

Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest

LISA NAUGHTON-TREVES*, ADRIAN TREVES†, COLIN CHAPMAN‡
and RICHARD WRANGHAM§

*Department of Geography, 550 N. Park Street, University of Wisconsin, Madison, WI 53706–1491, USA;

†Department of Psychology, University of Wisconsin, Madison, WI 53706, USA; ‡Department of Zoology,

University of Florida, Gainesville, FL 32611, USA; and §Department of Anthropology, Harvard University,

Cambridge, MA 02138, USA

Summary

1. Primates dominate lists of pests that damage crops around African parks and reserves. Beyond creating management problems, crop foraging is integral to the ecology of primates inhabiting forest–agriculture ecotones.

2. Twenty-three months of data from four villages around Kibale National Park, Uganda, revealed that redbtail monkeys *Cercopithecus ascanius*, olive baboons *Papio cynocephalus* and chimpanzees *Pan troglodytes* selected different crops or plant parts. Baboons took root and tuber crops ignored by other primates, and fed on the greatest variety of crops. All three species preferred maize and/or bananas. Redtails ate only banana fruit, baboons ate banana fruit more frequently than pith, and chimpanzees raided pith and fruit in equal proportions.

3. Each primate showed a distinct monthly pattern of crop foraging, significantly non-random for baboons and redbtail monkeys, weakly for chimpanzees. Large inter-monthly variation was observed for all three primates, but was least pronounced in redbtails.

4. Raiding frequency on maize peaked approximately 8 weeks after the onset of rains and was strongly correlated between the three primate species. Abundant forest fruit did not diminish primate appetite for maize.

5. Raiding frequency on bananas varied considerably despite continuous availability of fruit and pith. Peaks in banana consumption were unrelated to rainfall or maize raiding, but were associated instead with forest fruit shortages, specifically *Mimusops bagshawei*.

6. Chimpanzees consumed banana pith more frequently when forest fruits were scarce, whereas baboons targeted more banana fruits. The use of banana pith by chimpanzees supports the suggestion that energy-rich pith is crucial to chimpanzees during fruit scarcity.

7. Conservation of *Mimusops bagshawei* and other key forest fruit trees may lessen primate raiding intensity on perennial crops, e.g. bananas. Maize raiding appears unaffected by forest fruit abundance. Such highly palatable crops are best planted > 500 m from the forest edge.

8. Planting agroforestry buffers along park edges creates ideal habitat for crop-raiders. This management strategy is appropriate where human population density is low and crop raiding species are legal game. When dangerous or destructive wildlife species forage amidst densely settled subsistence farmland, managers are challenged to separate forests from agriculture using non-palatable plant barriers or electric fences.

Key-words: agroecology, primate pests, phenology, tropical forests, wildlife conservation.

Journal of Applied Ecology (1998) **35**, 596–606

Introduction

A daring foray by a chimpanzee into a field of ripe maize disturbs the farmer and ecologist alike. At risk is the survival of an endangered species and the livelihood of a poor farmer. The chimpanzee's act also undermines conventional views of natural behaviour in a pristine ecosystem. When a wild primate crosses into a farm to raid crops, it is typically viewed as a 'pest', 'weed', or 'ecological dislocate' (Sawarkar 1986; Richard, Goldstein & Dewar 1989; Else 1991). Seldom is crop-raiding incorporated into theoretical studies of primate feeding ecology or behaviour because of an emphasis on evolved plant-animal interactions (but see Richard, Goldstein & Dewar 1989). This separation of human-influenced from pristine behaviour is largely illusory.

In contrast to modern efforts to partition agriculture and wildlife, traditional shifting agriculturalists in tropical forests integrated farming with hunting of crop-raiding animals (Koch 1968; Linares 1976; Irvine 1987; Bahuchet & Garine 1990). Many animals inhabiting agro-forest systems have foraged on both crops and forest foods for centuries (Koch 1968; Donkin 1985; Sukumar 1989; Vansina 1990). As a result, certain species include crop foraging in their ecological strategy, which has probably influenced their distribution (Richard, Goldstein & Dewar 1989; Dove 1993). The significance of crops in the evolution and past ecology of wild primates will never be precisely ascertained, but certainly wildlife and agriculture have coexisted in tropical forests for millennia (Vansina 1990).

From an animal's perspective, fields of ripe maize may be analogous to the mast fruiting of forest trees (Janzen 1976). In fact, the Kantu of West Kalimantan report that bearded pigs *Sus barbatus* raid crops less heavily during mast-fruiting events in the forest (Dove 1993). Similarly, shifting agriculturalists in the Ituri forest of Zaire describe declines in crop damage by primates and bushpigs when fruit is abundant in the forest (Mubalama 1996). These anecdotes suggest that the timing of crop-raiding is influenced by the availability of fruit in the forest. Others attribute temporal peaks in raiding behaviour to crop availability, which in turn is driven by seasonal patterns of rainfall (Bell 1984; Sukumar 1989; Osborn 1993).

Most animals that forage on crops do not forgo wild foods, they instead add crop-raiding to their other foraging activities (Mohnot 1971; Masau & Strum 1984; Strum 1987; Sukumar 1989; Ganzhorn & Abraham 1991). Dismantling the conceptual barrier between studies of wild foraging and crop-raiding will reveal wildlife feeding strategies and improve management of the ecotone between agricultural lands and the forest edge. In environments with seasonal peaks in forest fruit availability, such information will permit managers to understand and predict periods of intense crop-raiding.

Primates are ideal subjects for a study that links wild feeding strategies with crop-raiding. Primates dominate lists of crop-raiders around African parks and reserves (Bell 1984; Balakrishnan & Ndhlovu 1992; CARE 1994; Newmark *et al.* 1994; Mubalama 1996; Naughton-Treves 1998) and a great deal is known about their wild diets. By ignoring crop-raiding or viewing it as a 'fall from grace', we may overlook an integral part of the ecology of these species (Richard, Goldstein & Dewar 1989; Dove 1992). Moreover, examining the temporal pattern of crop-raiding in comparison with the availability of wild and cultivated foods illuminates the foraging strategies of different primate species surviving in what is rapidly becoming the dominant land use in the tropics: secondary forest or agriculture/forest 'scrub' (Corlett 1995). Such investigations must proceed in the sober realization that, although some primate species thrive in the forest-agriculture ecotone (Maples *et al.* 1976; Kavanagh 1980; Horrocks & Baulu 1988; Else 1991; Baranga 1993), many more species are eliminated by the conversion of tropical forests to agriculture (Struhsaker 1981a; Butynski 1984; Marsh & Mittermeier 1987; Skorupa 1988; Decker & Kinnaird 1992; Fimbel 1994).

In this paper, we explore the temporal pattern of foraging on crops by three primate species (redtail monkey *Cercopithecus ascanius schmidtii*, Matschie 1892, olive baboon *Papio cynocephalus anubis*, Lesson 1827, and chimpanzee *Pan troglodytes schweinfurthii*, Giglioli 1872) over 23 months around Kibale National Park, Uganda. Kibale is a good site for such investigations, because the primates raiding crops at the edge of the park have been studied by ecologists inside the forest. Moreover, detailed data are available on the fruiting patterns of trees of Kibale. Crop consumption and temporal variability of raiding for each primate species is investigated. As rainfall affects both forest and agricultural habitat, and several previous studies suggest that crop-raiding is tied to rainfall (Bell 1984; Litoroh *et al.* 1992; Osborn 1993), we test for correlations between the frequency of raiding events and monthly rainfall. We then assess predictions that wild food availability modifies the timing of crop-raiding (Sukumar 1989; Dove 1993; Suarez 1993; Mubalama 1996), by testing for correlations between forest fruit availability and monthly crop raiding. Our analyses focus on primate foraging on two widely planted crops with distinct planting regimes: bananas *Musa* spp. and maize *Zea mays*. The main thrust of the paper is to investigate factors influencing the timing of crop-raiding and the foraging strategies of non-human primates inhabiting forest-agriculture ecotones.

Materials and methods

STUDY SITE

Kibale National Park, located in western Uganda (0°13'–0°41' N, 30°19'–30°32' E) encompasses 766

km² of moist, evergreen forest with undulating topography and great floristic variation across short distances (Struhsaker 1997; Chapman *et al.* 1997). From north to south, altitude and rainfall decline (1590–1110 m; 1600–1100 mm year⁻¹; Howard 1991), while temperatures increase (from 23.3 to 24.2°C annual mean daily maximum: Chapman *et al.* 1997).

Edge habitat is abundant at Kibale due to the park's elongate shape and previous logging and agricultural activities (*c.* 40% of the area is swamp, grassland thicket and colonizing forest: Skorupa 1988; Butynski 1990). The spatial heterogeneity of the forest derives from climatic, edaphic and human disturbance factors, which, in turn, create variation in the distribution of large vertebrates in space and time (Wing & Buss 1970; Skorupa 1988; Butynski 1990; Chapman *et al.* 1997; Struhsaker 1997).

Palynological evidence from south-western Uganda indicates forest clearing and agriculture for over 2000 years (Hamilton 1981). The prehistoric coexistence of agriculture and wildlife in the region was associated with low human population density. Wildlife foraged in a matrix of forest interspersed with small patches of agriculture (Vansina 1990). As recently as the 19th century, the region encompassing what is now Kibale was a vast forest inhabited by agriculturalists residing in scattered settlements (Taylor 1962). Subsistence farmers attempted to balance crop losses to wildlife with bushmeat gains from hunting. However, where wildlife were especially abundant, particularly elephants, settled agriculture was not possible (J. Vansina, personal communication; Uganda Game Department archives 1909–29).

Over recent centuries, the introduction of new crops and new political and economic systems has profoundly changed the human landscape of western Uganda. Maize was introduced to Uganda in the 17th century (Vansina 1990). Bananas appeared around 800, and by the mid 1900s dominated agriculture around Kibale (Vansina 1990). Changes in crops paralleled rapid changes in land use systems and growth in the human population. The human population around Kibale more than tripled between 1959 and 1991, outpacing the national annual growth rate (>7% vs. 3%, World Bank 1993). The loss of moist forest (such as that found at Kibale) has been particularly severe in Uganda, estimated at 86% reduction of its precolonial extent (World Resources Institute 1994). Forests now form the interstices between tracts of farmland.

Currently, 54% of land within 1 km of Kibale's boundary is used in smallholder agriculture (Mugisha 1994). Agriculturalists in the area belong to two predominant ethnic groups, the indigenous Batoro, and the immigrant Bakiga, who began arriving in the area during the 1950s (Turyahikayo-Rugyema 1974). Both groups plant a mixture of over 30 types of subsistence and cash crops; of which bananas, maize, beans *Phaseolus vulgaris*, yams *Dioscorea* spp., and cassava *Mani-*

hot esculenta cover the greatest area. Farm sizes are small (*c.* 1.4 ha per family) and population density is high (*c.* 272 individuals per km²)* (Naughton-Treves 1997). Farmers residing immediately on the park border (<500 m) absorb the majority of crop loss; accordingly many resent the presence of the park and its wildlife (Naughton-Treves 1996, 1997).

STUDY ANIMALS

Among the diverse wildlife of Kibale are species notorious for crop damage in Africa. The community of primates includes characteristic inhabitants of forest edge environments: olive baboons, redbtail, vervet *Cercopithecus aethiops*, blue *C. mitis*, and l'Hoest's monkeys *C. lhoesti* (Rowell 1966; Kavanagh 1980; Butynski 1984; Thomas 1991). Elephants *Loxodonta africana* have a long history of damaging timber stock, nurseries and crops in the area (Osmaston 1959). Also present are bushpigs (*Potamochoerus porcus* or *P. larvatus*), a little-studied animal responsible for considerable crop damage across Africa (Ghiglieri *et al.* 1982; Vercammen, Seydack & Oliver 1993). Information regarding the distribution and density of these species within Kibale is incomplete. Census data indicate that primate densities vary significantly between sites within Kibale (Struhsaker 1981b; Skorupa 1988; Butynski 1990).

Among the 17 wildlife species recorded damaging crops around Kibale during a 2-year period, primates accounted for 71% of damage events and 48% of the area of crop damage. Redtail monkeys were by far the most frequent raiders, while baboons damaged the greatest area of crops (Naughton-Treves 1998). Chimpanzees ranked third among primate raiders, but caused less than one-third the crop damage of baboons, and one-half the damage of redbtails (Naughton-Treves 1998). Black-and-white colobus *Colobus guereza*, vervet and l'Hoest's monkeys were also occasionally observed foraging on crops (Naughton-Treves 1996).

Olive baboons are characteristic inhabitants of forest-savanna edge environments (Rowell 1966), and are the most notorious crop-raiders among African primates (Else 1991). They are generally considered the worst crop-raiding animal at Kibale (Naughton-Treves 1996). Little is known about the diet of baboons at Kibale, but 200 samples of dung revealed that consumption of non-fig fruits correlated with their availability (Wrangham *et al.* 1991). Baboons inhabiting a gallery forest elsewhere in western Uganda had a home range of 3.8–5.1 km², and a mean dry range of 2 km (maximum of 6.4 km: Rowell 1966). Baboons in and around Kibale appear to have longer day ranges.

* Population densities are lower under other land uses around Kibale, such as forest fragments (24% of area), tea estates (10%) and grassland (10%) (Mugisha 1994).

Redtail monkeys also frequently inhabit forest edge environments and adjacent farmlands (Butynski 1984; Thomas 1991; Baranga 1993). Redtails and some of their congeners (vervet, blue and l'Hoest's monkeys) commonly feed on crops elsewhere in Africa (Kingdon 1979; Kavanagh 1980; Else 1991; Hill 1993; CARE 1994). Redtail monkeys use small home ranges intensively in the forest interior of Kibale (home range 0.22 km²; day range 1.5 km, varying from 0.9 to 2.7 km; Struhsaker 1978; Struhsaker & Leland 1988). Redtail groups which do not raid crops eat primarily ripe and unripe fruit, insects, flowers and young leaves (Struhsaker 1978; A. Treves & P. Baguma, personal observation). The most frequently eaten wild plant food for redtails, both absolutely and relative to tree abundance, was *Celtis durandii* (A. Treves, personal observation).

Chimpanzees demonstrate variable habitat preferences, but appear at highest densities in forested environments (Moore 1992). The home range of the Kanyawara chimpanzee community at Kibale was estimated between 7.8 and 14.9 km², not including farmland (Chapman & Wrangham 1993). Day range lengths at Kibale are not yet known, but, at Gombe, the median day range was 3–4 km for males and 2.7 km for females (Wrangham 1977). At Kibale, chimpanzees are ripe fruit specialists, but also eat leaves and herbs (Wrangham *et al.* 1991; Wrangham, Conklin-Brittain & Hunt, 1998). When ripe fruits were unavailable, chimpanzees spent more time eating the fibrous pith of terrestrial vegetation (Wrangham, Conklin-Brittain & Hunt 1998). Three trees (*Pseudospondias microcarpa*, *Mimusops bagshawei* and *Uvariopsis congensis*) are particularly important fruit sources for chimpanzees of the Kanyawara community and strongly influence their ranging and association patterns. In chimpanzee dung ($n = 839$ samples), the seeds of *M. bagshawei* were found in negative correlation with fibre (Wrangham *et al.* 1991). This fibre is thought to derive from terrestrial herbs, and may include banana pith. The significance of crops in chimpanzee diet at Kibale is unknown, although members of the Kanyawara community have been observed raiding crops.

FOOD AVAILABILITY IN AND AROUND KIBALE

Kibale experiences two dry and two rainy seasons each year. Inter-annual variation in the onset of the rainy season and supra-annual cycles contribute to unpredictability, but, each year rainfall typically increases during March through May, and again in August through November (Struhsaker 1997). Variability in rainfall appears to bear no relation to fruit availability within the forest (Struhsaker 1997), but, lack of seasonality does not signify uniform fruit availability. The fruit of fig trees is available quite evenly across the year, while non-fig fruits have peaks which are not related to any known annual cycles

(Wrangham *et al.* 1991). Intra-specific synchrony of fruiting occurs in several species and results in localized fruit abundance (Struhsaker 1997). In two species, *U. congensis* and *C. durandii*, fruiting synchrony was observed between trees up to 12 km apart. Other species showed little or no interior intraspecific synchrony (Struhsaker 1997).

Inter-annual variability in the onset of the rains at Kibale precludes the precise definition of planting seasons outside the forest. Local farmers generally follow a two-season planting regime each year, planting with the onset of rains in March and again in late August. Given the considerable year-to-year variability in rainfall, there is considerable risk involved in deciding when to plant, especially for grains, such as maize, millet and sorghum. Planting too early may result in desiccated crops—too late and seedlings may be drowned. Farmers attempt to cope with climatic variability at Kibale by incorporating flexibility in their planting calendar. Farmers may replant a failed crop if rains are delayed, or plant and harvest crops twice in a single season if rains are prolonged. Farmers do not plant crops in precise synchrony with their neighbours.

Maize and bananas are two common crops that demonstrate the variability in local planting regimes. Maize is planted at the onset of the rains in 'gardens' (average = 1012 m², range 50–8700 m², $n = 181$) that are harvested 3–4 months later. Bananas (including sweet, cooking and brewing types) are tended and harvested year round on family owned 'plantations' that average 4840 m² (100–66125 m², $n = 204$). Brewing bananas cover nearly 60% of the land under smallholder agriculture within 500 m of Kibale's western border (Naughton-Treves 1996). Farmers report no annual cycles of productivity for bananas. To test this, the size (diameter at breast height, d.b.h.) and density of banana stalks were randomly sampled in 100 m² plots on a weekly basis for 8 months. These data were later used to determine if primates selected banana stalks of a particular size or took them in relation to their availability.

MONITORING WILDLIFE FORAGING ON CROPS

Four villages and their surrounding fields located on the edge of Kibale were monitored for wildlife crop damage. A straight-line distance of approximately 10 km separated the northern- and southern-most village. At each village, a monitoring area stretching 1.0 km along the forest boundary and extending 0.5 km away from the forest edge was mapped at a resolution of 250 m².

For 23 months, each monitoring area was visited by two-person teams on a weekly basis and canvassed for crop damage. Animals were only occasionally viewed foraging in farms, therefore tracks, dung, dental impressions in plants, diggings, wadges and other physical remains were used to identify the animal

causing the damage. In the case of redtails and l'Hoe-st's monkeys, inter-observer reliability in the identification of the species responsible for a raid fell below 95%. In all analyses, we pool damage data for these congeners under redtails, because this species was responsible for 20 of 21 visually observed raids, and has a much higher population density in Kibale (Struhsaker 1981b).

An independent event was defined as all crop damage occurring during a single foray (exit from and return to natural vegetation: Naughton-Treves 1998). This provides a conservative estimate of raiding frequency (Naughton-Treves 1998). The amount of damage in a foray was recorded by counting damaged stems of individually planted crops (e.g. bananas, cassava, maize) and converting this to an area using average planting densities for each crop. Damage to sown crops (e.g. millet, beans) was measured directly in m² (Sukumar 1989). Crop maturity and parts consumed were noted. For bananas, the d.b.h. of each damaged stalk was measured and damaged shoots were counted.

ANALYSIS OF TEMPORAL VARIATION IN CROP FORAGING

We calculated monthly frequency of crop-raiding based on the number of independent forays by each species from July 1992 to May 1994 (23 months). Inter-monthly variability in the frequency of crop foraging was calculated in two ways: (i) the standard deviation of monthly events was calculated; (ii) the values for adjacent months were subtracted to yield a positive deviation representing the percentage change in the number of foraging events. The mean of these 22 values provides an index of month to month predictability of crop foraging, i.e. given damage in month t , it provides the average expected damage for month $t+1$. This index is used to compare variation in crop foraging frequency between species and crops.

Detailed data on forest fruit availability were collected concurrently with crop-raiding data. The total number of trees bearing ripe fruit in the sampling area of 4.8 ha was recorded in the first 10 days of each month. The forest sampling area lay within 5 km of the four study villages; a distance within the home range for chimpanzees and baboons, but exceeding that for redtails (Rowell 1966; Struhsaker & Leland 1988; Chapman & Wrangham 1993). Data for four tree species were used in the present analysis (*M. bagshawei*, *P. microcarpa*, *U. congensis* and *C. durandii*), because these species were most often eaten by chimpanzees and redtails during the study period (Wrangham, Conklin-Brittain & Hunt 1998); A. Treves & P. Baguma, personal observation). Operationally, the monthly total number of these trees bearing ripe fruit was tested against the total of independent events of crop-raiding for the same month.

Two-tailed tests were used throughout. For non-

parametric tests the Z -value of the Kendall rank correlation analysis is presented.

Results

All three primate species foraged on crops throughout the year but displayed peaks and troughs in the use of specific crops at the four study sites (Fig. 1). Bananas were constantly available, whereas maize was frequently, but not always available.

The primate species differed in crop preference, although bananas or maize figured as the preferred crop for all three (Table 1). Baboons took root and tuber crops that the other primates ignored, and also fed on the greatest variety of crops (15 types: Naughton-Treves 1996). Even when animals selected the same crop, there was variation in the specific plant part eaten or the age of the crop when eaten. For example, baboons foraged on maize throughout their life cycle (seedlings, inflorescence, pith fruit), while redtails ate maize fruit only close to harvest (Table 1). Redtails consumed only banana fruit, baboons damaged banana fruit more frequently than the pith, and chimpanzees raided pith and fruit in near equal proportions. On average, chimpanzees and baboons damaged significantly smaller banana stalks than were available in the fields (d.f. = 65: baboons unpaired $t = 11.7$, $P < 0.0001$; chimpanzees $t = 5.3$, $P = 0.0001$: Naughton-Treves 1996).

The three primate species showed distinct monthly patterns (Fig. 1). The temporal pattern of crop-raiding is significantly non-random for baboon and redtail monkeys, but not clearly so for chimpanzees. Large inter-monthly variation was a consistent pattern for all three primates, but was least pronounced for redtails (Table 2).

For each of the three primate species, the monthly frequencies of crop-raiding on maize and bananas were not correlated ($P > 0.1$ in all cases). Variation in monthly raiding frequency was greater for maize than for bananas, but this was only significant for redtail raiding (paired $t = -3.3$, $P = 0.003$).

RAINFALL AND SYNCHRONY OF RAIDING BETWEEN PRIMATES

For all three primates, crop-raiding on maize increased approximately 8 weeks after the onset of the rains, hence maize raiding was significantly negatively correlated with rainfall (Fig. 2). The c. 8-week lag between rainfall and maize raiding reflects the delay between planting and fruiting, when primates foraged most heavily (Table 1). As a result, maize crop-raiding was correlated between primate species ($Z > 2.0$ and $P < 0.05$ for all comparisons). In contrast, foraging on bananas was unrelated to rainfall ($P > 0.05$ in all cases), and was not correlated between the three primates.

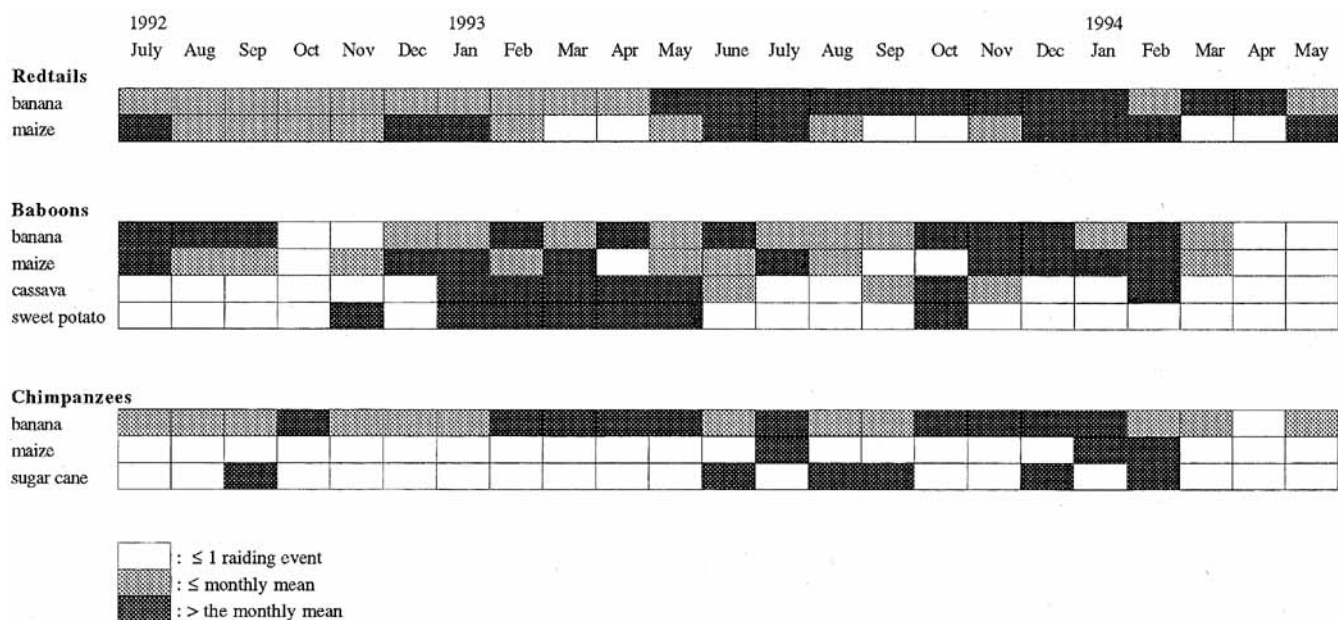


Fig. 1. Monthly intensity of crop-raiding by three primate species at Kibale National Park, Uganda: □ ≤ 1 raiding event; ▨ ≤ monthly mean; ■ > the monthly mean.

Table 1. Preferred crops and plant parts consumed by 3 primate species around Kibale National Park, Uganda

Animal	Top two preferred crops*	N*	Plant parts eaten (%)	Age of crops months (mean ± 1 SD)
Redtail	Sweet banana	169	95% fruit, 5% inflorescence	NA
	Maize	168	100% fruit	3.2 ± 0.5
Baboon	Maize	99	11% seedling, 7% flower, 82% fruit	1.9 ± 0.9
	Sweet potato	26	100% tuber	3.0 ± 1.7
Chimpanzee	Brewing banana	122	55% fruit, 45% pith†	NA
	Sweet banana	11	55% fruit, 45% pith†	NA

* Based on independent damage events (Naughton-Treves 1996).

† Pith = fibrous core of banana stalks. NA = not available.

Table 2. Intermonthly variation in frequency of primate crop-raiding

Species	N (events)	Intermonthly variation (% of annual total)*	
		Mean ± SD	Range
Redtail	1252	0.9 ± 0.7	0–2.4
Baboon	160	2.6 ± 1.9	0–7.4
Chimpanzee	146	2.2 ± 2.0	0–9.2

* Absolute value of the difference in frequency of raiding events between month *t* and month *t* + 1.

CROP-RAIDING AND FOREST FRUIT AVAILABILITY

In the phenology study area, *M. bagshawei* varied from 0 to 1.5 fruiting trees ha⁻¹ month⁻¹; *P. micro-*

carpa 0–0.4 ha⁻¹ month⁻¹; *U. congensis* 0–24.0 ha⁻¹ month⁻¹; and *C. durandii* 0–9.8 ha⁻¹ month⁻¹. The number of fruiting trees of each species was unrelated to rainfall ($P > 0.05$ in all cases).

The number of fruiting *M. bagshawei* trees in the current month was significantly negatively correlated with the monthly frequency of foraging on bananas by chimpanzees, baboons and redtail monkeys (Table 3). Only baboons responded to *C. durandii* availability. Crop-raiding on maize bore no relationship to forest fruit availability.

When banana foraging events by baboons were split by consumption of fruit or pith, the negative correlation with *Mimusops bagshawei* was significant only for fruits ($Z = -2.5$, $P = 0.01$). The opposite held for chimpanzees: *Mimusops bagshawei* fruiting correlated negatively with banana pith consumption only ($Z = -3.1$, $P = 0.002$). The tendency for chimpanzees and baboons to coincide in the timing of

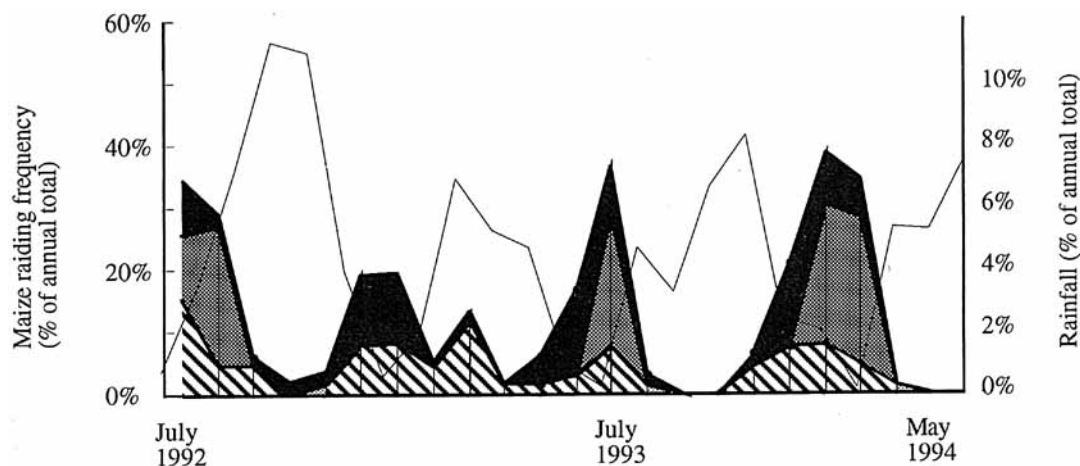


Fig. 2. Monthly rainfall (narrow line over shaded areas) superimposed on stacked monthly frequencies of maize raids by baboons (barred), chimpanzees (grey), redtails (black). The left y-axis indicates the number of independent events as a percentage of the annual total for each species. The right y-axis measures rainfall (mm) as a percentage of annual precipitation.

Table 3. The relationship between forest fruit availability and primate crop-raiding at Kibale National Park, Uganda

	Forest fruit tree species			
	<i>U. congensis</i>	<i>M. bagshawei</i>	<i>P. microcarpa</i>	<i>C. durandii</i>
Maize raiding				
Redtail	1.8	-0.1	-1.0	-0.2
Baboon	-0.2	-1.1	-1.6	0.5
Chimpanzee	1.5	-1.7	-0.2	1.1
Banana raiding				
Redtail	1.2	-2.0*	-0.1	1.4
Baboon	-0.5	-3.5**	-1.3	-2.2*
Chimpanzee	0.2	-2.4*	-1.8	0.2

Entries are Z-values of the Kendall rank correlation: monthly crop-raiding frequency tested against the number of fruiting trees per ha (July 1992–May 1994).

* $0.05 \geq P > 0.01$; ** $P \leq 0.01$.

their forays on bananas was due to fruit ($Z = 2.9$, $P = 0.007$), rather than pith ($Z = -1.8$, $P = 0.15$).

EFFECTS OF POOLING DATA ON CROPS

If raiding behaviour on all crops are pooled in analyses, the effects of forest fruit availability and rainfall are obscured. For example, pooling data on bananas and maize eliminates all correlations with rainfall and forest fruit availability for redtail monkeys. Using similarly pooled data, only the strongest correlations persist for the other two species (baboons: *M. bagshawei*, $P = 0.003$; rainfall, $P = 0.02$; chimpanzees: *M. bagshawei*, $P = 0.01$).

Discussion

Detailed analysis of primate crop foraging behaviour revealed links between the forest and agroecosystem at Kibale National Park. On the one hand, farmers'

maize planting decisions influenced the foraging behaviour of wild primates. On the other, fruiting events of *M. bagshawei* within the forest influenced primate foraging in nearby croplands.

Redtail monkeys, baboons and chimpanzees each exploited crops in the forest–agriculture ecotone in different ways. Redtail monkeys and chimpanzees targeted few crops, whereas baboons foraged on several different crops at varying stages of maturity. This conforms with studies of wild diets (Rowell 1966; Altmann & Muruthi 1988) and may help explain the broad habitat tolerance of baboons. All three primate species preferred bananas or maize over other crops. Redtails and baboons targeted banana fruit, while chimpanzees were as likely to consume banana pith as fruit. Redtails had the lowest intermonthly variation in raiding frequency, indicating the consistency with which they visited croplands, but this result may reflect the range size and intensity of use by the primates. Chimpanzee and baboon ranges are 10 or

more times larger than those of redtails, so their return visits to any given assemblage of crops would be expected to be less frequent.

Variation in ranging behaviour potentially confounds the identification of temporal peaks in raiding frequency. This confounding relationship was noted in Kalimantan, where the Kantu report considerable temporal variation in raiding behaviour of the far-ranging bearded pig, while more localized species (e.g. *Muntiacus muntjak* and *Cervus unicolor*) appear to forage continuously (Dove 1993). In the case of animals that move regionally, such as elephants, it becomes more difficult to separate the effects of temporal and spatial variation (Bell 1984; Sukumar 1989). Further confounding analysis of temporal variation is exaggeration or variability in farmers' evaluations of raiding intensity. For example, reported temporal peaks in elephant raiding over several years at Kenyan sites correlated with local farmers' perceived opportunities for compensation for crop damage (Gachago & Waithaka 1995). Identifying non-random frequencies in raiding behaviour requires systematic measurement of damage at the appropriate temporal and spatial scales.

Despite considerable variation in the timing of crop forays between primate species at Kibale, two consistent patterns underlay the exploitation of maize and bananas.

1. Maize. The synchrony in planting and ripening of maize results in peaks in food availability. All the primates responded similarly to these peaks by leaving the forest to raid maize fields. Abundance of forest fruit did not diminish primate appetite for maize. This appetite is all too familiar to farmers around Kibale, who guard maize intensely at harvest time and generally avoid planting maize at the forest boundary (Naughton-Treves 1996).

Numerous studies describe how ripening fields of maize attract primates and other wildlife (Maples *et al.* 1976; Milton & Binney 1980; Else 1991; Jorgenson 1993; Conover 1994). This pattern conforms to the popular explanation for raiding behaviour, namely that animals crop-raid whenever cultivars are available, because they are more palatable and nutritious than wild foods (Greenhood 1971; Marks 1976; Bell 1984; Booth, Kipuri & Zonneveld 1992; Damiba & Ables 1993; CARE 1994). Wildlife preference for maize may be due to its elevated protein content (dry matter of cob = 12% protein; Sukumar 1989). Elsewhere, wildlife exhibits similarly predictable peaks in foraging on highly seasonal grain crops, such as millet (Mascarenhas 1971; Sukumar 1989; Osborn 1993).

2. Bananas. Monthly frequencies of banana raiding bore no relation to rainfall. Yet, banana raiding by all three species declined with increases in *M. bagshawei* fruit availability, a forest species consumed by all three primates (Wrangham *et al.* 1991; A. Treves & P. Baguma, personal observation), and known to play a powerful role in the foraging ecology of chim-

panzees (Chapman, Wrangham & Chapman 1995). Previous analysis of chimpanzee and baboon dung revealed that both species consumed *M. bagshawei* fruit in relation to its abundance in the forest (Wrangham *et al.* 1991). When ripe fruits of *M. bagshawei* were unavailable, chimpanzee dung contained more fibre, evidence of their feeding on herbaceous vegetation such as *Aframomum* spp. (Wrangham *et al.* 1991; Wrangham, Conklin-Brittain & Hunt 1998). The present study indicates that some of this fibre could derive from banana pith, and supports the suggestion that energy-rich pith is crucial to chimpanzees during fruit scarcity (Wrangham 1986; Wrangham *et al.* 1991; Wrangham, Conklin-Brittain & Hunt 1998). The primate foraging pattern on bananas at Kibale conforms to explanations that wildlife use crops as 'fall-back' foods during times of wild food scarcity (Milton & Binney 1980; Ganzhorn & Abraham 1991; Dove 1993).

CONSERVATION IMPLICATIONS

The observed links between primate foraging on wild foods and cultivars around Kibale parallel accounts of wildlife crop foraging in tropical forest agricultural systems (Dove 1993; Mubalama 1996). Just as humans integrated hunting and agriculture, some wildlife species regularly used both wild foods and crops. Although crop-raiding is ancient, the context has changed drastically and the stakes are elevated for both the subsistence farmers and the wildlife. Due to land scarcity, farmers are often forced to farm at the forest edge, where they are prohibited from hunting the animals damaging their crops. Nonetheless, roughly 15% of farmers set traps illegally on their farms (Naughton-Treves 1998). The government also sponsors periodic 'vermin' eradication programmes outside the parks. Therefore, wildlife faces both habitat scarcity and danger in leaving protected areas.

The protected area manager is challenged to decouple the ancient relationship between farmers and the wildlife attracted to their crops. A Ugandan Game Warden summarized this chimaera:

... the lives of game keepers are wholly spent in the netherland of boundaries [where] two opposing forces meet. Their waking lives are spent darting about between the animals and the humans, across the no man's land between them. ... One day the humans are being warded off from the animals; the next day is spent separating the animals from the humans. ... (Graham 1973, p. 104).

Protected area managers' problems with crop-raiding wildlife are a subset of the larger question of how to manage edges. 'Agriculturalization' (Janzen 1987) and forest fragmentation increase edge habitat and decrease the ability of large animals to range widely without crossing agriculture (Sukumar 1989). Fuelled by the bitter complaints of farmers, Kibale's managers

are searching for means to limit wildlife forays into farmlands and elevate local tolerance for incursions.

Edge management strategies lie along a continuum. On one extreme, a complete physical barrier separates wildlife from humans; on the other, no edge exists between humans and wildlife. In practice, protected areas typically have permeable edges. The appropriate edge management strategy depends upon the prevailing physical and social context and conservation objectives. A highly permeable edge may be appropriate where crop-raiding species are highly valued as game to local populations and are not critically endangered. Such conditions typically occur in areas of low human population density, such as the Peruvian Amazon or the southern African drylands (Ascorra 1996; Matzke & Nabane 1996). Where forest abuts densely settled farms, hunting is prohibited, and raiding animals threaten farmers' lives and livelihoods, a harder edge may be necessary. Such is the case around many Kenyan and Ugandan forested parks, where managers build fences, trenches and thorn walls to deter elephants and other animals from entering surrounding farmlands (Bell 1984; Booth, Kipuri & Zonneveld 1992). Despite these efforts to partition forests and agroecosystems, certain primate species continue to cross into farmlands to forage (Gachago & Waithaka 1995; Mwathe & Waithaka 1995).

Species that can exploit edges and circumvent barriers (such as the three primates of this study) appear to benefit relative to forest interior species (Else 1991; Thomas 1991). Widespread and recurrent complaints about crop-raiding cercopithecines and baboons reflect their abundance in the region (Hill 1993; CARE 1994; Mubalama 1996; Ugandan Wildlife Authority reports 1990–96). Exploitation of crops has allowed some primates to colonize new sites (e.g. *Cercopithecus aethiops tanzanus*: Kavanagh 1980). Baboon and vervet populations elsewhere have increased due to access to human foods (Horrocks & Baulu 1988; Else 1991). However, the animals' use of crops often results in eradication or control operations (Mascarenhas 1971; Altmann & Muruthi 1988; Horrocks & Baulu 1988).

Wherever wildlife habitat neighbours agriculture, there will be some risk of crop losses. Ameliorating these losses and elevating local tolerance for wildlife incursions will require a sophisticated blend of technical, social and economic interventions. The results of this study indicate that deliberate conservation of some wild food species (e.g. *Mimusops bagshawei*) could alleviate crop-raiding in some seasons. To avoid heavy losses or high guarding investment, highly palatable seasonal crops such as maize, should not be planted on the forest edge. Sharing tourism revenue with local communities may elevate tolerance for losses (Damiba & Ables 1993). On a broader level, conserving large blocks of forest and reducing edge habitat should be a management priority in western Uganda.

Acknowledgements

This research was approved by the Ugandan National Research Council, and received generous support from the Fullbright-Hays Programme, the Makerere University Biological Field Station, the Wildlife Conservation Society, and the American Association of University Women. A MacArthur Foundation post-doctoral fellowship at CIS, Princeton University, supported L. Naughton-Treves during write-up and analysis. P. Baguma, F. Mugurusi and P. Kagoro provided first rate field assistance. K. Redford, D. Kammen and four anonymous referees offered critical analysis.

References

- Altmann, J. & Muruthi, P. (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, **15**, 213–221.
- Ascorra, C.F. (1996) *Evaluacion de fauna en sistemas agroforestales de Tambopata para el majejo sostenido*. Annual report. Conservation International, Lima, Peru.
- Bahuchet, S. & Garine, I. (1990) The art of trapping in the rainforest. *Food and Nutrition in the African Rainforest* (eds C.M. Hladik, S. Bahuchet & I. Garine), pp. 25–49. UNESCO, Paris.
- Balakrishnan, M. & Ndhlovu, E.E. (1992) Wildlife utilization and local people. A case-study in Upper Lupande Game Management Area, Zambia. *Environmental Conservation*, **19**, 135–144.
- Baranga, D. (1993) *The ecology and conservation status of the redtail monkey (Cercopithecus ascanius schmidti) in the Kampala area*. PhD thesis, Makerere University, Kampala, Uganda.
- Bell, R.H.V. (1984) The man-animal interface: an assessment of crop damage and wildlife control. *Conservation and Wildlife Management in Africa* (eds R.H.V. Bell & E. McShane-Caluzi), pp. 387–416. US Peace Corps Office of Training and Program Support, Malawi.
- Booth, V.R., Kipuri, N.N. & Zonneveld, J.M. (1992) *Environmental impact of the proposed fencing programme in Kenya*. Elephant and Community Wildlife Programme, Kenya Wildlife Service, Nairobi, Kenya.
- Butynski, T.M. (1984) *Ecological survey of the Impenetrable (Bwindi) Forest, Uganda, and recommendations for its conservation and management*. Field Report, New York Zoological Society, Bronx, New York.
- Butynski, T.M. (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecological Monographs*, **60**, 1–26.
- CARE (1994) *The people of Bwindi Impenetrable National Park*. Report, CARE, Kibale, Uganda.
- Chapman, C.A., Chapman, L.J., Wrangham, R.W., Isabirye-Basuta, G. & 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. & Wrangham, R.W. (1993) Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *American Journal of Primatology*, **31**, 263–273.
- Chapman, C.A., Wrangham, R.W. & Chapman, L.J. (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59–70.
- Conover, M.R. (1994) Perceptions of grass-roots leaders of

- the agricultural community about wildlife damage on their farms and ranches. *Wildlife Society Bulletin*, **22**, 94–100.
- Corlett, R.T. (1995) Tropical secondary forests. *Progress in Physical Geography*, **19**, 159–172.
- Damiba, T.E. & Ables, E.D. (1993) Promising future for an elephant population—a case study in Burkina Faso. *Oryx*, **27**, 97–103.
- Decker, B.S. & Kinnaird, M.F. (1992) Tana river red colobus and crested mangabey: results of recent censuses. *American Journal of Primatology*, **26**, 47–52.
- Donkin, R.A. (1985) *The Peccary: with observation on the introduction of pigs to the New World*. American Philosophical Society, Philadelphia, PA.
- Dove, M.R. (1992) The dialectical history of 'jungle' in Pakistan: an examination of the relationship between nature and culture. *Journal of Anthropological Research* **48**, 231–253.
- Dove, M.R. (1993) The responses of Dayak and bearded pig to mast-fruiting in Kalimantan: an analysis of nature-culture analogies. *Tropical Forests, People and Food: Biocultural Interactions and Application to Development* (eds C.M. Hladik, A. Hladik, O.F. Linares, H. Pagezy, A. Semple & M. Hadley), pp. 113–123. Parthenon Publishing, Paris.
- Else, J.G. (1991) Non-human primates as pests. *Primate Responses to Environmental Change* (ed. H.O. Box), pp. 155–165. Chapman and Hall, London.
- Fimbel, C. (1994) Ecological correlates of species success in modified habitats may be disturbance- and site-specific: the primates of Tiwai Island. *Conservation Biology*, **8**, 106–113.
- Gachago, S. & Waithaka, J. (1995) *Human-elephant conflict in Kiambu, Murang'a, Kirinyaga, Embu and Meru Districts*. Field Report, Kenya Wildlife Service, Nairobi, Kenya.
- Ganzhorn, J.U. & Abraham, J.-P. (1991) Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. *Folia Primatologica*, **56**, 171–176.
- Ghiglieri, M.P., Butynski, T.M., Struhsaker, T.T., Struhsaker, T.T., Leland, L., Wallis, S.J. & Waser, P. (1982) Bush pig (*Potamochoerus porcus*) polychromatism and ecology in Kibale Forest, Uganda. *African Journal of Ecology*, **2**, 231–236.
- Graham, A.D. (1973) *The Gardeners of Eden*. George Allen & Unwin Ltd., London.
- Greenhood, W.F. (1971) *Diets and ecology of crop-raiding baboons*. MSc thesis, University of Florida, Gainesville, FL.
- Hamilton, A.C. (1981) The quaternary history of African forests: its relevance to conservation. *African Journal of Ecology*, **19**, 1–6.
- Hill, C.M. (1993) *Crop-raiding by wildlife: its impact on a farming community in Uganda*. Field Report, Institute of Biological Anthropology, University of Oxford, Oxford, UK.
- Horrocks, J.A. & Baulu, J. (1988) Effects of trapping on the vervet (*Cercopithecus aethiops sabaues*) population in Barbados. *American Journal of Primatology*, **15**, 223–233.
- Howard, P.C. (1991) *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland, Switzerland.
- Irvine, D. (1987) *Resource management by the Runa Indians of the Ecuadorian Amazon*. PhD thesis, Stanford University.
- Janzen, D.H. (1976) Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics*, **7**, 347–391.
- Janzen, D.H. (1987) Habitat sharpening. *Oikos*, **48**, 3–4.
- Jorgenson, J. (1993) *Gardens, wildlife densities, and subsistence hunting by Maya Indians in Quintana Roo, Mexico*. PhD thesis, University of Florida, Gainesville, FL.
- Kavanagh, M. (1980) Invasion of the forest by an African savannah monkey: behavioral adoptions. *Behaviour*, **73**, 238–260.
- Kingdon, J.S. (1979) *East African Mammals*. Academic Press, London, U.K.
- Koch, H. (1968) *Magie et Chasse dans la Forêt Camerouaise*. Berger-Lerrault, Paris.
- Linares, O.F. (1976) Garden hunting in the American tropics. *Human Ecology*, **4**, 331–349.
- Litoroh, M., Sakwa, J., Omondi, P. & Reuling, M. (1992) *A survey of the Marmanet Forest Complex*. Elephant and large mammal populations. Kenya Wildlife Service/EC, Nairobi, Kenya.
- Maples, W.R., Maples, M.K., Greenhood, W.F. & Walek, M.L. (1976) Adaptations of crop-raiding baboons in Kenya. *American Journal of Physical Anthropology*, **45**, 309–316.
- Marks, S.A. (1976) *Large Mammals and a Brave People*. University of Washington Press, Seattle, WA.
- Marsh, C.W. & Mittermeier, R.A. (1987) Primate Conservation in the Tropical Rain Forest. Alan R. Liss, New York.
- Masau, J.M. & Strum, S.C. (1984) Response of wild baboon troops to incursion of agriculture at Gilgil. *Kenya. International Journal of Primatology*, **5**, 364.
- Mascarenhas, A. (1971) Agricultural vermin in Tanzania. *Studies in East African Geography and Development* (ed. S.H. Ominde), pp. 259–267. University of California Press, Berkeley.
- Matzke, G.E. & Nabane, N. (1996) Outcomes of a community controlled wildlife utilization program in a Zambezi Valley community. *Human Ecology*, **24**, 65–85.
- Milton, J.P. & Binney, G.A. (1980) *Ecological planning in the Nepalese Terai*. World Wildlife Fund and Sierra Club Foundation, Washington, DC.
- Mohnot, S.M. (1971) Ecology and behaviour of the Hanuman langur, *Presbytis entellus*, invading fields, gardens and orchards around Jodhpur, western India. *Tropical Ecology*, **12**, 237–249.
- Moore, J. (1992) Savanna chimpanzees. *Topics in Primatology, 1. Human Origins* (eds T. Nishida, W.C. McGrew, P. Marler, M. Pickford & F.B.M. de Waal), pp. 99–118. University of Tokyo Press Tokyo, Japan.
- Mubalama, L. (1996) *An assessment of crop damage by large mammals in the Reserve de Faune—Ituri Forest-Zaire—with special emphasis on African forest elephant (Loxodonta africana)*. MSc thesis, University of Kent at Canterbury.
- Mugisha, S. (1994) *Land cover/use around Kibale National Park. Analysis of 1988 Aerial Photographs*. Uganda Forestry Department (Sheet no. BP 1939), MUIENR, RS/GIS Lab, Kampala, Uganda.
- Mwathe, K.M. & Waithaka, J. (1995) *An assessment of the elephant-human conflict situation in Shimba Hills National Reserve in Kenya*. Kenya Wildlife Service, Nairobi, Kenya.
- Naughton-Treves, L. (1996) *Uneasy neighbors: wildlife and farmers around Kibale National Park, Uganda*. PhD thesis, University of Florida, Gainesville, FL.
- Naughton-Treves, L. (1997) Vulnerable places and people around Kibale National Park, Uganda. *Geographical Review*, **87**, 27–47.
- Naughton-Treves, L. (1998) Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology*, **12**, 156–169.
- Newmark, W.D., Manyaza, D.N., Gamassa, D.G.M. & Sariko, H.I. (1994) The conflict between wildlife and local people living adjacent to protected areas in Tanzania: human density as a predictor. *Conservation Biology*, **8**, 249–255.
- Osborn, F.V. (1993) *The ecology and deterrence of crop raiding elephants*. Report, Department of National Parks and Wildlife Management Zimbabwe.
- Osmaston, H.A. (1959) *Working plan for the Kibale and Itwara Central Forest Reserves, Toro District, W. Province*,

- Uganda. Report No. 1, Forest Department, Uganda Protectorate.
- Richard, A.F., Goldstein, S.J. & Dewar, R.E. (1989) Weed macaques: the evolutionary implications of macaque feeding ecology. *International Journal of Primatology*, **10**, 369–594.
- Rowell, T.E. (1966) Forest living baboons in Uganda. *Journal of the Zoological Society (Lond.)*, **149**, 344–365.
- Sawarkar, V.B. (1986) Animal damage: predation on domestic livestock by large carnivores. *Indian Forester*, **112**, 858–866.
- Skorupa, J.P. (1988) *The effects of selective timber harvesting on rainforest primates in Kibale Forest Uganda*. PhD thesis, University of California, Davis, CA.
- Struhsaker, T.T. (1978) Food habits of five monkey species in the Kibale Forest, Uganda. *Recent Advances in Primatology* (eds D.J. Chivers & J. Herbert), pp. 225–248. Academic Press, London.
- Struhsaker, T.T. (1981a) Forest and primate conservation in East Africa. *African Journal of Ecology*, **19**, 99–114.
- Struhsaker, T.T. (1981b) Polyspecific associations among tropical rain-forest primates. *Zeitschrift für Tierpsychologie*, **57**, 268–304.
- Struhsaker, T.T. (1997) *Ecology of an African Rain Forest*. University of Florida Press, Gainesville, FL.
- Struhsaker, T.T. & Leland, L. (1988) Group fission in redtail monkeys (*Cercopithecus ascanius*) in the Kibale Forest, Uganda. *A Primate Radiation: Evolutionary Biology of the African Guenons* (eds A. Gautier-Hion, F. Bourliere, J.-P. Gautier & J. Kingdon), pp. 364–388. Cambridge University Press, Cambridge.
- Strum, S.C. (1987) *Almost Human*. Elm Tree Books, London.
- Suarez, I.M.T. (1993) *Ecología de los grupos de sapos (Tayassu tajacu) y danos que ocasionan en los cultivos vecinos a la Estacion Biologica de la Selva, Costa Rica*. MSc thesis, Universidad Nacional de Costa Rica, Heredia, Costa Rica.
- Sukumar, R. (1989) *The Asian Elephant*. Cambridge University Press, Cambridge.
- Taylor, B.K. (1962) *The Western Lacustrine Bantu*. Sidney Press Ltd, London.
- Thomas, S.C. (1991) Population densities and patterns of habitat use among anthropoid primates of the Ituri forest, Zaire. *Biotropica*, **23**, 68–83.
- Turyahikayo-Rugyema, B. (1974) *The history of the Bakiga in southwestern Uganda and northern Rwanda, 1500–1930*. PhD thesis, University of Michigan, Ann Arbor, MI.
- Vansina, J. (1990) *Paths in the Rainforests*. University of Wisconsin Press, Madison, WI.
- Vercammen, P., Seydack, A.H.W. & Oliver, W.L.R. (1993) The bush pigs (*Potamochoerus porcus* and *P. larvatus*). *Pigs, Peccaries and Hippos* (ed. W.L.R. Oliver), pp. 93–101. IUCN, Gland, Switzerland.
- Wing, L.D. & Buss, I.O. (1970) Elephants and forests. *Wildlife Monographs*, **19**, 1–92.
- World Bank (1993) *Uganda. Agriculture*. World Bank Country Study, The World Bank, Washington, DC.
- World Resources Institute (1994) *World Resources 1994–5*. Oxford University Press, NY.
- Wrangham, R.W. (1977) Feeding behavior of chimpanzees in Gombe National Park, Tanzania. *Primate Ecology* (ed. T.H. Clutton-Brock), pp. 503–538. Academic Press, New York.
- Wrangham, R.W. (1986) Ecology and social relationships in two species of chimpanzee. *Ecology and Social Evolution: Birds and Mammals* (eds D.I. Rubenstein & R.W. Wrangham), pp. 352–378. Princeton University Press, Princeton, NJ.
- Wrangham, R.W., Conklin, N.L., Chapman, C.A. & Hunt, K.D. (1991) The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society of London, Series B*, **334**, 171–178.
- Wrangham, R.W., Conklin-Brittain, N.L. & Hunt, K.D. (1998) Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology* (in press).

Received 14 August 1997; revision received 9 July 1998