figure 2a,b. The percentage of trees bearing ripe fruit for the 10 most common species in Kibale National Park, Uganda over a 12-year period (Uvariopsis congensis 60.4 tree/ha, Markhamia platycalyx 50.0 tree/ha, Bosqueia phoberos 50.0 tree/ha, Celtis durandii 47.1 tree/ha, Diospyros abyssinica 40.0 tree/ha, Funtumia latifolia 33.8 tree/ha, Chaetacme aristata 17.1 tree/ha, Strombosia scheffleri 12.5 tree/ha, Pancovia turbinata 10.8 tree/ha, and Dombeya mukole 9.2 tree/ha).

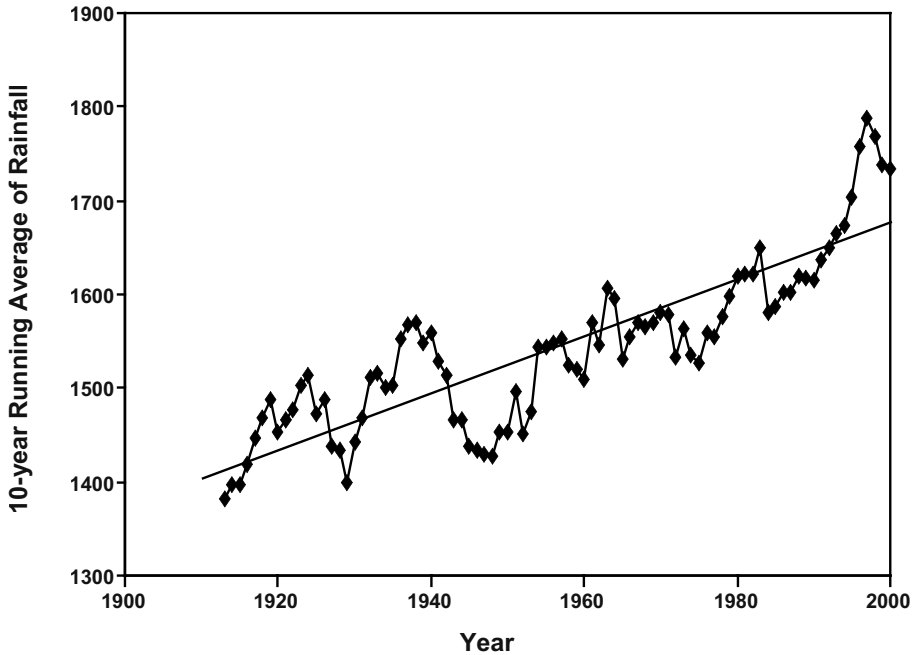


Figure 3. The 10-year running average of the annual rainfall in the area of Kibale National Park, Uganda.

### Phenology

We quantified patterns of fruit availability over a 12-year period in Kibale National Park, Uganda to begin to understand the potential importance of periods of fruit scarcity in determining frugivore population dynamics. Over the 12 years there was a great deal of temporal variability in fruit availability. In addition, the frequency and duration of periods of fruit scarcity varied dramatically over the years. The nature of this variability has a number of implications for our understanding of frugivore population dynamics. First, the variability indicates conclusions from studies that are less than 3 or 4 years should be made with caution. This applies issues, such as competition, dietary adaptations, territoriality, and population regulation. For example in a 45-month study of red colobus (*Procolobus badius*) Chapman et al. (2002c) found consistent increased use of particular plant parts.

### DISCUSSION

Second, over this 12-year period, there were 13 periods (34 months) when less than 1% of monitored trees fruited. The average period of fruit scarcity was 2.4 months, but fruit scarce periods lasted as long as 9 months. These data suggest that the

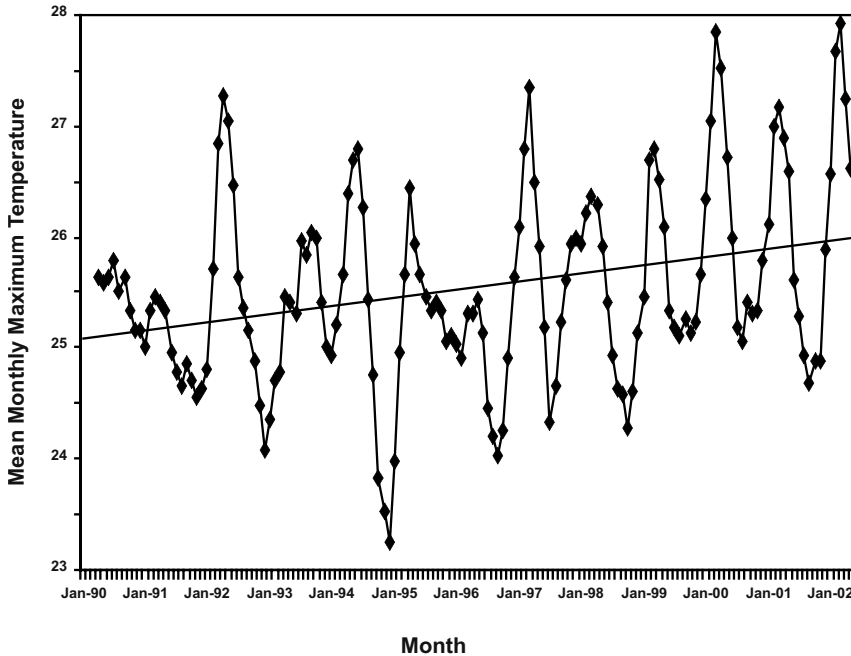


Figure 4. The 4-month running average of the monthly mean maximum temperature ( $^{\circ}\text{C}$ ), measured at Kibale National Park, Uganda.

availability of fruit greatly exceed the consumptive capacity of the frugivores of Kibale during periods of abundance, but these periods alternate with times of scarcity when frugivores are obliged to feed on alternative resources, likely of inferior quality. Given the frequency and duration of these periods of fruit scarcity, it is quite possible that they have an important regulatory function on primate densities.

#### *Figs as Fallback Foods*

Terborgh (1986) suggested that palm nuts, figs, and nectar play an important role in the nutrition of frugivorous vertebrates during periods of fruit scarcity in one Neotropical forest. This suggestion was based on the low interannual variation in fig production, irregular timing of their fruiting period, and the high rate of fig consumption by frugivorous animals. The perception that figs constitute an important fruit resource for many frugivorous species is supported by a number of studies from different geographical regions (Janzen, 1979; Foster, 1982; Milton et al., 1982; Leighton & Leighton, 1983; Lambert & Marshall, 1991; O'Brien et al., 1998; Goodman et al., 1997; Kannan & James; 1999). Many frugivores consume

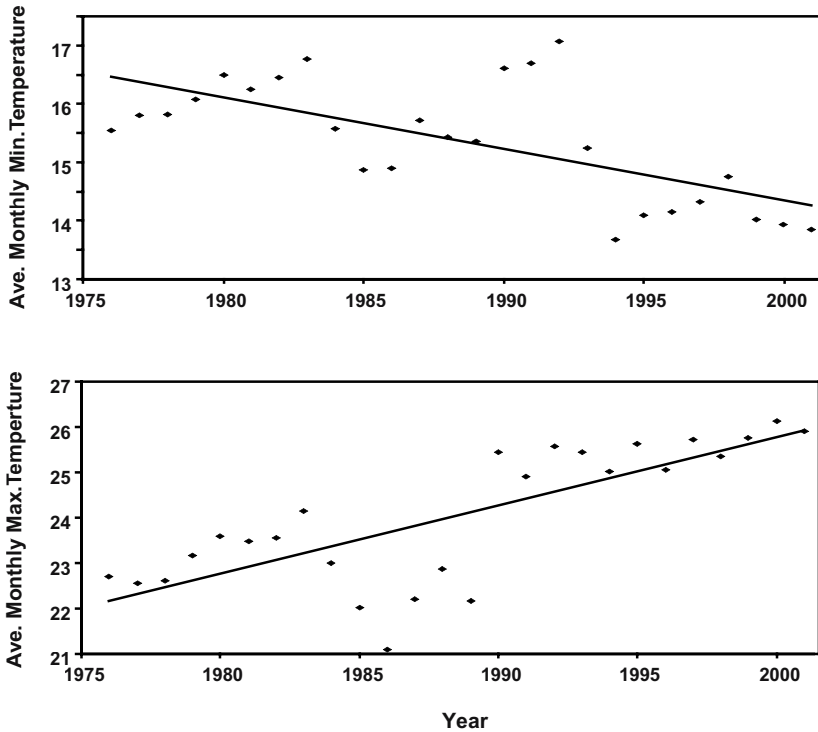


Figure 5. The average monthly (a) minimum and (b) maximum temperature ( $^{\circ}\text{C}$ ) measured at Kibale National Park, Uganda.

figs in Kibale (Conklin & Wrangham, 1994). However, for figs to act as a fallback food for frugivores they must consistently produce abundant fruit during fruit scarce times. In this study, no figs fruited in the area we monitored in 17 out of 34 fruit-scarce months, suggesting that figs do not consistently fruit during fruit-scarce times. Thus, figs may provide fruit resources during some fruit-scarce months, but the number of trees is probably not adequate nor the fruiting phenology consistent enough to sustain all frugivore populations, particularly territorial species with relatively small home ranges. It seems likely that the role of figs as a fallback food is scale dependent. Borges (1993) studied the giant squirrel (*Ratufa indica*), a solitary, territorial species, and found figs were important only to those individuals who had access to figs in their territories. This is likely the case for the frugivorous primates of Kibale. During periods of fruit scarcity, figs can best be exploited by mobile species with large home ranges and the ability to track fruiting figs. For species with small feeding ranges, like redtail monkeys, figs are unlikely to be important resources for all groups during periods of fruit scarcity.

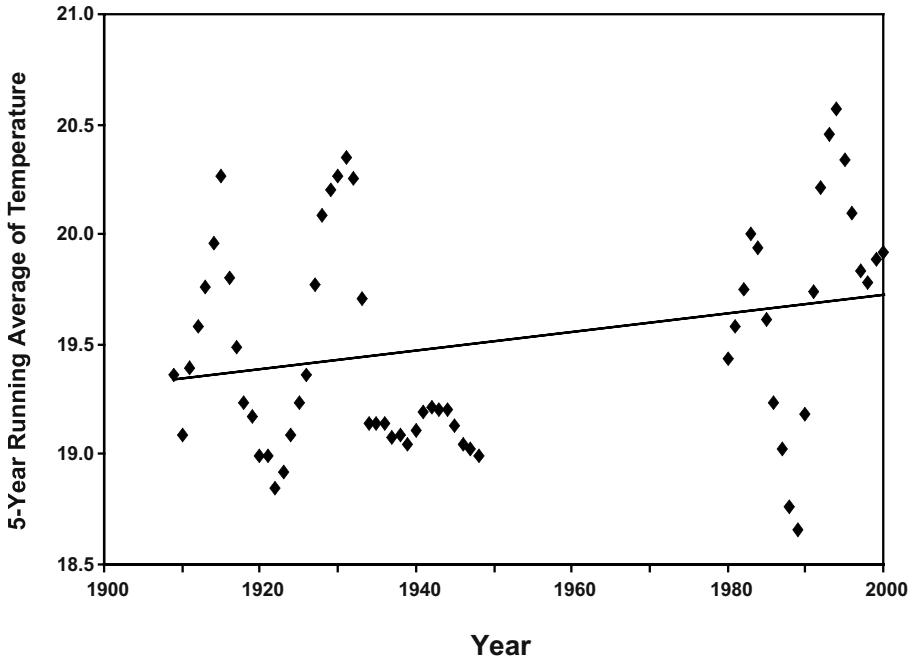


Figure 6. The average of the minimum and maximum daily temperatures ( $^{\circ}\text{C}$ ) recorded at Fort Portal (1905-1948) and Kibale National Park, Uganda (Kanyawara 1976-2001).

Similarly, Gautier-Hion & Michaloud's (1989) study in Gabon showed that figs were infrequently eaten by most species, occurred at very low densities, and had unpredictable fruiting patterns. They concluded that fig fruits were not staple foods and could not sustain most populations of frugivorous species during periods of low fruit availability. At least for African frugivores, there may not be a single resource on which frugivore populations rely. Gautier-Hion & Michaloud (1989) determined that monkeys and large birds in Gabon depend on the fruit of two species of Myristicaceae and one species of Annonaceae. Other studies from central Africa have demonstrated that large birds may migrate to track fruit resources during fruit scarce times, whereas frugivorous monkeys shift their diets to seeds, leaves, and insects (Poulsen et al., 2002).

### *Climate Change*

Rainfall data collected since 1903 indicate that the region is becoming moister, and droughts are less frequent. There has also been an increase in maximum mean monthly temperature and a decrease in minimum mean monthly temperature since we started recording these data in 1990. The higher temperatures and increased rainfall recorded over 12 years at Kibale may be indicative of larger global patterns. The earth's climate has warmed by approximately  $0.6^{\circ}\text{C}$  over the past 100 years

with two main periods of warming (1910 – 1945 and 1976 – present), and the 1990's is the warmest decade on record (Walther et al., 2002). Of course, ecological communities do not respond to global averages. Rather, regional changes, which are highly spatially heterogeneous, are more relevant in the context of ecological response to climatic change. The climate change documented from the Kibale region, suggests that regional changes can be much larger than the global average.

Over the past 12 years, we documented that fruit has become more available, fruit scarce months have declined in frequency, and the duration of periods of fruit scarcity has decreased. These changes correspond to local changes in climate. There is a growing body of literature that suggests that recent climatic changes have differentially affected a broad range of organisms with diverse geographical distributions (Hughes, 2000; Wuethrich, 2000; Ottersen, 2001). For example, the average first flowering date of 385 British plant species has advanced by 4.5 days over the past decade compared to the previous four decades (Fitter & Fitter, 2002). In Borneo a severe drought linked to the El Nino-Southern Oscillation event of 1997-1998, caused a substantial break in the production of inflorescences on dioecious figs, and led to the local extinction of the wasp pollinators at Lambir Hills National Park (Harrison, 2000). Changes in phenology and fruit production of trees will likely have a cascading effect on frugivorous animals and pollinating insects that are directly dependent on plant resources.

Three species, *Markhamia platycalyx*, *Bosqueia phoberos* and *Pancovia turbinata*, all fruited in the first few years of our study; however, only a small proportion of each populations fruited. These are all common species, and one would expect a greater proportion of the population to fruit. It is possible that the climatic conditions found in the early half of the century were more favorable for these species (see Struhsaker (1978) for an alternative explanation for *Markhamia platycalyx*). At our Dura River site in Kibale which is approximately 12 km south of Kanyawara and has less rainfall (1500 mm), a large proportion of the *Bosqueia phoberos* population has repeatedly fruited in recent years (Chapman et al. 2002a, Chapman unpublished data).

### *Conservation Implications*

Unfortunately, it is relatively rare that long-term data are available from tropical forest systems. Given this and the fact that tropical forest systems are being rapidly transformed, it seems useful to speculate on the conservation implications of our findings. First, we documented that fruit production is highly variable among years, periods of fruit scarcity occur on a superannual basis and the frequency and duration of fruit-scarce periods are such that they may limit the size of frugivore populations. Thus, a study in any single year will unlikely provide the needed insights to understand relationships between frugivore numbers and fruit availability.

Second, since figs tend to occur at a low density, the importance of figs during periods of fruit scarcity will likely be limited to frugivores that have access to figs in their territories or feeding ranges. During periods of fruit scarcity, figs can best be exploited by mobile species with large home ranges and the ability to track fruiting

figs. For species with small feeding ranges, like redbellied monkeys, figs are unlikely to be important resources for all groups during periods of fruit scarcity. Thus, suggestions to manage fig abundance in areas should be viewed with extreme caution, since the management strategy will only affect a small subset of the frugivore community. Also, evidence from elsewhere in Africa suggests that there may not be a single resource on which frugivore populations rely, rather the important fallback resources may vary among areas (Gautier-Hion & Michaloud, 1989; Poulsen et al., 2002).

Finally, our data build on the findings of Struhsaker (1997) and indicate that the climate of the Kibale region is changing. Whether this represents consistent long-term changes associated with global warming, or shorter-term fluctuations is not known. Regardless, the plant phenological patterns and the animals dependent on these plants are experiencing changes. Responses to this climate change are likely complex and vary among species. In general, fruit production in the Kibale region is increasing, but for certain species the current conditions appear unsuitable for flowering or fruiting. Thus, we may see the local loss of those species.

#### ACKNOWLEDGMENTS

Funding for this research was provided by grants to CC, LC, and Richard Wrangham (Wildlife Conservation Society CC,LC), the National Science Foundation ((CC) grant number SBR-9617664, SBR-990899), USAID internal support grants (CC, LC, RW), a PSTC USAID grant (RW,CC), and the National Geographic Society (CC)). Permission to conduct this research was given by the Office of the President, Uganda, the National Council for Science and Technology, the Uganda Wildlife Authority, and the Ugandan Forest Department. Funding to Richard Wrangham assisted in the initial establishment of the phenology transects and his initial contribution to designing this monitoring was critical. We would like to give special thanks to Tom Struhsaker for being so generous with his long-term data in this instance and in many others: the value of Kibale as a research site is greatly increased by his generosity. Tom Gillespie and Tom Struhsaker provided helpful comments on the project.

## REFERENCES

- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Borges, R. M. 1993. Figs, Malabar giant squirrels, and fruit shortages within two tropical Indian forests. *Biotropica* 25, 183-190.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Canadian Journal of Zoology* 68, 203-220.
- Bush, M. B. 2000. *Ecology of a changing planet*. Prentice Hall, Upper Saddle River, New Jersey.
- Butynski, T. M. 1988. Guenon birth seasons and correlates with rainfall and food. In A. Gautier-Hion, F. Bourliere, J-P. Gautier, and J. Kingdon (Eds.). *A primate radiation: evolutionary biology of African guenons*, pp. 284-322. Cambridge University Press, Cambridge, England.
- Chapman, C. A. 1987. Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica* 49, 90-105.
- Chapman, C. A. and Chapman, L.J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29, 396-412.
- Chapman, C. A. and Chapman, L. J. 1990. Dietary variability in primate populations. *Primates* 31, 121-128.
- Chapman, C. A., Chapman, L.J., Bjornndal, K. A., and Onderdonk, D.A. 2002a. Application of protein to fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology* 23, 283-310.
- Chapman, C. A., Chapman, L. J., Cords, M., Gauthua, M., Gautier-Hion, A., Lambert, J. E., Rode, K. D., Tutin, C. E. G., and White, L. J. T. 2002b. Variation in the diets of *Cercopithecus* Species: Differences within forests, among forests, and across species. In M. Glenn and M. Cords (Eds.). *The guenons: Diversity and adaptation in African monkeys*, pp. 319-344. Plenum Press, New York, New York.
- Chapman, C. A., Chapman, L.J., and Gillespie, T. R. 2002c. Scale issues in the study of primate foraging: Red colobus of Kibale National Park. *American Journal of Physical Anthropology* 117, 349-363.
- Chapman, C. A., Chapman, L.J., Wrangham, R., Isabirye-Basuta, G., and Ben-David, K. 1997. Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology* 35, 287-302.
- Chapman, C. A., Chapman, L.J., Naughton-Treves, L., Lawes, M. J., and McDowell, L. R.. Predicting folivorous primate abundance: Validation of a nutrition model. *Conservation Biology* (Submitted).
- Chapman C. A. and Lambert, J. E. 2000. Habitat alteration and the conservation of African primates: A case study of Kibale National Park, Uganda. *American Journal of Primatology* 50, 169-186.
- Chapman, C. A. and Peres, C. 2001. Primate conservation in the new millennium: The role of scientists. *Evolutionary Anthropology* 10, 16-33.
- Chapman, L. J., Chapman, C. A., Brazeau, D., McGlaughlin, B., Jordan, M. 1999a. Papyrus swamps and faunal diversification: Geographical variation among populations of the African cyprinid *Barbus neumayeri*. *Journal of Fish Biology* 54, 310-327.
- Chapman C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., and Zanne, A. E. 1999b. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* 15, 189-211.
- Conklin, N. L. and Wrangham. R. W. 1994. The value of figs to hind-gut fermenting frugivores - A nutritional analysis. *Biochemical Systematic Ecology* 22, 137-151.
- Cords, M. 1987. Forest guenons and patas monkeys: Male-male competition in one male group. In D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker (Eds.). *Primate societies*, pp. 98-111. University of Chicago Press, Chicago, Illinois.
- Davies A. G. 1994. Colobine populations. In A. G. Davies and J. F. Oates (Eds.). *Colobine monkeys: Their ecology, behaviour and evolution*, pp. 285-310. Cambridge University Press, Cambridge, England.
- Fitter, A. H. and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. *Science* 296, 1689-1692.



- Foster, R. B. 1982. The seasonal rhythm of fruit fall on Barro Colorado Island. In E. G. Leigh, A. S. Rand Jr, and D. M. Windsor (Eds.). *Ecology of a tropical forest*, pp 151-172. Smithsonian Institution Press, Washington, DC.
- Gautier-Hion, A. 1988. The diet and dietary habits of forest guenons. In A. Gautier-Hion, F. Bourliere, and J-P. Gautier (Eds.). *A primate radiation: Evolutionary biology of the African guenons*, pp. 257-283. Cambridge University Press, Cambridge, England.
- Gautier-Hion, A., Gautier, J-P. and Maisels, F. 1993. Seed dispersal versus seed predation: An inter-site comparison of two related African monkeys. *Vegetatio* 107/108, 237-244.
- Gautier-Hion, A. and Michaloud, G. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70, 1826-1833.
- Goodman, S. M., Ganzhorn, J. U., and Wilme, L. 1997. Observations at a *Ficus* tree in a Malagasy humid forest. *Biotropica* 29, 480-488.
- Harrison, R. D. 2000. Repercussions of El Nino: Drought causes extinction and the breakdown of mutualisms in Borneo. *Proceedings of the Royal Society of London B. Biological Sciences* 267, 911-915.
- Hughes, L. 2000. Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution* 15, 56-61.
- Janzen, D. H. 1979. How to be a fig. *Annual Review of Ecology and Systematics* 10, 13-51.
- Kannan, R. and James, D. A. 1999. Fruiting phenology and the conservation of the Great Pied Hornbill (*Bucerus bicornis*) in the Western Ghats of southern India. *Biotropica* 31, 167-177.
- Kingston B. 1967. Working plan for Kibale and Itwara Central Forest Reserves. Uganda Forest Department, Entebbe, Uganda.
- Krebs, C. J. 1978. A review of the Chitty hypothesis of population regulation. *Canadian Journal of Zoology* 56, 2463-2480.
- Lambert, F. R. and Marshall, A. G. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *Journal of Ecology* 79, 793-809.
- Lambert, J. E., Chapman, C. A., Wrangham, R. W., Conklin-Brittain, N. L. The hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology* (Submitted).
- Lee, P. C. 1987. Nutrition, fertility and maternal investment in primates. *Journal of Zoology (London)* 213, 409-422.
- Leighton, M. and Leighton, D. R. 1983. Vertebrate response to fruiting seasonality within a Bornean rain forest. In S. L. Sutton, T. C. Whitmore, and A. L. Chadwick (Eds). *Tropical rain forest ecology and management* (pp. 584-596). Blackwell, Oxford.
- McKey, D. B. 1978. Soils, vegetation, and seed-eating by black colobus monkeys. In G. G. Montgomery (Ed.). *The ecology of arboreal folivores* (pp. 423-437). Smithsonian Institution Press, Washington, DC.
- Melnick, D. J. and Pearl, M. C. 1987. Cercopithecines in multimale groups: Genetic diversity and population structure. In D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker (Eds.). *Primate societies* (pp. 121-134). University of Chicago Press, Chicago.
- Milton, K. 1979. Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *American Naturalist* 114, 363-378.
- Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest* (pp. 273-289). Smithsonian Institution Press, Washington, DC.
- Milton, K. 1996. Effects of bot fly (*Alouattomyia baeri*) parasitism on a free-ranging howler (*Alouatta palliata*) population in Panama. *Journal of Zoology (London)* 239, 39-63.
- Milton, K. 1998. Physiological ecology of howlers (*Alouatta*): Energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology* 19, 513-547.
- Milton, K., van Soest, P. J., and Robertson, J. B. 1980. Digestive efficiencies of wild howler monkeys. *Physiological Zoology* 53, 402-409.
- Milton, D., D. M. Windsor, D. W. Morrison, and M. Estribi. 1982. Fruiting phonologies of two Neotropical *Ficus* species. *Ecology* 62: 752-762.
- National Research Council. 1992. *Conserving biodiversity: A research agenda for development agencies*. National Academy Press, Washington, D.C.
- Nicholson, A. J., 1933. The balance of animal populations. *Journal of Animal Ecology* 2, 132-178.

- Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P.G., Green, S. M., Dasilva, G. L., and Mole, S. 1990. Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology* 71, 328-343.
- O'Brien, T. G., Kinnaird, M. F., Darenfeld, N. L., Conklin-Brittain, R. W., and Silver, S. C. 1998. What's so special about figs? *Nature* 392, 668.
- Osmaston, H.A. 1959. *Working plan for the Kibale and Itwara Forests*. Uganda Forest Department, Entebbe.
- Ottersen, G. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* 128, 1-14.
- Peres, C. A. 2000. Identifying keystone plant resources in tropical forests: The case of gums from *Parkia* pods. *Journal of Tropical Ecology* 16, 1-31.
- Poulsen, J. R., Clark, C. J., and Smith, T. B. 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology* 54, 91-105.
- Poulsen, J. R., Clark, C. J., Connor, E. F., and Smith, T. B. 2002. Differential resource use by hornbills and primates: implications for seed dispersal. *Ecology* 83, 228-240.
- Power, M. E., Tilman, D., Esters, J. A., Menges, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., and Paine, R. T. 1996. Challenges in the quest of keystone. *Bioscience* 46, 609-620.
- Skorupa J. P. 1988. *The effect of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda*. Ph.D. Dissertation, University of California, Davis, California.
- Sokal R. R. and Rohlf. F. J. 1981. *Biometry*. Freeman, San Francisco, California.
- Struhsaker, T. T. 1975. *The red colobus monkey*. University of Chicago Press, Chicago, Illinois.
- Struhsaker, T. T. 1978. Interrelations of red colobus monkeys and rain-forest trees in the Kibale Forest, Uganda. In G.G. Montgomery (Ed.). *The ecology of arboreal folivores*. (pp. 397-422). Smithsonian Institution Press, Washington, DC.
- Struhsaker, T. T. 1997. *Ecology of an African rain forest: Logging in Kibale and the conflict between conservation and exploitation*. The University Press of Florida, Gainesville, Florida.
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. In M.E. Soule (Ed.). *Conservation biology: The science of scarcity and diversity* (pp. 330-344). Sinauer, Sunderland.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416, 389-395.
- Waterman, P.G., Ross, J.A.M., Bennett, E. L., and Davies, A. G. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biological Journal of the Linnean Society* 34, 1-32.
- Wrangham, R. W., Roders, M. E., and Basuta, G. I. 1993. Ape food density in the ground layer in Kibale Forest, Uganda. *African Journal of Ecology* 31, 49-57.
- Wuehrlich, B. 2000. How climate change alters rhythms of the wild. *Science* 287, 793-795.

Department of Zoology, University of Florida, Gainesville, Florida, USA; Wildlife Conservation Society, Bronx, New York, USA.