Population structure and behaviour of crop-raiding elephants in Kibale National Park, Uganda

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Abstract

We examined patterns of crop raiding by elephants across gender and age classes in relation to elephant life history and sociobiology and estimated the quantitative contribution of crops to elephant diet in Kibale National Park (KNP). Elephant dung-boli sizes were used to estimate age and sex, while the presence of crop remains in the dung of crop-raiding elephants was used as evidence of repeated raiding. To estimate the expected proportion of elephants raiding per age class, the age distribution of raiders was compared with the age distribution of all KNP elephants. Elephants raiding crops were predominantly males. They began raiding in expected proportions at 10–14 years while a higher than expected proportion raided crops at 20–24 years. These results suggest that crop raiding is initiated at an age when male elephants leave their families and a large proportion of elephants raid when they are approaching reproductive competition. Evidence from dung of crop raiders, suggests that repeated raiding increases with age. Crop raiders derived 38% of their daily forage from the short time spent raiding, consistent with expectations of foraging theory. Males may be more likely to learn crop raiding because they are socially more independent and experience intense mating competition than females.

Key words: behaviour, conflict, crop raiding, elephants, life history, Uganda

Résumé

Nous avons examiné les modèles de l'incursion des cultures par les éléphants en prenant en compte le sexe et l'ge ainsi que l'histoire de vie et la sociobiologie, et avons estimé la contribution qualitative des cultures à la diète des éléphants au parc national de Kibale (KNP). La taille des crottins fut mesurée afin d'estimer l'ge et le sexe, tandis que la présence des restes des cultures fut prise comme évidence des incursions à de nombreuses reprises. Afin d'estimer la proportion attendue d'élèphants pilleurs dans chaque groupe d'ge, la distribution en ge des pilleurs fut comparée àla distribution en ge de tous les éléphants de KNP.En grande partie, les pilleurs étaient des mles. Ils commencèrent les incursions à l'ge attendu de 10 à 14 ans alors qu'un nombre inattendu firent des incursions à 20-24 ans. Les résultats suggèrent que les incursions sont initiées à l'ge où les mles quittent leurs familles et qu'une grande proportion font les incursions quand ils approchent de l'ge de la concurrence reproductrice. D'après les analyses des crottins la fréquence d'incursions augment avec l'ge. Les pilleurs retirent 38% de leur fourrage quotidien en peu de temps, ce qui conforme aux théories du fourrage. Il se peut que les mles soient plus susceptibles à faire des incursions parce qu'ils sont plus indépendants et connaissent de plus forte concurrence d'accouplement que les femelles.

Introduction

Conflict between elephants and farmers because of crop raiding is an important issue in elephant conservation in Africa (Haigh *et al.*, 1979; Bell, 1984; Thouless, 1994; Hoare, 1999). With diminishing elephant habitats, crop raiding is anticipated to increase and to play a significant role in the decline of elephant populations (Hoare, 1999). In areas where elephants and humans are in proximity, repeated raiding of crops by elephants can lead to local human displacement. Elephants and humans are often injured or killed in attempts to discourage crop raiding (Thouless, 1994; Barnes, 1996; Tchamba, 1996). If solutions to alleviate the negative impacts of elephants on humans are not found, persistent raiding of crops will

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compromise elephant conservation. In order to devise long-term techniques for managing crop raiding, some basic information on age and sex structure, foraging patterns and behavioural dynamics of crop-raiding elephants is required. This information can be a valuable starting point for deducing patterns and possible mechanisms driving the initiation, propagation and development of habitual raiding behaviour, and can offer insight in planning and designing management strategies aimed at reducing crop raiding.

To date, there is limited information on the age and sex structure of these crop-raiding elephants relative to the age-sex distribution of source populations. Because in most locations elephants raid at night, it is difficult to obtain data on the age, and sex of individual crop-raiders. We therefore used indirect techniques to obtain this information. We specifically examined the age when elephants start raiding, when a greater proportion are raiding, and when many individuals are raiding repeatedly. We related crop-raiding patterns to elephant life history events in order to identify factors that may be influencing the initiation and development of habitual raiding behaviour. Similarly, we compared foraging on crops to foraging on wild plants inside KNP in order to assess the relative contribution of crops to elephant diet and consequently to detect the motivation for crop-raiding from the perspective of optimal foraging theory.

Materials and methods

Study area

The KNP with an area of 766 km^2 is located in south-western Uganda, (Fig. 1) and consists of a medium altitude tropical forest interspersed with areas of swamp, grassland and degraded and regenerating forests (Chapman *et al.*, 1999). A portion of the KNP southern boundary is contiguous with Queen Elizabeth National Park, while the rest of the park is surrounded by extensive small-scale agriculture. The elephant population has declined from an estimated 450 animals in the 1960s (Wing & Buss, 1970) to an estimated 262 animals in 2000 (Plumptre *et al.*, 2001) because of illegal poaching and control shooting in the 1970s and 1980s (Struhsaker, 1997). Until the late 1980s, elephants in KNP were shot and killed in crop fields by the game department staff. Currently, killing elephants is illegal in Uganda even when elephants are involved in raiding crops. However, when they are able to get to the location of raiding, KNP guards chase elephants out of the crop-fields into the park using noise from rifle shots. Crop-raiding occurs throughout the year because of the prevalence of perennial banana plantations.

Estimation of age–sex structure, group size, repeated raiding and forage utilization

Because elephants in KNP raid exclusively at night, it was impossible to estimate the age and sex of elephants in the field by direct observation. In addition, direct observation during the day is difficult as after raids elephants enter the forest where it is dangerous to follow closely on foot. We therefore used indirect measures such as elephant dung characteristics, paths and footprints to estimate the age structure and group sizes of crop-raiding elephants and to establish the incidence of repeated raiding.

To estimate the age of an elephant from dung, we obtained two perpendicular diameter measurements (i.e. maximum and minimum breadth) in centimetres from at least two intact dung boli in each dung pile encountered in crop fields or inside KNP. Dung bolus circumference was calculated from the mean diameter of these intact boli. The age of elephants voiding these boli was determined using bolus circumference to age conversion curves (Jachmann & Bell, 1984). The age structure was then determined from the frequency of dung-boli sizes corresponding to age estimates. The utility of dung boli measurements for estimating age in elephants has been validated in African elephants whose ages were estimated from photogrammetric techniques (Jachmann & Bell, 1984), and in semi-captive Asian elephants (Reilly, 2002). These studies determined that dung bolus size can be used to reliably estimate age in elephants 0–25 years old. Above 25 years of age, dung boli size is unreliable for detecting age differences (Jachmann & Bell, 1984) hence dung from individuals >25 years was lumped into one age category.

Because male and female elephants older than 15 years differ in bolus size, we needed to know the sex of individuals in order to estimate age from dung (Jachmann & Bell, 1984). To construct age structure when the sex of individuals voiding dung is unknown however, we need to know the sex ratio of the elephant population. In this study, we assumed a 1 : 1 sex ratio (Moss, 2001) and used a method provided by Jachmann & Bell (1984) to construct the age structure for the KNP elephant population and for crop-raiding family groups. Although the use of dung measures to estimate age in elephants can be limited to populations in which this technique has been validated due growth variation between populations, we do not,

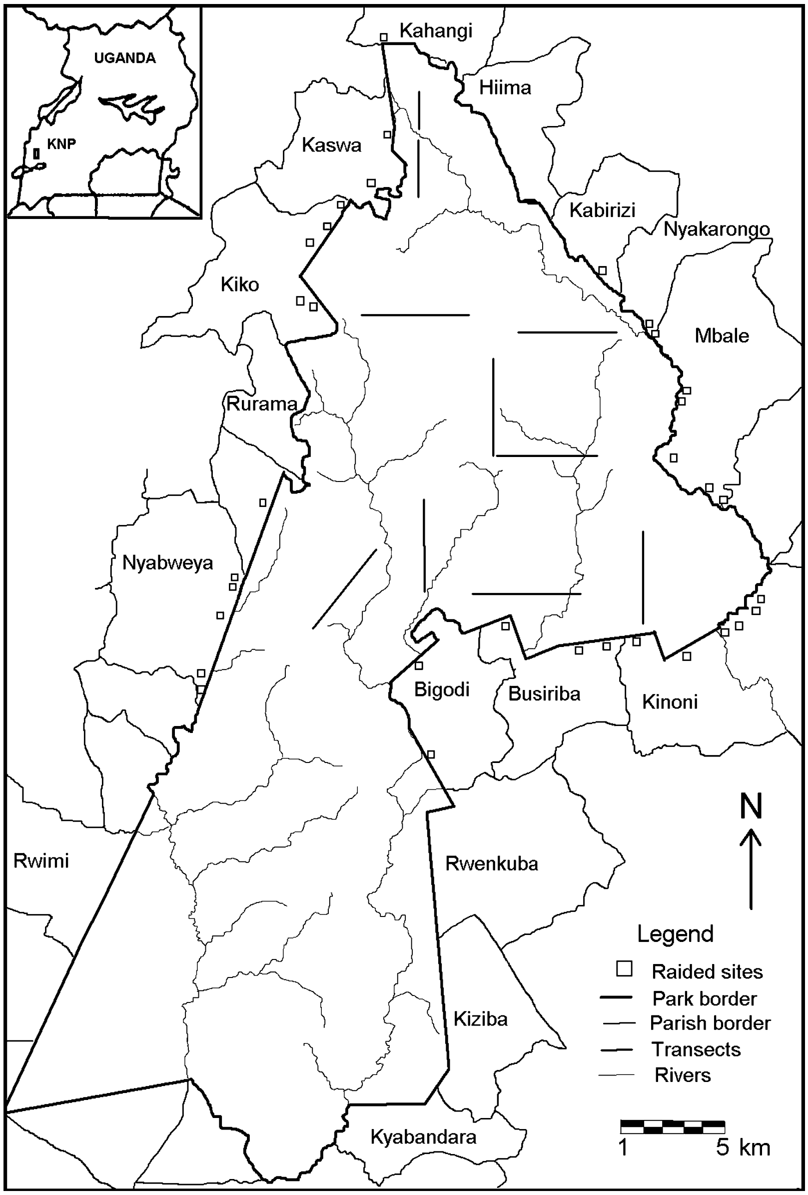

Fig 1 Map of KNP showing the location of sites raided by elephants and transects used to census dung. The location of KNP is shown (inset)

suspect any significant growth variation between Kasungu and KNP elephants because a few dung measurements taken from adult KNP elephants (Wing & Buss, 1970) are comparable with measurements from similarly aged Kasungu elephants (Jachmann & Bell, 1984).

We distinguished between male and female elephant groups raiding crops from the presence or absence of dung and footprints from elephants ≤6 years, as male elephants between 6 and 8 years begin to spend 25% of their time outside their family groups in the company of other males (J. Poole, P. Lee & C. Moss, unpublished data). Given that the common calving interval in elephants is 3–5 years (Moss, 2001) and that calves in this age category always stay close to maternal family groups (Owen-Smith, 1988; Lee & Moss, 1999), family groups were expected to consist of at least a 6-year-old calve. Raiding groups with a calf (<6 years old) were therefore assumed to be composed of family groups, while the absence of dung from individuals under this age was interpreted as involvement of mostly male groups. This method of inferring male and female elephant groups has been successfully used by Balasubramanian *et al.* (1995) and is likely more reliable in populations with a high proportion of juveniles as most adult females would likely have a calf (see Results).

The group sizes of crop-raiding elephants were primarily determined from the number of entrance and exit paths in the crop field and secondarily from footprint and dung characteristics. For each raid, we counted the number of entrance and exit paths at the KNP and farm interface. For the maximum number of paths counted, we followed each path and examined the footprint characteristics (size, shape and stride pattern), dung characteristics (size, texture and composition) and the number of other paths branching off from these paths. We then used this information to determine the number of elephants using each path and from this estimated the group size of crop raiders. For any raiding incident, dung from different individuals could be determined based on variation in size (boli diameter), texture (fibrous, woody or watery), and composition (whether dominated by leaves, grass, wood, bark, fruit, or crop remains). Although these techniques are difficult to employ when group sizes are large, they were useful during this study because, elephant group sizes were small.

The incidence of repeated raiding by the same elephants was evaluated using the presence of identifiable crop remains (e.g. maize kernels, millet grains and banana leaves) in dung sampled from crop fields. Given a food passage rate in an elephant's gut of about 21–46 h (Rees, 1982), the presence of crop remains in dung found inside crop fields was used as evidence of repeated raiding by the same individuals within a period of 24–40 h. Additional data on the incidence of repeated raiding by elephants were collected by tracking groups of crop-raiding elephants. Elephant tracks were followed from crop fields into KNP for a minimum distance of 5 km or until elephant tracks could not be traced. The distance moved by crop-raiding elephants per day was then calculated for groups that were successfully followed from crop field through forest and back to crop field.

We quantified the number of stems that elephants fed on by tracking their paths through crop fields and inside KNP. After a raid, we followed a single path in crop fields and forests, counting and identifying all the plants fed on by elephants. In forests, elephants eat specific plant parts, so it is straightforward to count the number of plants eaten from browsing signs (Short, 1981). Although this technique may underestimate the amount of forage elephants consume, it is the only practical technique available for assessing the diet of elephants in forest habitats. Similarly, we could count the number of crop stems eaten by elephants because elephants ate mostly maize fruit and banana leaves or stems, leaving behind other plant parts. The time elephants spent foraging on crops was estimated from incidental accounts of farmers who observed when elephants entered and exited crop fields.

Data sampling and analysis

Data on the age structure estimates from dung boli measurements for all KNP elephants were collected from nine 5-km transects (Fig. 1). These transects were located to represent major vegetation types. Once every 2 months between November 1996 and November 1997, we enumerated and measured dung along transects. Data on the age structure of crop-raiding elephants were collected between January 1999 and June 2001. We collected data on crop raiding in the northern parishes that received intensive raiding (Kiko, Kaswa and Kahangi, Fig. 1). The KNP boarder with these parishes was monitored three times a week for elephant incursions into crop fields. For each observed incursion, we estimated the ages and group sizes of elephants.

Age structure of elephants in KNP was estimated from the frequency of dung boli sizes corresponding to different age classes. For crop raiders, however, a higher frequency of dung from some age classes can result either from repeated raiding by members of the respective age classes or many individuals raiding from those age classes. Because the frequency of dung from crop fields does not directly reflect the number of raiding individuals in the respective age classes, we estimated the probability of finding crop remains in the dung of crop raiders from each age as a proxy for repeated raiding using logistic regression (Agresti, 2002).

We used our estimated probability of repeated raiding by members of an age group and data from the age distribution of dung boli from the entire park to calculate the expected age distribution in crop fields (Table 1). The relative frequency of individuals from different age classes raiding was inferred by comparing the observed age distribution of crop raiders with the expected age distribution (i.e. age ratios from the entire KNP elephant population). To make this comparison while controlling for bias in age distribution because of differences in sampling time, we calibrated the age data for all KNP elephants, including crop raiders, to reflect age distribution in 2000 by adding or subtracting 1–3 years from age data collected prior to or after 2000 respectively. We chose the year 2000 because 56% of the age data from crop-raiding elephants was collected in 2000. We then used this calibrated elephant age data in our analysis and employed chi-square analyses with Bonferroni confidence intervals (Byers & Steinhorst, 1984) to evaluate whether elephants from all age groups raided in proportion to their availability in the entire KNP population. We interpreted a significantly higher than expected dung frequency for an age class as a higher than expected proportion of individuals from that age class raiding.

Results

The youngest recorded age estimate of an elephant raiding crops was 7 years (0.4% of dung for this age from crop raiders, n = 213), whereas the youngest recorded age from the entire elephant population inside KNP, including raiders and nonraiders, was <1 year. Dung from ≤6 years old elephants constituted 36% of dung inside KNP and was absent from the dung of crop raiders (Fig. 2). From these data we infer that crop raiders are likely to be predominantly males, because dung from young animals would likely be present if females raided crops.

The age distribution of crop raiders based on dung measured in crop fields was significantly different from the expected age distribution based on the size distribution of dung piles measured inside KNP adjusted for the variation of repeated raiding by age (Table 1) and the difference in sampling time. Dung from crop raiders occurred at the expected frequency for elephants 10–14 years of age and at higher than the expected frequency for elephants 20–24 years of age (Table 1). This result suggests that higher than expected proportions of individuals in the 20–24 years age class are raiding crops. Dung from elephants 15 years or older constituted 71% of dung sampled from crop fields, suggesting that most crop raiders are pubertal and postpubertal males.

The presence of crop remains in dung piles found in crop fields revealed that repeated raiding by some animals was common. The probability of obtaining crop remains from the dung of crop raiders was significantly predicted by the age of elephants ($\chi^2 = 9.358$, $P = 0.002$, n = 213) with the occurrence of crop remains increasing with age (Fig. 3). This result suggests that the incidence of repeated raiding increases as elephants grow older.

By following elephant tracks we confirmed that some male elephant groups raided repeatedly for two to four successive nights (Table 2). These repeatedly raiding groups stayed near cultivation during the day and made

Table 1 Chi-square analysis for goodness of fit between observed and expected age frequency estimates of crop raiders in KNP in 2000

Age class	Observed dung frequency	Expected dung frequency (±95% Bonferroni intervals)	χ^2-value	P-value (d.f. = 1)
5–9	13	57 ± 17	33.965	0.000
10–14	59	57 ± 17	0.070	0.791
15–19	61	48 ± 16	3.521	0.061
20–24	50	14 ± 10	92.571	0.000
≥25	30	36 ± 15	1	0.317
All	213	213	131.127	0.000 (d.f. = 4)

Observed frequency is the relative frequency of dung piles from crop raiders within each age class counted from crop fields in 2000 plus data from 1999 and 2001 ± 1 year (n = 213). Expected frequency is the relative frequency of dung piles from various age categories derived from dung counted inside the park in 1997 with 3 year added to each data point to account for the temporal differences in sampling. For each age class we added the proportion of dung resulting from repeated raiding and estimated the expected proportion of dung piles expected per age class from the crop fields (equation below).

$$E_x = \frac{P_x N + P_x N R_x}{\sum_{i=1}^{n} (P_x N + P_x N R_x)} N$$

Ex is the expected frequency of dung piles from age class x, Px is the proportion of dung from age class x determined from all KNP elephants, N is the total number of dung piles enumerated in crop fields, Rx is the probability of repeated raiding by individuals in age class x (from the logistic regression) and n is the number of age classes.

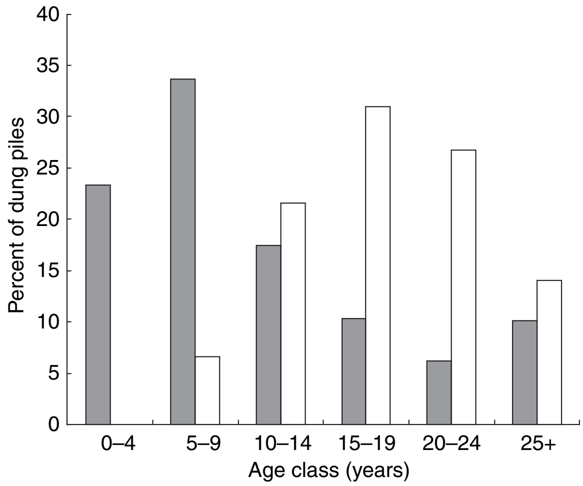

Fig 2 Age structure of the elephant population in KNP in 1997, compared with that of crop raiders determined in 1999–2001. Dark bars represent the age structure of all KNP elephants and open bars represent the age structure of crop raiders. Age was determined from boli diameters of dung piles sampled inside the park (n = 242) and from crop fields (n = 213)

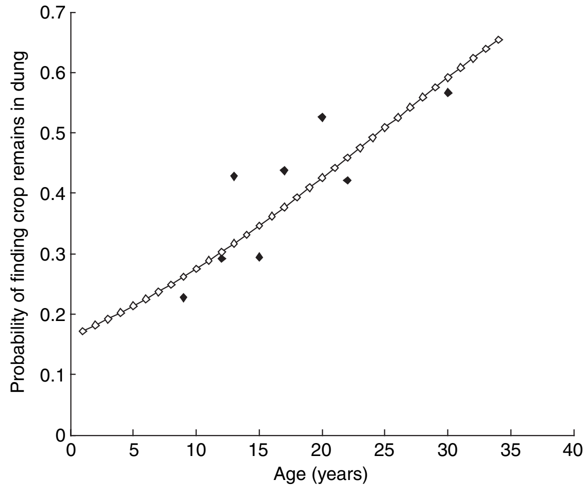

Fig 3 Incidence of habitual raiding expressed as a probability of finding crop remains in dung from elephants of a given age in KNP. The line connecting open squares shows the predicted probability derived from dung piles enumerated in crop fields (n = 213) using a logistic regression model. The open squares show the observed probability derived as a ratio of dung in each age class containing crop remains

Table 2 Evidence of habitual raiding from follows of crop-raiding elephants in KNP, Uganda. Distance in kilometres moved per day is calculated from groups followed from crop field to KNP and back to the field whose date for crop damage was known

Date of crop-raiding	Group size	Number of consecutive raids	Distance moved (km day^{-1})
9/2/97	2	3	3.00
9/3/97	4	3	2.05
11/3/97	4	3	2.20
6/4/97	5	2	–
3/5/97	2	4	2.80
4/5/97	2	4	1.90
19/5/97	8	2	–
6/7/97	3	2	–
3/8/97	7	1	–
5/8/97	4	1	–
7/8/97	8	1	–
17/8/97	1	1	–
1/4/01	5	3	5.40
19/5/01	6	2	5.90
25/5/01	5	2	–
Mean ± SD			3.32 ± 1.65

nightly incursions into crop fields. During the day, these groups foraged within 5 km inside the park boundary, moving on average 3.3 km daily (Table 2). The mean (±SD) number of plant stems consumed inside KNP by crop-raiding elephants was 220 ± 89 (n = 5) tree and shrub stems per elephant per day. While in crop fields raiders ate on average 137 ± 91 banana stems per day during an average of 2.6 h (n = 36) of raiding. This observation suggests that crop-raiding elephants derive 38% of their daily intake of plant stems during a short period of time foraging on crop fields. These observations were confirmed by following one group, consisting of a sub-adult and an adult male 13 and 25 years old respectively. This pair visited crop fields for three consecutive nights and derived about 18–31% of daily food intake from approximately 0.5–1.0 h per night of foraging in crop fields.

Elephants raided in groups of one to eight individuals per raiding event (mean = 4, median = 4.5, mode = 5). Few lone raiders were observed during this study (Fig. 4). From raiding events in which the age of all elephants were assessed (n = 22 raiding events), the oldest individuals were often ≥25 years old in 32% of events or ≥20 years old in 54.5% of events. However the oldest individual was ≤15 years of age in only 13.6% of raiding events. These results suggest that although young males may occasionally venture to raid alone, they most often raid in the company of older males.

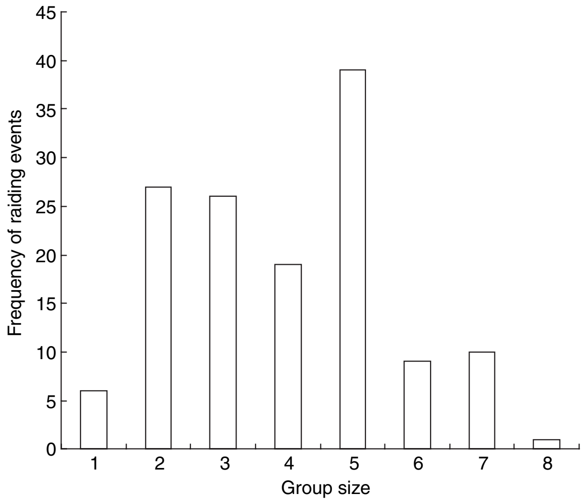

Fig 4 Group sizes of crop-raiding elephants observed in crop fields between 1997 and 2001 in KNP, based on 137 raiding incidences

Discussion

Results suggest that crop raiding is related to dispersal and other developmental events in the life history of male elephants. At the age of 6–8 years, coinciding with the age when they start raiding for the first time, male elephants start becoming peripheral to their natal families, spending up to 25% of their time in the company of other males (J. Poole, unpublished data). In addition, male elephants initially raid in frequencies concordant with their abundance at 10–14 years of age. This age class includes the mean age of natal dispersal observed in male elephants (13.8 ± 1.7 years in Amboseli elephants, J. Poole, unpublished data). During this study, the greatest proportions of elephants involved in raiding were in the 20–24 years age class. This age class coincides with the postpubertal period of 20–25 years of age when males are approaching reproductive age and are starting to show distinct periods of sexual activity (Poole, 1994).

Crop-raiding in elephants appears to begin when male elephants leave their maternal family units. During this time, they begin to seek for new feeding areas, and this activity may bring them into contact with crops. Without knowledge of foraging areas, these males will find crops a reliable and predictable resource that is less likely to be competed for with large dominant bulls. In addition, dispersing males may begin crop raiding as a result of increases in exploratory drive, in risk-taking behaviour, in caloric intake, and in growth commonly experienced by many mammals during the pubertal period (Spear, 2000; Macri *et al.*, 2002; Romeo, Richardson & Sisk, 2002). This pubertal behaviour has been observed to increase the probability of crop raiding in sub-adult males relative to other age-sex groups in primates (Forthman-Quick, 1986; Chapman, Lawes & Macleod, 1998; Saj, Sicotte & Paterson, 1999).

Males raiding crops when they are approaching reproductive age, and beginning to show distinct periods of sexual activity and thereafter may benefit from increased nutrition as crops are known to be rich in nutrients than wild forage (Sukumar, 1989; Osborn, 1998). Improved nutrition from raiding can lead to increased body size and extended musth periods which in turn enhances a bull's competitive ability during mating (Poole, 1989). Although females would also benefit from crop raiding, with improved nutrition leading to shorter inter-birth intervals and healthier babies, the risks of crop raiding are higher for females as they live in groups consisting of kin. In addition to risking their lives during crop raiding, matriarchs would risk the lives of their offspring and siblings as well (Sukumar & Gadgil, 1988). Females invest enormously in their offspring than males and if these offspring are juveniles, they risk being trampled or lost when the herd is frightened during raiding. In Kenya for example, female elephants reduced their frequency of raiding crops more than males did when the risk of raiding increased through the installation of an electric fence around crop fields (Thouless & Sakwa, 1995).

Habitat quality may also affect a female group's decision to raid crops. For example, female Asian elephants, raid more often in fragmented habitats than in optimal habitats, whereas males will raid in both optimal and fragmented habitats (Sukumar, 2003). The tendency for males to raid more than females in optimal habitats is thought to result from intense mating competition among males relative to females such that any slight nutritional advantage gained from crops translates into larger size or extended duration of musth providing raiders with a competitive edge over nonraiders (Sukumar & Gadgil, 1988). Female elephants in KNP may be reluctant to take risks involved in raiding crops partly because forage resources inside KNP may be optimal, an observation supported by the remarkable diversity of habitats in KNP (Wing & Buss, 1970).

Our results are also consistent with the idea proposed by Sukumar (1989) and Osborn (1998) that crop-raiding is an optimal foraging strategy. Crop raiding may help maximize foraging efficiency by reducing time spent and distance travelled while foraging. Evidence from daily foraging of repeat crop raiders demonstrates that elephants consume more food during short crop raids than during the time spent foraging in KNP assuming that these elephants spend an average of 16 h feeding as observed in other populations (Owen-Smith, 1988). As a result of gaining a great deal of their nutritional needs while raiding, raiders may also travel shorter distances compared with nonraiders. Daily ranging of KNP crop raiders was low (3 km) compared with known daily ranging of non-crop-raiding elephants in areas with vegetation similar to that observed in KNP (e.g. 6 km in Theuerkauf & Ellenberg, 2000 for the Bossematie Forest and 12 km in Merz, 1986 for the Tai forest). Results from this study are however, comparable with a mean daily distance of about 2 km travelled by crop-raiding elephants in Bia National Park, Ghana (Martin, 1991).

This study also confirmed that repeated raiding occurs in KNP, as observed elsewhere across Africa (Bhima, 1998; Hoare, 1999) and Asia (Sukumar, 1994). Evidence of repeated raiding was most common in postpubertal male elephants, suggesting that crop raiding is learnt behaviour. Males may be more susceptible to learning crop raiding because they are socially more independent, and their behaviour is driven by mating competition than females. Similarly, the need to find new feeding sites, and occasional associations with older and experienced raiders during dispersal, may predispose young males to develop crop-raiding behaviour. Once exposed to crop raiding, some elephants may grow accustomed to obtaining nutritious forage easily and may adopt crop raiding as a primary form of foraging. In older postpubertal males that have begun raiding, the increasing nutritional demands for growth and maintenance of musth may reinforce repeated raiding behaviour.

Compared with many studies (e.g. Sukumar, 1994; Bhima, 1998; Hoare, 1999), a low frequency of solitary bulls was observed raiding in KNP but was similar to group sizes of two to eight elephants reported for crop-raiding forest elephants in West Africa (Jeffrey, 1970). In other studies, large solitary males caused most damage to crops and their frequency of raiding was higher than that of younger bulls, which raided in groups of two to six individuals (Sukumar, 1994). The low frequency of solitary individuals raiding crops in KNP could be the result of poaching in the 1970s and 1980s removing the majority of older males in the population (Moss, 1990).

The results from this study provide the first attempt to link crop-raiding by African elephants to life history events, and in addition to Osborn (1998), to suggest that crop-raiding is an optimal foraging strategy. These findings imply that, for areas in which raiding is caused in part or entirely by males, raiding will remain a management problem that will demand continued attention as young males leave their family units or as males enter reproductive competition.

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