Socio-Ecology and Behavior of Crop Raiding Elephants in the Amboseli Ecosystem, Kenya

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor of Philosophy in the Department of
Biology in the Graduate School
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2010

<u>ABSTRACT</u>

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Abstract

Risky foraging is a male reproductive tactic in most polygynous mammals. It is speculated to result from intense intra-sexual reproductive competition. Consequently this behavior has been speculated to increase a male's reproductive competitiveness. However, individual males may differ in their propensity to take foraging risks.

We therefore conducted a study on crop raiding behavior (a risky foraging strategy) in African elephants from the greater Amboseli ecosystem, in southern Kenya. We specifically examined the population sizes, gender and patterns of raiding elephants and investigated the effect of crop-raiding and genetic heterozygosity on male body size. We also examined the influence of age and genetic relatedness on observed patterns of association. Finally, we examined the role of life history milestones, association patterns and social structure on the acquisition of crop raiding behavior among wild free ranging male African elephants. With regard to the influence of association patterns on crop raiding behavior, we were specifically interested in understanding the mechanisms by which social learning might occur among male elephants.

Our results showed that 241 elephants from different populations in the ecosystem converged to raid farms. Approximately 35% of raiders were from Amboseli National Park, and the rest were other populations in the ecosystem. We observed only post-pubertal males but not females to raid. About one third of post-pubertal males from the Amboseli population were raiders. We found evidence of habitual raiding by some individuals. Crop raiding predicted post-pubertal male size, with raiders being larger than non-raiders. This result suggests that taking risks pays off for males. Our results also showed that other variables known to influence growth like genetic heterozygosity had no effect on size-for-age in male elephants, because low-heterozygosity males were rare. The probability that an individual male is a crop raider was greater for older individuals than young males. The probability that a male is a raider was greater when his two closest associates were raiders versus when they were not raiders and when a male's second closest associate was older, versus when his second closest associate was of similar age or younger. These results suggest that increasing energetic demands associated with life history milestones and social learning play a significant role in the initiation of crop raiding behavior. Raiders did not cluster into separate social units from non-raiders, probably due to the nature of social learning exhibited by this species and due to the diffuse nature of male elephant social units.

These results have implications for understanding the evolution of risky foraging behavior in males, and for understanding the role of kin selection, dominance hierarchies and social learning in male elephant social systems. Results also have implications for understanding the spread of adaptive complex behavior in natural populations.

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Acknowledgements

Many individuals and organizations contributed to the development and successful completion of this dissertation. Here, I acknowledge their contributions and support.

First I like to thank my advisor Susan Alberts for her terrific mentorship, scientific insight and guidance throughout the development of the ideas presented here, their implementation and finally her help during the writing of this dissertation. Secondly, I would like to thank members of my academic committee, James Clark, Stephen Nowicki, Stuart Pimm and Will Wilson for their thoughtful comments during the proposal development and throughout the implementation of this research. Their ideas and comments helped shape the questions addressed in this dissertation.

This work would have been inconceivable without the support of Cynthia Moss, Joyce Poole and Phyllis Lee of the Amboseli Elephant Research Project (AERP), the research arm of the Amboseli Elephant Trust (ATE). Cynthia Moss founded AERP in 1972 and has directed the project since its inception. AERP has maintained complete data on individual elephant life histories and has the longest data of this kind on elephants. I am grateful to Cynthia for giving us access to this data. As I was developing research questions for this dissertation, most research ideas addressed in this dissertation were conceived during a meeting between Joyce, Susan and I in 2004. I am grateful to Joyce Poole for her support during the entire course of this study. The study

on the effects of crop-raiding on elephant size (Chapter two) was made possible in part by the availability of data from the ongoing research on growth of African elephants conducted by Phyllis Lee. This chapter was written in collaboration with Phyllis Lee who provided her long-term data on elephant footprint sizes.

In the field, Norah Njiraini, Katito Sayialel and Soila Sayialel, were more than, a knowledge base on elephants and the Amboseli ecosystem but they also provided logistical support during the field season. First, they provided their expert knowledge on elephant bull identification and I by the end I was able to learn and benefit from this knowledge. Second they showed me around Amboseli National Park and areas to find elephant bulls.

Outside of the Park and for the work on elephant crop raiding in farms, I was introduced to the farmers by John Kioko. I am thankful to Kioko for this role and for identifying the field assistants that I worked with. I am grateful to my field assistants, Timothy Saigilu, Elijah Lekeni and John Teete for their help in collecting data on the crop raiders. I would not have been able to collect elephant dung from such a wide area of farmland or track and identify raiders without their help.

While carrying out field work, AERP camp was my home during the first year of field work and the Kimana bush camp of the School for Field Studies (SFS) was my home during the last two years of field work. I am thankful to Cynthia Moss and Simon Ole-Seno, the directors of AERP and SFS respectfully for providing me accommodation in their camps. I would also like to thank Josephat Makanga, Peter (AERP) and James Waome for the wonderful meals while I resided in these camps.

While at Duke University, I am grateful to the staff of the biology department for ensuring that I had all I needed as a student and for helping me keep track of routine requirements from the graduate school. Particularly, I would like to thank Anne Lacey, Jill Foster, Johanna Bernhardt, Jim Tunney, Renee Puryear, Jennifer Foreman, Lisa Bukovnik and Andrew Turnier. I am grateful to the members of the Alberts lab, past and present for their intellectual stimulation. This work benefited greatly from past genetic work on elephants by members of the lab; Beth Archie and Julie Hollister-Smith.

This project would not have been implemented without generous funding from the US Fish and Wildlife Service grant number AFE-0314/6-G085, the National Science Foundation (IBN0091612) to S.C. Alberts, the Amboseli Trust for Elephants (ATE). My studies at Duke University were funded by the Duke University Graduate School and the Biology Department.

We thank the Office of the President of the Government of Kenya for permission to conduct this research through permit number MOEST 13/001/35C 225. We thank Kenya Wildlife Services (KWS) and Amboseli National Park staff for their hospitality and support during the study.

Finally, I would like to acknowledge the support of my family and many friends in Kenya, and North Carolina. From my family I like to thank my father for his encouragement, mother for caring about my wellbeing and to James for being a friend and a colleague.

1. Introduction

1.1 Risk Behavior as a male reproductive tactic

More males than females in most polygynous species studied so far have been observed to take crop raiding risks. Examples include, Hanuman langurs (Chhangani & Mohnot 2004), vervets (Saj et al. 1999), African elephants (Bhima 1998), Asian elephants (Sukumar & Gadgil 1988), Chimpanzees (Hockings 2007; Wilson et al. 2007) and Anubis baboons (Forthman-Quick 1986; Maples et al. 1976). Parallel behaviors in the wild where males are more likely than females to risk predation in order to forage in food-rich patches or habitats where predators are present is common. Examples include, fallow deer, (Apollonio et al. 2005) roe deer (Mysterud et al. 1999), Dall's sheep (Corti & Schackleton 2002), bighorn sheep (Berger 1991; Mooring et al. 2003), African buffalo (Hay et al. 2008), western grey kangaroo (MacFarlane & Coulson 2007), mountain sheep (Bleich et al. 1997), elk (Winnie & Creel 2007) moose (Miquelle et al. 1992) and Eurasian lynx (Bunnefeld et al. 2006; Odden et al. 2002). In all these situations males seem to be maximizing nutrient intake to enhance growth at the expense of mortality risk from predation. Studies looking at vigilance rates and habitat use in relation to predation risk have also observed males to be risk prone and females to be risk averse. Examples include, elk (Childress & Lung 2003), fallow deer (Cuiti et al. 2004), alpine ibex (Grignolio et al. 2007), thinhorn sheep (Loehr et al. 2005), rhino (Berger & Cunningham

1995), Columbian blacktailed deer (Stankowich & Coss 2006), impala (Matson et al. 2005), and Thompson's gazelle (Walther 1969).

Risky foraging can therefore be considered a male reproductive tactic in most polygynous mammals. It is speculated to result from intense intrasexual reproductive competition (Trivers, 1985). Consequently this behavior has been speculated to increase a male's reproductive competitiveness (Sukumar & Gadgil 1988). In most polygynous mammalian systems male reproductive competitiveness is influenced by body size and social dominance (Pelletier & Festa-Bianchet 2006). Larger and more socially dominant males achieve higher reproductive success than smaller subordinate males. However, body size and social dominance are highly influenced by numerous factors including notably age, nutrition and genetic quality. In elephants, and most ungulates, males experience condition dependent reproductive strategies like musth and rut respectively. Most mating in these mammalian groups occurs during musth, or rut. Large males receiving good nutrition can sustain long episodes of musth and rut during the breeding season. Very little empirical research has been undertaken to assess the reproductive benefits of risky foraging behavior.

Individual males may differ in their propensity to take foraging risks such as crop raiding (Sukumar 1995). The processes that generate individual differences in risk taking are well understood from a psychological and evolutionary perspective. For example, risk taking is a trait correlated with a suite of other behaviors such as exploratory behavior, neophilia, impulsivity and dispersal (Jones & Godin ; Sih et al. 2004; van Oers et al. 2004). However, much less is known regarding individual differences in risk in a population from an ecological perspective. Social learning from peers or older individuals and energetic demands associated with some life history stages such as age at dispersal, age of first reproduction and age of attainment of reproductive peak are likely motivating factors. Association patterns likely modulate the spread of this behavior in populations through social learning (Boogert & Reader 2008).

We therefore conducted a study on crop raiding behavior (a risky foraging strategy) in African elephants from the greater Amboseli ecosystem, in southern Kenya. We had four major objectives in this study. First we wanted to establish the number of elephants that raid crops, their gender, and their patterns of raiding (Chapter 2). Secondly we investigated the effect of high-risk foraging behavior (crop-raiding) and genetic heterozygosity on male body size (Chapter 3). Finally, we investigated the role of life history milestones, association patterns and social structure on the acquisition of crop raiding behavior among wild free ranging male African elephants. We also investigated the mechanisms by which social learning might occur among male elephants (Chapter 5).

2. Crop-raiding elephants: population sizes and raiding patterns estimated from molecular and observational techniques

2.1 Introduction

Conflict between humans and wildlife is a major conservation concern because a number of protected species frequently come into conflict with humans through their depredations on crops and livestock, including some whose conservation status is considered endangered, threatened or vulnerable such as elephants, chimpanzees, gorillas, lynxes, lions and cheetahs (Basille et al. 2009; Hoare 1999; Hockings & Humle 2009; Hockings 2007; Marker et al. 2003; Patterson et al. 2004). This conflict can be a major cause of wildlife mortality, thereby accelerating the demise of populations that are already experiencing dramatic declines from habitat loss (Andren et al. 2006; Tumenta et al. 2009). Sometimes entire local populations are decimated as farmers secure their crops or livestock from depredation by killing or injuring wildlife that may represent a threat (Example; Haigh et al. 1979). The prevailing paradigm for the management of large protected vertebrates that come into conflict with humans is the selective culling or translocation of offending individuals. This approach assumes that a few 'problem individuals' cause most of the conflict with humans and that their removal will dramatically reduce the level of conflict (Linnell et al. 1999; Sukumar 1991; Sukumar 1995). However, in spite of the threat to protected species' populations posed by human-wildlife conflict, very little is known about the demographics of animals causing conflict in large natural wildlife populations. Information on the proportion of animals that cause conflict, their gender and individual frequency of involvement in conflict, is important information for designing potential measures for alleviating conflict as well as for inferring the ultimate drivers of behavior that causes conflict. For example, data on the propensity of individual animals to cause conflict is useful for identifying targets for aversive conditioning, translocation, culling or monitoring movement patterns to provide early warning systems for crop and animal protection. This may consequently enhance species conservation and survival in human dominated landscapes.

For elephants, crop-raiding is a major form of conflict with humans and poses a threat to their conservation (Hoare 2000). Although there is evidence to suggest that in Asian elephant populations a few elephants cause the most damage to crops in a given area (Sukumar 1995), there has been no systematic attempt to estimate the population sizes of crop raiders in African elephant populations. Attempts to examine gender and patterns of crop raiding by African elephants have relied on either indirect evidence (Chiyo & Cochrane 2005) to establish sex and raiding patterns of the offending elephants or on reports from farmers (Jackson et al. 2008). Because crop-raiding by elephants appears to occur exclusively at night, determining elephant sex and individual identities or estimating elephant numbers can be difficult, often leading to inaccurate reports from farmers or incomplete information in case of indirect methods.

Recent advances in non-invasive molecular censusing techniques make it possible to estimate population sizes of crop-raiding elephants. However, the costs associated with non-invasive molecular censusing can be high, and sample sizes and mean recapture rates are often small. Moreover, the probability of capture is likely to vary for individual elephants, and molecular census data from crop raiding elephants will therefore have a capture probability bias. This bias in capture probability poses problems for population estimation models because males that raid repeatedly will be over-represented in the census and those that raid rarely will become increasingly under-represented. In these circumstances, population size is not identifiable and population estimates are model dependent (Link 2003). This is because the observed distribution of raiding by individual elephants will not contain a reliable count distribution for making inference on the unobserved number of raiders (Link 2003). Confronted with this dilemma, it is important to choose a model for estimating population *a priori* using data simulations.

In this study, we had four goals. The first goal was to estimate the total population size of raiders in the Amboseli ecosystem. The second goal was to estimate the proportion of total raiders originating from the elephant population from Amboseli National Park, because the agricultural areas we monitored are in proximity to three contiguous elephant populations. To achieve these two goals, we had to determine *a priori* a suitable model for estimating population size from data characterized by small sample sizes, low mean recapture rates and heterogeneity in capture probabilities among individuals. To do this, we tested two classes of models through simulations; three asymptotic models (specifically, negative exponential, Michaelis-Menten and Chessel; (Examples: Eggert et al. 2003; Kohn et al. 1999; Meijer et al. 2008) and three count models known to be robust to heterogeneity in the probability of individual recaptures (i.e., poisson-mixture, Zelterman and Chao; examples can be found in (Böhning et al. 2005; Chao 1987; Zelterman 1988). Although the performance of asymptotic regression models is well established for small sample sizes and mean recapture rates (Frantz et al. 2004), their performance when capture probability varies among individuals has not been investigated. Similarly, the performance of count models when sample sizes are less than 100 such as some samples in this study is unknown. Our third goal was to investigate the patterns of crop raiding by individually identified elephants. We were interested in testing for the presence of habitual raiding behavior using the distribution of individual raiding frequencies. Finally, our fourth goal was to determine gender differences in raiding patterns.

2.2 Methods

2.2.1 The study population and study area

Farms that we monitored for crop raiding were located where three major elephant populations are contiguous in their range. These populations include the Amboseli National Park elephant population (hereafter the "Amboseli NP population" or “Amboseli NP elephants”, the Kilimanjaro National Park population (hereafter the “Kili population” or “Kili elephants”), and lastly, the elephant population centered in Kimana Sanctuary and the adjacent Tsavo and Chyulu National Parks (hereafter the “Kimana-Tsavo” population” or “Kimana-Tsavo elephants”; see (Douglas-Hamilton et al. 2005; Figure 1). In this study we were most interested in raiding elephants originating from the Amboseli National Park (ANP), for several reasons. First, this population has been studied since 1972 by the Amboseli Elephant Research Project (AERP) and all elephants that have been born to the Amboseli NP population are individually known and recognizable from pinnae and tusk characteristics, natural body marks, and body shape. Secondly, all Amboseli NP elephants have ages assigned to them, allowing us to examine raiding behavior in relation to age. Elephants born in 1975 onwards have their ages estimated to within 2 weeks whereas those born between 1972 and 1974 have ages estimated to within 3 months. However, elephants born before 1972 have their ages estimated to within 5 years using measurements of shoulder height, hind footprint length and body shape (Lee & Moss 1995; Moss 2001). Lastly, about 50% of the adult elephant population in Amboseli NP have been genotyped (Archie et al. 2008; This study) including 251 genotypes from a total of 471 adult females (≥12 years old), and 110 genotypes from a total of 275 adult males (≥15 years).

2.2.2 Field recognition of raiding elephants and fecal sample collection

We monitored frequently raided farms in Namelok, Isinet and Sompet (see Figure 1) between September 2005 and December 2007 with the help of three assistants. We collected two types of data depending on whether we followed and located raiders or not.

When we followed and located raiders, we determined their sex, took photos of their left and right ears for identification and lastly, we classified raiders as either Amboseli NP, Kili or Kimana-Tsavo elephants. Amboseli NP elephants are individually known and have a well documented recognition photo database. Kili elephants tend to be smaller and have relatively smaller ears and tusks than Amboseli NP or Kimana-Tsavo elephants. Elephants that we could not classify as Amboseli NP or Kili were classified as Kimana-Tsavo elephants. We counted 130 elephants during 37 raiding events in Sompet and Namelok. We were not able to follow elephants raiding Isinet because raiders always entered the Kimana Wildlife Sanctuary after leaving the farms, where it was difficult to track them. From the 130 raiders we saw, we were able to recognize individually (as Amboseli NP males) or classify (as Kili or Kimana-Tsavo elephants) 107 elephants. These 107 elephants included only 50 unique individuals (Figure 2) because some individuals raided multiple times. Of these 50, we identified forty two Amboseli NP males and classified one as a Kili male and 7 as Kimana-Tsavo males.

When we did not follow or locate raiders, we collected fecal samples from raided farms. Fecal collection was opportunistic, because raiders did not always defecate in crop fields when they raided. In most raiding events where elephants deposited dung, there was dung present for only some of the raiders. In order to minimize the collection of duplicate samples and increase the chance of collecting dung from as many different individuals as possible, our dung collection strategy involved locating two types of elephant tracks in or just outside fields. First we located all the tracks that were used by single individuals and for each of these tracks we collected one dung sample and assumed that all the dung on each track was deposited by a single elephant. Secondly, we located all tracks used by more than one elephant, and we collected multiple dung samples. In tracks used by multiple elephants, we subjectively treated dung as coming from two different animals if its' bolus size, consistency and composition seemed different from dung that has been collected from the same track. For each dung pile suspected to be from a different individual, we collected the outer layer of feces (rich in mucus and dead cells) into a 15ml plastic capped tube containing 95% ethanol 6-24 hours after defecation. In the field, we kept these fecal tubes at room temperature for 6-12 months and once they arrived at the lab they were stored in a -80'c freezer. We collected 175 dung samples in 68 raiding events from Namelok, Sompet and Isinet farms during the 2005 and 2006 crop growing seasons.

2.2.3 Identification of raiding elephants from genotyping fecal DNA

We extracted DNA from feces using a QIAamp DNA Stool Mini Kit (Qiagen) following a modified Qiagen DNA extraction protocol (See Archie et al. 2003). All fecal DNA samples from this study were genotyped at a minimum of 5 loci and up to 8 loci. These loci included one dinucleotide loci (LAFMSO2; Nyakaana & Arctander 1998), and 8 tetranuclotide loci (LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18, and LaT24; Archie et al. 2003). We used the PCR protocols detailed in Archie et al. (2003) to amplify DNA from the loci of interest and PCR products were separated using Applied Biosystems 3730XL DNA Analyzer and run on Genemapper v.3.7 Aplied Biosystems. Microsatellites alleles were scored using GeneMarker v.1.6. (SoftGenetics). In order to minimize error due to spurious alleles and due to allelic dropout, we genotyped each sample twice if the initial PCR product was scored as a heterozygote and three to four times if it was a homozygote (Archie et al. 2006). We successfully amplified 112 of 175 fecal samples we collected from farms.

Genotype matching was a two stage process. At the first stage, we wanted to discover repeated crop raiders by identifying dung deposited by the same crop-raider from multiple raiding occasions; to do this; we matched genotypes from feces collected in farms. At the second stage we wanted to identify crop raiders by matching genotypes from fecal DNA extracted from feces collected in farms with genotypes of known Amboseli elephants. In order to match genotypes, we had to determine the minimum number of loci required to discriminate between genetic samples collected from different individuals. We determined the minimum number of loci by calculating the probability of identity (PI) or the probability that a dyad will match at a specified number of loci. Previous studies identified a PI threshold of 0.0001 to sufficient for discriminating between genotypes of different individuals (Creel et al. 2003; Waits et al. 2001) and we thought to identify the number of loci to would provide a similar threshold for our study population. We calculated PI as the ratio of the number of matches from all dyadic comparisons of 586 Amboseli elephants for a specified number of loci. We also calculated PI from a theoretical expectation based on Hardy-Weinberg equilibrium and allele frequency using the formulae provided by Waits et al (2001). From calculated PI values, genotyping four loci (i.e. PI =0.00004) was sufficient for individual identification (Table 1). We therefore treated two genotype samples as coming from the same individual if four or more loci matched. We also allowed for a mismatch at a maximum of one additional locus for matched pairs to account for possible genotyping errors. Using this criterion, we matched similar genotypes using the CERVUS software (Kalinowski et al. 2007; Marshall et al. 1998).

We matched genotypes from 112 fecal samples and found 67 unique genotypes. Twenty unique genotypes matched Amboseli NP males and 47 genotypes did not match any known genotypes of Amboseli NP elephants.

2.2.4 Effect of variation in mean recapture and recapture probability on population estimates

In order to choose an appropriate model for our data, we tested the accuracy and precision of asymptotic regression and count model estimators when the mean of recapture is small and recapture probability varies across individuals using simulated data. These simulated data enabled us to compare the population size estimates from the different models with the true value that they are estimating. We generated data using poisson and negative binomial distributions to simulate random (each individual is equally likely to be captured) and non-random (some individual are more likely to be captured) recapture probabilities respectively. For both the poisson and negative binomial distribution, we generated 31 data sets of size N=100 random integers, each with a mean equal to 2, 1 and 0.5. For these data, the number of integers (N) represents the population size and each random integer represents the number of recaptures for each individual, whereas the mean represented the mean number of recaptures per individual in the population. For the negative binomial, we generated data using two levels of dispersion parameters; K=1 and K=0.5 for each mean parameter. The parameter K introduces variation in individual recaptures. We deleted zeros from all the datasets because zero values represent the unobserved raiders. We then used the remaining non-zero positive integer values, which are equivalent to the number of raiders counted, to estimate the number of deleted zeroes using asymptotic regression and count models. We describe these models below under population estimation of crop raiding elephants.

For the asymptotic regression models, we used the median instead of the mean as a measure of the average population since the distribution of means was influenced by a few large point estimates particularly when sample sizes are small (Frantz & Roper 2006). We assessed the accuracy of the models using model coverage and model bias. We considered a model accurate if it had good coverage, i.e. 95% confidence interval included the simulated population and a small model bias, i.e. the difference between the simulated population and the estimated population is smaller compared to other models.

2.2.5 Estimation of population sizes of raiding elephants

We estimated the population size of raiding elephants separately from observation counts and from genotype counts because we could not consolidate these two data sources for two reasons. First we lacked known genetic samples for some individuals that we knew to be crop-raiders: dung from these individuals may have occurred in our samples of dung from unknown individuals, but we could not confirm this. Second, observation counts and genotype counts were not uniformly sampled spatially (Figure 2). For each type of data we estimated the total population size of raiders from all three populations, as well as the population size of raiders originating from the Amboseli NP population. We used two classes of models to estimate population sizes; the count models and asymptotic regression models. For the count models, we fitted a finite poisson mixture model, Zelterman's model, and Chao's model.

Population size, N, was estimated from a finite poisson mixture model, using the Horvitz-Thompson formulation; ($N = n/(1-P_o)$), where N is the total population size of raiding elephants, n is the number of individuals that were observed raiding, and P_o is the probability that some raiders were not observed. For the Poisson count models, P_o is estimated as the exponent of lambda ($e^{-\lambda}$). The parameter(s) λ for the Poisson (mixture) was determined by a nonparametric maximum likelihood using an EM algorithm (Böhning et al. 2005). We fitted a finite poisson mixture to data and choose the best mixture model from many alternative mixture models using Bayesian Information Criteria (BIC).

Similarly, we estimated population size $\overline{N}_z$ from the Zelterman's model using the Horvitz-Thompson formulation.

$\overline{N}_z = \frac{n}{1-e^{(-\lambda_1)}}$, (Zelterman 1988), where $\lambda_1 = \frac{2f_2}{f_1}$

f_1, and f_2, are the number of individuals or genotypes sampled once or twice respectively. Population size for the Chao's model (Nc) was estimated using the equation;

$\overline{N}_c = n + \left(\frac{f_1^2}{2f_2}\right)$ (Chao 1988)

The variance (Var) and standard error (SE) and consequently the 95 confidence interval of the population size estimates for the Zelterman's and Chao's models were determined using the formulation of Böhning (2008) as follows,

$$\widehat{Var}_{\lambda|n}(\bar{N}_z) = nG(\lambda)\left[1 + nG(\lambda)\lambda^2\left(\frac{1}{f1} + \frac{1}{f2}\right)\right] \text{ where } nG(\lambda) = \frac{\exp(-\lambda)}{(1-\exp(-\lambda))^2} .$$

$$\widehat{Var}_{\lambda|n}(\bar{N}_C) = \frac{1}{2}\frac{f1^2}{f2}\left(1 - \frac{f1^2}{2f2n+f1^2}\right) + \frac{f1^3}{f2^2}\left(1 + \frac{1}{4}\frac{f1}{f2}\left(1 - \frac{f2}{n}\right)\right) \text{ and}$$

$$S.E. = \sqrt{\widehat{Var}_{\lambda|n}(\bar{N}_{CorZ})}$$

The 95% confidence interval for the poisson mixture was estimated as the 2.5 and 97.5 percentiles from 1000 bootstrap samples using a parametric procedure (Böhning et al. 2005). All these calculations of population point estimates and confidence intervals were implemented using the software CAMCR (Kuhnert & Bohning 2009).

The second class of models used to estimate the population size of the crop-raiders was asymptotic regression models. These models, also referred to as rarefaction models, estimate population size from an asymptote of the accumulation curve of unique individuals with sample size using three regression equations;

the negative exponential, $y = a(1 - e^{-bx})$, (Eggert et al. 2003),

Michaelis-Menten, $y = \frac{ax}{b+x}$, (Kohn et al. 1999), and

Chessel, $y = a - a(1 - \left(\frac{1}{a}\right))^x$, (Valiere 2002).

In these equations, y is the cumulative number of unique individuals or genotypes, x is the cumulative number of samples, a is the asymptotic value of y or population size and b is a rate of change in slope of the accumulation curve. The parameters a and b are then estimated by iterative non-linear least squares function (nls), in the r software. We randomized the order in which unique genotypes or individual frequencies are added to the accumulation curve 500 times. We iterated these randomizations 1000 times for each data set, while estimating parameter a per iteration. We present the mean, median and 2.5 and 97.5 percentiles for the 1000 iterations. These analyses were carried using r software (see Valiere 2002).

Testing for the presence of habitual raiders and estimating their numbers

We examined our data for the presence of habitual raiders by testing whether the distribution of raiding frequencies by individual elephants fitted a poisson or a negative binomial distribution. If all elephants are raiding with equal probability, we expect the distribution of raiding events across individuals to fit a poisson distribution but if individual elephants are not raiding with equal probability such that some animals are raiding more frequently compared to others, we expect the distribution of raiding frequencies across individual animals to fit a negative binomial distribution.

We fitted the frequency of raiding incidents to a zero truncated poisson and a zero truncated negative binomial distribution separately for genotype data and for observational data. To fit a truncated poisson distribution to the data, we calculated the maximum likelihood estimate of λ by numerical optimization using the nlm function in the r software. We then calculated the expected frequency for the Poisson distribution using the formulae for the zero truncated Poisson distribution,

$$P(Y_i = j|Y_i > 0) = \frac{\lambda_i^j}{(1-(e^{\lambda_i}))j!}$$

To fit a zero truncated negative-binomial distribution to the raiding frequency data, we estimated the maximum likelihood of dispersion parameter k and mean raiding frequency, m by numerical optimization in r using the nlm function in the r software. We used estimates of these parameters to calculate the expected frequencies from zero truncated negative binomial parameterization (Clark 2007; White & Bennett 1996);

$$P(x_i = j|x_i > 0) = \frac{z(k+j)}{j!\,z(k)}\left(\frac{m}{k}\right)^j \left(1+\frac{m}{k}\right)^{-(j+k)} \left(1-\left(1+\frac{m}{k}\right)^{-k}\right)^{-1}$$

We then tested the best model for the distribution of raiding events by comparing values from the observed distribution with values expected from either the truncated poisson or a negative binomial distribution using Fisher's exact test. To determine the number of elephants that are raiders, we fitted the distribution of raiding incidents to a truncated finite poisson mixture. We then used the estimated weight of the largest λ component of the finite poisson mixture to represent the proportion of habitual raiders in the estimated population.

2.3 Results

2.3.1 Simulation results: Effect of mean and variance in recapture on population estimates

Our simulations showed that all models except the Michaelis-Menten produced accurate estimates of the true population size (N=100) when data were generated by a poisson process and when mean recapture frequency was greater than 2 or 1 compared to when it was 0.5 (Figure 3, Table 2). However, when the data was generated by a negative binomial process all models produced underestimates of population size. Underestimation was severe when K was small. Michaelis-Menten performed best when the dispersion parameter K=1; it was less biased and had good confidence interval coverage. It was comparable to the Zelterman model for K=0.5 as the relatively less biased model, although the Zelterman estimator had better coverage. The negative exponential and Chessel models consistently under-estimated population size relative to other estimators when data were generated by a negative binomial process. Specifically, the Chessel and negative exponential models produced estimates less than half the true value when the data were dispersed.

Change in mean number of captures produced negative or positive bias depending on the process used to generate data. Population size was overestimated when data was generated from a poisson distribution, and when mean recapture rate became smaller, whereas population size was underestimated when data was generated from a negative binomial distribution and when mean recapture rates became smaller.

From these results, the Zelterman model performed better than other models when data was generated either from poisson or a negative binomial distribution and also when recapture rates were small. The Michaelis-Menten model performed best only when data were generated by a negative binomial process and when recapture rates became small, but not when the data was generated by a poisson process. We therefore used population estimates from the Zelterman's model in the interpretation of population estimates from our crop raiding elephant data since this model performed well in all situations we examined.

2.3.2 Population size estimates of crop raiding elephants

Our population estimates of elephants coming from Amboseli NP determined from observational data (N=84) was twice as large as our estimates from genetic data (N=41). This result was expected because we had genotypes for only half of the Amboseli NP population. So we expected to detect about half of the Amboseli NP raiders using genotype counts. This estimate (84) of Amboseli NP raiders reveals that one third of the 275 post pubertal males in this population raid crops.

When we considered population estimates of all crop raiders, the population size estimate from genotype data (N=241) was nearly twice that estimated from observational data (N=108; Table 3). This difference between estimates from the observational and the genotype data suggests that, while the data from observations detected mostly raiders from the Amboseli NP population, the data from genotyping was a representative sample of raiders from all three populations in the Amboseli ecosystem. In fact, population size estimates for all raiders based on observational data were similar to population size estimates of Amboseli elephants obtained from observations suggesting detection bias of observational data favoring Amboseli NP population. In other words, we were much more likely to see raiders from Amboseli than from any other population, but our dung collection samples represented all three populations.

2.3.3 Habitual raiding patterns

The distribution of crop raiding across genotypes marginally deviated from a poisson distribution with a mean=1.00 (p = 0.060, Fisher's test) but was similar to a negative binomial distribution of mean=0.005, and k=0.003 (p = 0.789, Fishers' test, Figure 4). Similarly, the distribution of crop-raiding across elephants identified from observations of raiders matched a negative binomial distribution with mean=0.030 and k=0.010, (p = 0.987) compared to a poisson distribution of mean=1.779, (p= 0.097; Figure 4). The distribution of raiding patterns was therefore non-random, indicating that some individuals raided more often than expected by chance, i.e., they were habitual raiders. We estimated the number of habitual raiders using the zero truncated poisson mixture to be 50 individuals from the Amboseli ecosystem and 10 of these are from Amboseli NP. For example, from observational data, the individuals with the most raids and the second most raids that originated from Amboseli NP contributed to 10% and 9.5% of the total observed elephant raiding frequency per elephant.

2.3.4 Gender of crop raiders

Through our combined genotype and observational data, we identified a total of 61 raiders of known identify and/or population. Fifty two of these were known Amboseli NP males, one was a Kili male, and 8 were Kimana-Tsavo males. All raiders were post pubertal male elephants 16 years of age or older and no females were ever observed raiding. Similarly, the genotypes from fecal samples collected from farms did not match any known female genotypes. These data strongly suggest that virtually all raiding in the Amboseli ecosystem is done by males.

2.4. Discussion

2.4.1 Population estimates of raiders and their origins

Our results show that the population of raiders in the Amboseli ecosystem is large and drawn from multiple populations. We estimated a total of 241 raiders in the Amboseli ecosystem. Amboseli NP elephants appear to comprise about 35% (n=84) of these raiders while the rest come from Kimana-Tsavo and Kili elephant populations. Our data provide clear evidence of these. We obtained accurate estimates of population sizes of raiders for the entire ecosystem from genetic data but detected most raiders from Amboseli NP through observations more than other populations.

Counts of crop raiders obtained from observations adequately sampled raiders originating from the Amboseli NP because raiding elephants were observed when raiders stayed in woodland refuges between farms and Amboseli NP suggesting that most raiders that we detected were from Amboseli NP and less likely from other adjacent protected areas. Similarly, we collected more samples from Namelok through observations and because Namelok is in the proximity of Amboseli NP, more Amboseli NP elephants were counted by this method. In fact the results of all raiders and Amboseli raiders estimated using data from observations were nearly similar, suggesting that observational data consisted of largely elephants from Amboseli NP.

Genotype counts provided a representative sample of the Amboseli ecosystem raiders. We obtained adequate genotype counts of raiders over a wider area (Sompet, Namelok and Isinet). Genotype count data showed that 60% of individuals who raided Namelok also raided Isinet, but the 74% of individuals that raided Isinet were exclusively from Isinet (Figure 2). Most raiders in Isinet came from Kimana Santuary and are mostly part of the Kimana, Tsavo and Chyulu elephant populations. Because of the care we took in developing our genotype-based estimates, we are confident that they do not suffer from the common problems of molecular censusing. In particular, we amplified each sample multiple times in order to reduce the error that a genotype from a single animal is scored as coming from multiple animals. In addition, because genotyping error cannot be completely eliminated when dealing with many loci, we accounted for this genotyping error when matching samples, by allowing a mismatch at one locus for samples that matched at four or more loci (Waits & Paetkau 2005).

From our genotype data, we estimated that Amboseli NP males represent approximately 17% of the raiding population in the Amboseli ecosystem, somewhat less than we present above. We expected this because we had genotypes from only 50% of males of raiding age and males that have not been genotyped could not be included in the count of Amboseli NP elephants sampled through fecal genotyping. If this is the case and if genotyped and ungenotyped elephants are equally likely to raid and if 35% of total raiders are Amboseli NP males, we would predict that the proportion of Amboseli NP raiders estimated from genotypes to be 17%. Our data support this prediction.

2.4.2 Patterns of habitual raiding behavior

Our results provided strong support for non-random raiding by individual elephants in the Amboseli ecosystem. We estimated about 50 habitual raiders from the Amboseli ecosystem and 10 of these come from the Amboseli NP. In addition, we observed that 2 individuals from observational data caused 20% of all the total elephant raiding events. Our data strongly supported a negative binomial distribution of raiding incidents more than a poisson distribution of raiding incidents. These findings on habitual raiding are comparable to results from a study of Asian elephants (Sukumar 1995) where, 2 bulls caused nearly 30% of the total raiding incidences by elephants.

2.4.3 Gender differences in crop-raiding

In this study only males were documented raiding crops. If females raided crops, then their raiding frequency was too low to be detected. This finding is consistent with results that more males than females in most polygynous species studied so far take crop-raiding risks. Examples include Hanuman langurs (Chhangani & Mohnot 2004), vervet monkeys (Saj et al. 1999), African elephants (Bhima 1998), Asian elephants (Sukumar & Gadgil 1988), chimpanzees (Hockings 2007; Wilson et al. 2007), and Anubis baboons (Forthman-Quick 1986). These gender differences have been hypothesized to result from differences in intrasexual competition and raiding costs and benefits for males and females. Because males in polygynous social systems have a larger variance in reproductive success than females; sexual selection is expected to enhance behaviors that increase reproductive success. In male elephants, reproductive success is greatly influenced by social dominance and the onset and duration of musth (Poole & Moss 1981), which are in turn dependent on age and nutritional state (Sukumar 2003). It is therefore postulated that sexual selection should favor bulls that adopt foraging strategies that maximize nutrient gains. These nutrient gains can then be allocated for growth and maintenance of musth. Our data on size for age in male elephants show that raiders were larger for age than non raiders as a result of raiding (chapter 2). Females probably raid crops less than males because they are likely to incur even higher risks that cannot be offset by raiding gains because most adult females are either pregnant or are accompanied by their infants. These states make females more vulnerable to being killed or injured by farmers, left behind or trampled upon during the stampede associated with escape from angry farmers protecting their crops.

2.4.5 Management implications

This study revealed that farms attract males from different populations and that there is a large pool of crop raiders and a few that raid habitually. These results suggest that although targeted culling may provide, at best, temporary relief in populations where habitual raiders are well known, it has high risks of misidentifying the animals involved. This is because the numbers of habitual raiders are smaller relative to occasional raiders. For populations where habitual raiders are known, using satellite and GPS collar technology placed on habitually raiding elephants holds promise as a conflict management tool. For example, GPS collar technology can be used to report locations of the raiders and this can provide an early warning system for wildlife protection agencies or farmers (Venkataraman et al. 2005). This study also highlights the potential value of molecular censusing for the estimation of population sizes of animals in conflict with humans.

Table 1. The predicted probability and observed frequencies of two individuals having identical genotypes at a specified number of loci (or theoretical Probability of Identity, PI) calculated from allele frequencies of 586 known Amboseli elephants. Two predicted probability measures were computed from allele frequencies, (1) assuming a random mating population of unrelated individuals in Hardy-Weinberg equilibrium, and (2) when full siblings are present using the formulae in waits et al (2001). The observed frequencies of identical genotypes were determined from actual data (matching 170,236 dyads) and are shown in the last column (Observed data).

Number of identical loci between two individuals	Predicted PI under Hardy Weinberg	Predicted PI for full siblings	Observed data
0	0.146372171	0.706891048	0.641450692
1	0.129700000	0.429900000	0.298203670
2	0.015745580	0.180558000	0.054453817
3	0.000881123	0.064224481	0.005468878
4	0.000043730	0.022311585	0.000417068
5	0.000001685	0.007463225	0.000005874
6	0.000000053	0.002433758	0.000000000

Table 2: A comparison of Mean, 95% Confidence Interval (C.I.) and estimation bias of six Capture-recapture models for data from a simulated population of size (N=100). These population data were generated using three different mean recapture frequencies (0.5, 1 and 2) and three different distributions (Poisson, and the negative binomial distributions with parameter (K=1, and K=0.5)).

Data generators		Mean=2		Mean=1		Mean=0.5	
	Population Model	Mean ±CI	%Bias	Mean ±CI	%Bias	Mean ±C.I	%Bias
Poisson							
	Chessel	99±2	-1	101±5	1	110±12	10
	Neg.Exponential	98±2	-2	100±4	0	104±10	4
	Michaelis-Menten	143±4	-3	166±8	6	189±20	89
	Chao	98±3	-2	102±5	2	113±15	13
	Zelterman	99±3	-1	102±7	2	116±17	16
	Poisson Mixture	98±2	-2	104±8	4	3±13	13
Negative binomial (K=1)							
	Chessel	66±1	-34	58±3	42	57±5	-43
	Neg. Exponential	71±1	-29	63±3	37	58±4	-42
	Michaelis-Menten	99±2	-1	97±5	3	98±9	-2
	Chao	86±5	-14	75±5	25	72±10	-28
	Zelterman	96±8	-4	80±6	20	75±12	-25
	Poisson Mixture	86±5	-14	81±8	19	66±7	-34
Negative binomial (K=0.5)							
	Chessel	52±2	-48	46±2	54	42±3	-58
	Neg. Exponential	57±2	-43	51±3	49	45±3	-55
	Michaelis-Menten	77±3	-23	76±4	24	73±6	-27
	Chao	70±3	-30	66±6	34	63±9	-37
	Zelterman	80±7	-20	74±10	-26	68±12	-32
	Poisson Mixture	72±8	-28	67±8	33	55±8	-45

Table 3: Population estimates of raiding elephants (1) from Amboseli NP only and (2) from all three source populations (Amboseli, Kilimanjaro and Kimana-Tsavo) in the Amboseli ecosystem. Population sizes were estimated from opportunistic counts of raiding elephants and from genotype counts based on fecal samples taken from raided farms. Opportunistic elephant sightings were collected in Sompet and Namelok farms whereas fecal samples were collected from Isinet, Sompet and Namelok farms. Estimates from six models are shown but the most reliable results according to simulations are the Zelterman and Michaelis-Menten model estimates, indicated in bold

	Model	**Estimates from observations**		**Estimates from genotypes**	
		Mean, (95% CI)	Median	Mean, (95% CI)	Median
Amboseli raiders	Count models				
	Zelterman	**84, (34-134)**	**86**	**41, (6-76)**	**41**
	Chao	75, (40-110)	77	38, (12-64)	39
	Poisson mixture	62, (49-111)	64	31, (23-64)	36
	Asymptotic models				
	Michaelis-Menten	**84, (63-133)**	**80**	**57, (37-130)**	**49**
	Neg. Exponential	54, (44-78)	53	34, (23-73)	30
	Chessel	45, (39-50)	45	31,(24-39)	30
All raiders	Count models				
	Zelterman	**108, (47-170)**	**109**	**241, (81-401)**	**247**
	Chao	97, (52-142)	97	217, (88-347)	221
	Poisson mixture	83, (63-158)	85	262, (112-9.3x10^{5})	331
	Asymptotic models				
	Michaelis-Menten	**106, (79-162)**	**101**	**222, (144-448)**	**199**
	Neg. Exponential	67, (55-95)	65	129, (91-241)	117
	Chessel	55, (48-62)	55	98, (84-114)	97

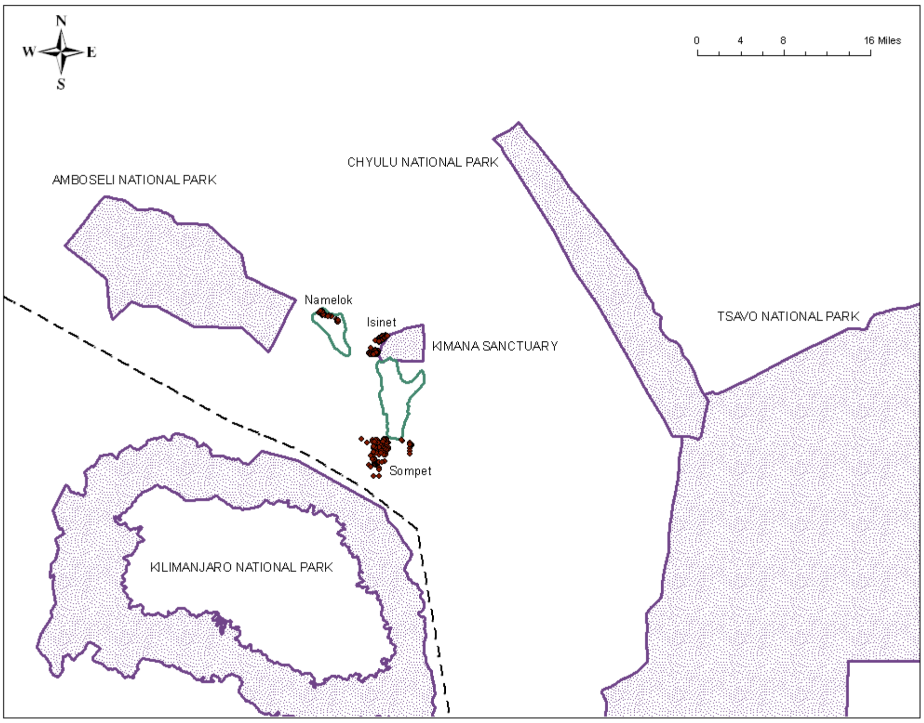
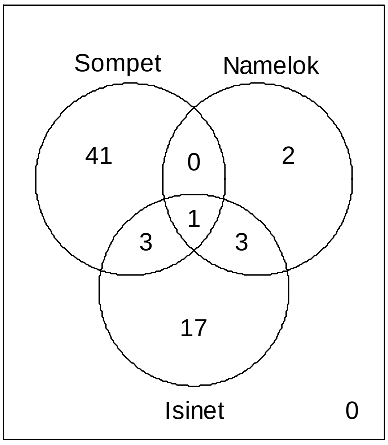


Figure 1: Map of the Amboseli ecosystem showing protected areas in grey shade containing three major elephant populations in the ecosystem. Farming areas that we monitored for crop raiding are shown using red dots and the dashed line shows the Tanzania and Kenya National boarder



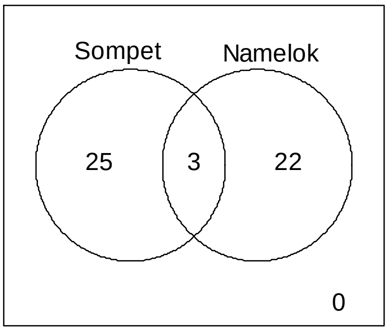


Figure 2: Venn diagrams showing the spatial distribution and sampling intensities of unique genotypes (top) and unique individuals recognized through observations (bottom). Circles represent farming areas (Sompet, Namelok and Isinet) where samples were collected from. The numbers inside the circles indicate the number of unique individuals observed to raid in a farming area; the number where two circles intersect show the number of unique individuals observed to raid in the two or more farming areas indicated in the region of intersection of the circles.

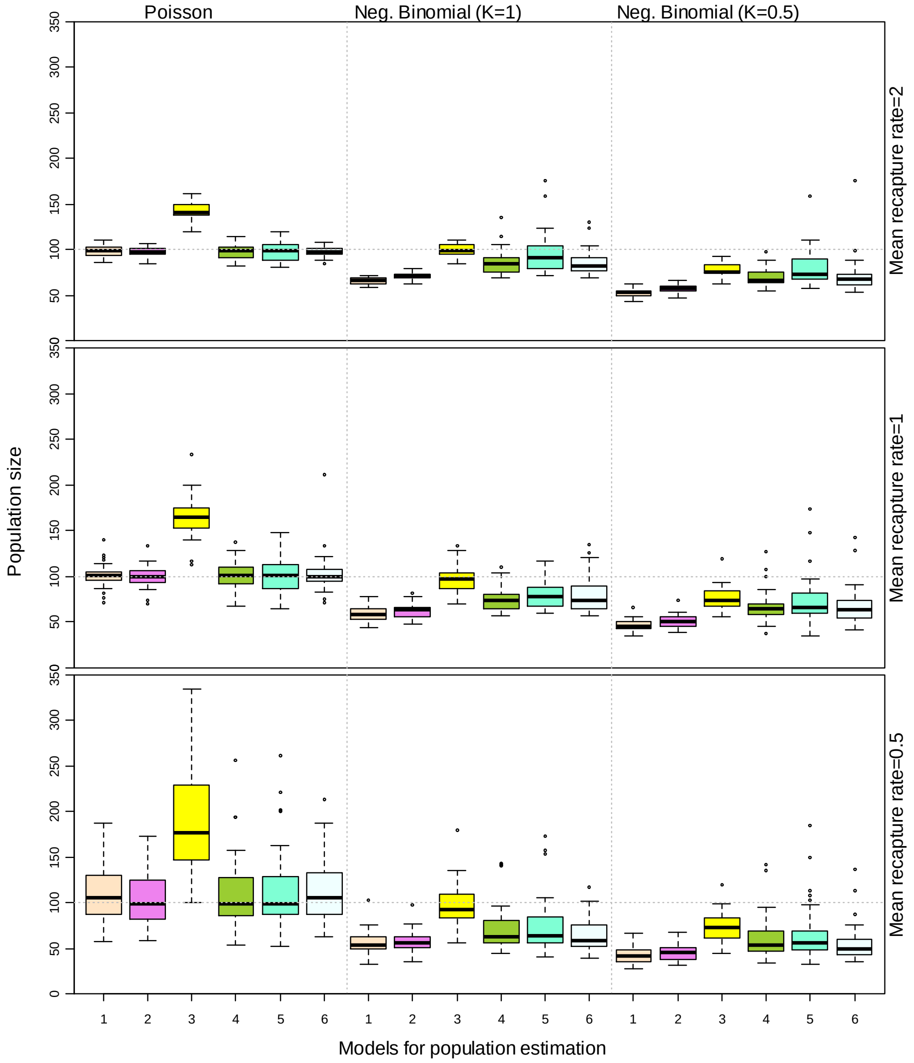


Figure 3: A boxplot comparing the median(dark line) and quartiles (boxes) of mean population size estimates (n=31) of six Capture-recapture models (1-Chessel, 2-Neg.Exponential, 3-Michaelis M, 4-Poisson mixture, 5-Zeltermann, and 6-Chao) around the median for a simulated data set with a population size of 100. The expected population size (100) is indicated by a dotted, light-grey, horizontal line in each box plot panel. Each of the three stacked boxplot pannels represent summaries for data with a recapture mean of 2 (top), 1 (middle) and 0.5 (bottom). Each panel is divided into 3 parts . They for each of the six capture-recapture models data generated by a poisson distribution (left part), a negative binomial distribution with K=1 (middle) and K=0.5 (right)

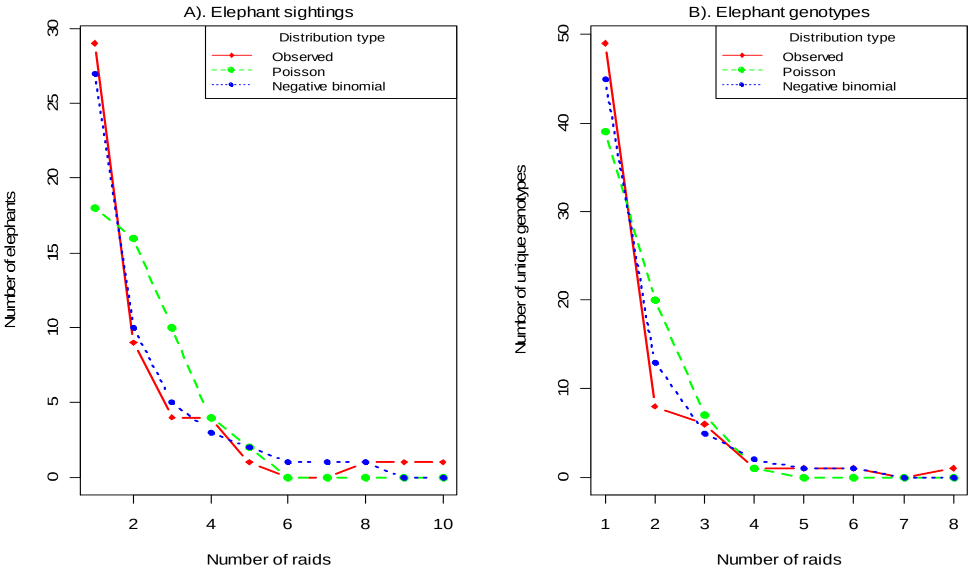


Figure 4: The distribution of number of raids per raider based on the number of observed raiding incidences using data on (a) elephant sightings or (b) genotypes data compared with predicted distribution under a poisson distribution and under a negative binomial distribution.

3. No risk, no gain: effects of crop-raiding and genetic heterozygosity on body size in male African elephants

3.1 Introduction

Body size is an important life-history related trait in polygynous mammals, often influencing survival early in life, fighting ability and dominance at maturity and consequently reproductive success (Kovach & Powell 2003; Lee & Moss 1986; Loison et al. 1999; McElligott et al. 2001; Mysterud et al. 2004; Zedrosser et al. 2007). In polygynous mammals, males are usually larger than females and intra-sexual competition is more intense among males than among females, resulting in a large variance in reproductive success among males compared to females (Alberts et al. 2003; Boesch et al. 2006; Fabiani et al. 2004; McElligott & Hayden 2000; Setchell et al. 2005; Slate et al. 2000). A common feature of polygynous social systems is the presence of bias in maternal investment, with mothers investing more towards a higher birth weight or increased growth of male offspring compared to that of female offspring (Bercovitch et al. 2000; Birgersson et al. 1998; Clutton-Brock et al. 1981; Lee & Moss 1986). Bias in female mate choice for larger males is also common (Bowyer et al. 2007; Poole 1989). These observations taken together with the fact that larger males have a higher reproductive success, indicates more intense selection for large body size in males than in females. For example, in most polygynous species males have delayed reproductive maturation compared to females. This delay creates an opportunity for males to invest in growth and size and for females to invest in earlier reproduction, body condition and parental care in order to enhance their reproductive competitiveness (Field et al. 2007; Isaac 2006; Post et al. 1999; Whitehead 1994). In spite of strong selection for large size, male size remains variable even within populations. Identifying factors that generate this variation is critical for understanding male reproductive success and life history strategies.

In this paper, we investigate the influence of two factors on male size-for- age in African elephants. One of these factors, crop-raiding, occurs in all elephant populations that border agricultural areas and is a major source of human-elephant conflict (Williams et al. 2001). Crop-raiding is sex-biased and is undertaken more by males compared to females (Sukumar & Gadgil 1988). However, not all male elephants raid crops even when their home ranges abut agricultural areas (Sukumar 1995; Williams et al. 2001). Crop raiding among independent males is initiated after they have dispersed from their maternal families at approximately 14 years of age (Lee & Moss 1999) and we therefore predicted raiding to affect adult growth and hence size after dispersal. The second factor we examined is multi-locus heterozygosity at microsatellite loci. Multi-locus heterozygosity has been demonstrated to influence infant survival and to correlate with body size or growth in some species. We therefore expected the effects of heterozygosity on male body size to occur throughout life.

3.1.1 Crop raiding as a high-risk foraging behavior

When male-male competition is intense, males are expected to take risks that enhance investment in growth or enhance social dominance, consequently increasing their reproductive competitiveness (Trivers 1985). Several studies on sexually dimorphic mammals have demonstrated that males will seek more abundant, high quality forage at the risk of predation, whereas females will sacrifice forage abundance to minimize predation risk when there is a positive correlation between food abundance and predation risk (Apollonio et al. 2005; Berger 1991; Bleich et al. 1997; Corti & Schackleton 2002; Croft et al. 2006; Hay et al. 2008; MacFarlane & Coulson 2007). Elephants display a similar male bias in high-risk foraging in that males are more likely than females to raid crops (Sukumar & Gadgil 1988). While male elephants engage in a variety of high-risk foraging tactic, their propensity to raid crops is variable (Sukumar 1995). Crop raiding is a high-risk foraging strategy for elephants because Crop-raiders are often killed or injured by farmers and sometimes by wildlife authorities when they are detected raiding (Haigh et al. 1979; Hoare 2001; Moss 2001; Obanda et al. 2008). In Amboseli 10% of raiders were seen with spear injuries during this study. Elephants appear to recognize these risks. For example although elephants forage both during the day and night, foraging on crops invariably occurs at night (Graham et al. 2009) and particularly during moonless nights (Barnes et al. 2007), probably to minimize risks of detection by farmers. On the other hand, crop-raiding compared to foraging on wild plants offers high nutritional returns (Rode et al. 2006; Sukumar 1990) and raiders can obtain 38% of their daily forage intake in 10% of their foraging time (Chiyo & Cochrane 2005) while raiding crops compared to foraging on wild plants.

Trading-off safety from predators for forage abundance has been speculated to provide a nutritional pay off that could accelerate growth or increase body size and consequently reproductive success (Corti & Schackleton 2002; Hay et al. 2008; Mooring et al. 2003). In a species with indeterminate growth, and high energetic costs of sustained growth, such as elephants, sustaining these growth rates may be especially critical to reproductive output. However, no study has demonstrated a causal relationship between body size and such high-risk foraging behavior. Here we test for the effect of high-risk foraging behavior on body size by specifically examining whether independent male crop-raiders are larger for age compared to non-raiders and whether males that raid crops are initially smaller or larger for age.

3.1.2 Microsatellite heterozygosity effects on life history traits

Multi-locus heterozygosity at microsatellite markers has been linked to fitness measures such as growth, infant survival and reproductive success in a number of species (Bean et al. 2004; Coltman et al. 1998; Da Silva et al. 2006; Gage et al. 2006; Hoffman et al. 2004; Slate et al. 2000; Zedrosser et al. 2007). These multilocus heterozygosity and fitness correlations have been shown to result either from locus specific effects for loci linked to functional genes that influence fitness and are under balancing selection, or from inbreeding depression associated with genome wide loss in allelic variants that influence fitness (Amos & Acevedo-Whitehouse 2009; Gage et al. 2006; Hansson et al. 2004). Some studies have found positive correlations between microsatellite heterozygosity and growth rates or size for age in vertebrates (Hildner et al. 2003) while other studies have found no correlations between heterozygosity and size or growth rate (Curik et al. 2003; Overall et al. 2005; Zedrosser et al. 2006). A limited number of studies have investigated the effects of multi-locus heterozygosity of neutral loci on size for age or growth in natural free ranging large mammals, specifically males (Charpentier et al. 2006; Curik et al. 2003; Zedrosser et al. 2007), but no similar studies have been done on elephants. Here we test the hypothesis that elephants with a high multilocus genetic heterozygosity are larger for age.

3.2 Material and Methods

3.2.1 Study population and age estimation

This study focused on the Amboseli elephant population currently consisting of ~1,400 elephants. This population has been studied continuously since 1972 by the Amboseli Elephant Research Project (AERP). All elephants born to the Amboseli population are individually known and recognizable from natural tears, notches, holes and vein patterns on pinnae, tusk characteristics, natural body marks and shape. This population is free ranging and uses an area nearly 8000 km^2 of Maasai ranches (Moss et al. in press) surrounding Amboseli National Park and is connected to elephant populations from Kimana, Tsavo and Chyulu in the east and those of Kilimanjaro and Longido controlled hunting area in the south and southwest (Douglas-Hamilton et al. 2005). All known Amboseli elephants have ages assigned to them; elephants born since

1975 have their ages estimated to within 2 weeks, those born between 1972 and 1974 have ages estimated to ± 3 months, and elephants born between 1969-1971 have ages estimated to within one year. Elephants born before 1969 have ages estimated to within 2-5 years, depending on familiarity, longevity of the male, and duration of observations. All age estimations are validated from long-term observations of growth and body shape, as well as tooth ages when dead (Moss 2001).

3.2.2 Estimation of elephant size from footprint measurements

Footprint measurement is a reliable and well-established non-invasive method for determining elephant size (Western et al. 1983). Elephant hind footprint length is highly correlated with height at the shoulder, accounting for up to 93% of the variance in male elephant height in African elephants (Lee & Moss 1995) and 94% in Asian elephants (Kanchanapangka et al. 2007). Footprint length is also highly correlated with body mass in both species of elephants. In Asian elephants forefoot circumference was found to account for 86% of variance in body weight (Kanchanapangka et al. 2007). We estimated the length of the hind foot from measurements of footprint impressions left on the soil by known individuals. Specifically, we measured the linear distance perpendicular to the short foot axis from the outer rear edge of the footprint to the internal arch of the toe excluding the toe nail imprint. For any given sighting, we took several opportunistic measurements of footprints whenever the soil substrate allowed delineation of footprints and whenever we were able to observe footprints for target individual elephants. We used 650 footprint size measurements from 302 unique individuals collected between 1976 and 2005 (Lee & Moss 1995) and again between 2005 and 2007. These include 120 measurements collected from 36 unique individuals that we observed to raid crops in 2005 to 2007. Forty six unique males measured in 1976/1991 were also measured again in 2005/2007.

3.2.3 Genetic analysis and sample collection

We used two sets of genetic data in this paper. First, we used genotypes of known individuals from recent genetic studies on this population (See Archie et al. 2007; Archie et al. 2008) for whom we had footprint measurements (n = 119 males). Second, we collected fecal samples from 50 known males that were not previously genotyped for a genetic analysis. From these fecal samples, we extracted DNA using a QIAamp DNA Stool Mini Kit (Qiagen™) following a modified protocol (Archie et al. 2003). All individuals were genotyped at a minimum of 8 loci and up to 11 loci from previous studies. These included one dinucleotide locus (LAFMS02; Nyakaana & Arctander 1998), and ten tetranuclotide loci (LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18, LaT24, LaT25 and LaT26; Archie et al. 2003). We used the PCR protocols detailed in Archie et al (2003) to amplify DNA from the loci of interest. PCR products were separated using Applied Biosystems 3730XL DNA Analyzer and analyzed using Genemapper v.3.7 by Applied Biosystems. Microsatellites alleles were scored using GeneMarker v.1.6. (SoftGenetics). For each sample, we ran PCR and genotyping twice if the initial PCR product was scored as a heterozygote and three to four times if it was a homozygote, in order to minimize error associated with spurious alleles and allelic drop out (Archie et al. 2006). We tested all loci for Hardy-Weinberg equilibrium and for the presence of null alleles (non amplifying alleles) using CERVUS software (Kalinowski et al. 2007; Marshall et al. 1998; see supplemtary material S1). We calculated a weighted multilocus homozygosity index (HL) for 119 male elephants where we had both footprint measurements and genetic data. We used the method of Aparicio et al (2006) to calculate homozygosity. We then derived multilocus heterozygosity by subtracting the homozygosity value for each individual from one.

3.2.4 Identification of crop-raiders

Identification of crop raiders was a multi-step process. In the field we either identified crop raiders by tracking elephants for several hours following a farm raid or, when we were not able track raiders, by collecting their dung from raided farms. For elephants that we tracked and located, we could visually identify known members of the Amboseli-born elephant population. In cases where we were not immediately able to ascertain their identities, we took photos and later matched these photos with a database of all Amboseli-born males. Dung collected from raided farms was preserved in 95% ethanol in the field and later brought to the lab at Duke University. In the lab, we extracted and genotyped DNA from the dung of these unknown crop raiders that we collected from raided farms. We genotyped on average 6 loci (LAFMS02, LaT05, LaT08, LaT13, LaT16, LaT24) for samples collected from farms. We then compared the genotypes of crop-raiding elephants collected over a period of two years with genotypes of 586 known male and female elephants. We matched a raiding sample to a known individual in the database if four or more loci matched between the two. We used 4 loci because our data indicated that a dyad would match by chance at 4 loci with a probability of 0.00004 (this represents the probability of identity, PI; Waits et al. 2001). We used a minimum match at four loci for samples genotyped at not more than five loci. In addition, we allowed for only one mismatch at the remaining loci to account for potential genotyping errors such as allelic drop out. All matching of fecal samples with similar genotypes and genotype assignments to known individuals was carried out using the software CERVUS.

3.2.5 Statistical analyses

Our footprint size data consisted of repeated measurements from many individuals taken at irregular intervals. Consequently, we used a linear mixed effects model framework to determine the effects of raiding behavior and multi-locus heterozygosity on elephant size for age. We carried out these analyses on log-transformed male age ln(Xi+1) and footprint ln(Yi) data because the relationship between footprint size and age was nearly asymptotic. We added one to each male age (Xi) because some values for male age were close to zero at the time of footprint measurement, making it impossible to normalize data through a log transformation. Multi-locus heterozygosity was also transformed using arcsine transformation.

We ran two separate models based on male life stages with footprint size as a response variable and male age, male raiding status and multi-locus heterozygosity as covariates. We used elephant's identity as a nesting factor (or random effect) because we had repeated measurements for some elephants. We separated the models based on male life stages because we expected that different covariates affected male size at different life stages. The first model included males 16 years and older. We choose 16 years of age as the minimum age because males at this age are independent and spend most of the time away from their mothers with other males where they may initiate raiding. Sixteen years of age is the youngest age an elephant was observed to raid in Amboseli and follows the mean age at independence from the natal family in Amboseli (average age is 14 years, and range is from 8-19 years; Lee & Moss 1999). We expected to detect the effects of crop raiding on size-for-age at this life stage. In a second model we included only males aged 0 to 10 years old because males in this age category are still with their natal family and are thus spending most of their time with their mothers. We did not expect to detect a size bias for males that become crop raiders versus those that don't become raiders.

For each male life stage (0-10 years and 16+ years), we first ran a full mixed effects model that included age, raiding status and heterozygosity as fixed effects and then dropped non significant fixed effects in a stepwise manner starting with the least significant until we were left with a model with only significant fixed effects (Pinheiro & Bates 2004). For all these full covariate model analyses, the intercept, male age and only raiding status and not heterozygosity were significant for either age set, and so formal model selection was not necessary. However, to confirm that covariates that were non-significant in the full model were not influencing body size, we ran additional independent fixed effects models including each non-significant covariate, either crop-raiding or multi-locus heterozygosity with age. For each significant fixed effects model, we tested for different random effects and nesting factors using the likelihood ratio test (Crawley 2005).

All statistical analyses were carried out in S+, 8.1 (TIBCO software, 2008).

3.3. Results

3.3.1 Crop raiding effects on size

Crop raiding had a positive effect on foot size for age for males sixteen years and older but not for males 0-10 years (Table 4), such that males observed to raid crops were larger for age than those not observed to raid (Figure 5). However, males that became raiders were not larger for age when young (0-10 years old) compared to same-aged males that were not subsequently observed to raid (Figure 5).

3.3.2 Microsatellite heterozygosity effects on size

Multi-locus heterozygosity had no significant effect on size for age for males ten years or younger or males sixteen years and older (Table 4). We did not explore locus specific effects because of a lack of a general effect or trend in the predicted direction as well as the lack of *a priori* expectations of locus specific heterozygosity on size for age. The distribution of multilocus heterozygoisty in the Amboseli population was skewed towards higher values (Figure 6). The mean (± standard deviation) heterozygosity for 119 males from this population was (0.8 ± 0.147).

3.4. Discussion

Our results indicate that foraging behavior such as raiding crops with a high risk of injury or mortality can lead to gains in body size. This supports our hypothesis that high-risk foraging has an energetic pay off, and suggests that the relative dearth of females among crop raiders relates to the fact that only males, the sex experiencing high variance in reproductive success (Poole 1989), are more likely to take on these mortality risks in order to obtain the energy and growth payoff. An enhanced size for age as a result of crop raiding is likely to confer reproductive benefits to male elephants for two reasons. First, their age at the onset of musth, the physiological state of heightened sexual and aggressive behavior, will be younger for larger males resulting in a longer breeding lifespan (Lee et al. in press). Male elephants commence spermatogenesis at the age of 10 years (Laws 1966), are physiologically capable of siring offspring at 15-17 years of age (Owen-Smith 1988), but do not typically sire their first offspring until they are 26-30 years of age (Hollister-Smith et al. 2007; Poole 1989) due to intense competition from larger older males. This extended period of maturation provides an opportunity for investment in growth and size. Second, annual reproductive performance is positively correlated with musth duration (Hollister-Smith et al. 2007; Poole 1989) and the duration of musth is dependent on condition and body size, as well as age of individual males. Males with access to reliable, easily digested, and high energy human crops experience longer musth episodes while those with limited energy are less likely to experience musth (Poole 1989; Sukumar 2003). Larger males may also have increased reproductive success because they are preferred by females as mates (Hollister-Smith et al. 2007; Moss 1983; Poole 1989).

Microsatellite heterozygosity has been shown to be positively correlated with fitness traits in many populations, but in this study, mean individual heterozygosity of microsatellites loci was not correlated with size. Correlations between heterozygosity of neutral markers and fitness traits such as size and growth rate are weak or absent in out-bred populations and stronger in inbred populations (Hildner et al. 2003; Overall et al. 2005; Rowe & Beebee 2001). The lack of a relationship between multi locus heterozygosity and size for age in the Amboseli elephant population may simply reflect the high heterozygosity and extensive out-breeding in this population.

This out-breeding is a consequence of inbreeding avoidance (Archie et al. 2007) and extensive gene flow between Amboseli and adjacent elephant populations.

Our findings on the sex-specific nature of high-risk behavior and the gains of such behavior may generalize to other sexually dimorphic species with high reproductive variance because high-risk foraging is widespread among males of many sexually dimorphic species such as in fallow deer, (Apollonio et al. 2005) roe deer (Mysterud et al. 1999), Dall's sheep (Corti & Schackleton 2002), bighorn sheep (Berger 1991; Mooring et al. 2003), African buffalo (Hay et al. 2008), mountain sheep (Bleich et al. 1997), elk (Winnie & Creel 2007) and moose (Miquelle et al. 1992) .The prevalence of additional physiological traits in species exhibiting this behavior such as condition dependent mating strategies (musth and rut) and prolonged growth in males suggests that these traits are related to the evolution of high-risk foraging behavior in males of sexually dimorphic species. Our findings suggest that males of polygynous mammals compared to females are more likely to come into conflict with humans. Since high-risk foragers or crop raiders grow large, culling of males for purposes of reducing conflict is likely to eliminate individuals that are larger and reproductively competitive, and this will have implications for mating behavior and possibly genetic diversity and genetic quality in affected populations.

Table 4: Model parameter summaries for the effect of crop-raiding status, maternal-age and genetic heterozygosity on foot-size for age in male elephants. Male age in years (+1) and foot-size in cm were transformed into the natural logarithm. We used a random intercept for all the models displayed.

Covariate	Fixed effects	Coefficient (S. Error)	d.f.	P-value
Crop-raiding effects				
On males 0-10 years	Intercept	2.856 (0.016)	29	<0.0001
	Ln(Age+1)	0.291 (0.010)	29	<0.0001
	Raiding status	-0.012 (0.022)	101	0.6039
On males 16-60 years	Intercept	3.141 (0.025)	236	<0.0001
	Ln(Age+1)	0.219 (0.008)	236	<0.0001
	Raiding status	0.028 (0.008)	195	**0.0002**
Heterozygosity effects				
On males 0-10 years	Intercept	2.910 (0.052)		<0.0001
	Ln(Age+1)	0.274 (0.019)	11	<0.0001
	Arcsine(Heterozygosity)	-0.015 (0.041)	26	0.7211
On males 16-60 years	Intercept	3.145 (0.033)	154	<0.0001
	Ln(Age+1)	0.218 (0.010)	154	<0.0001
	Arcsine(Heterozygosity)	0.007 (0.014)	97	0.6458

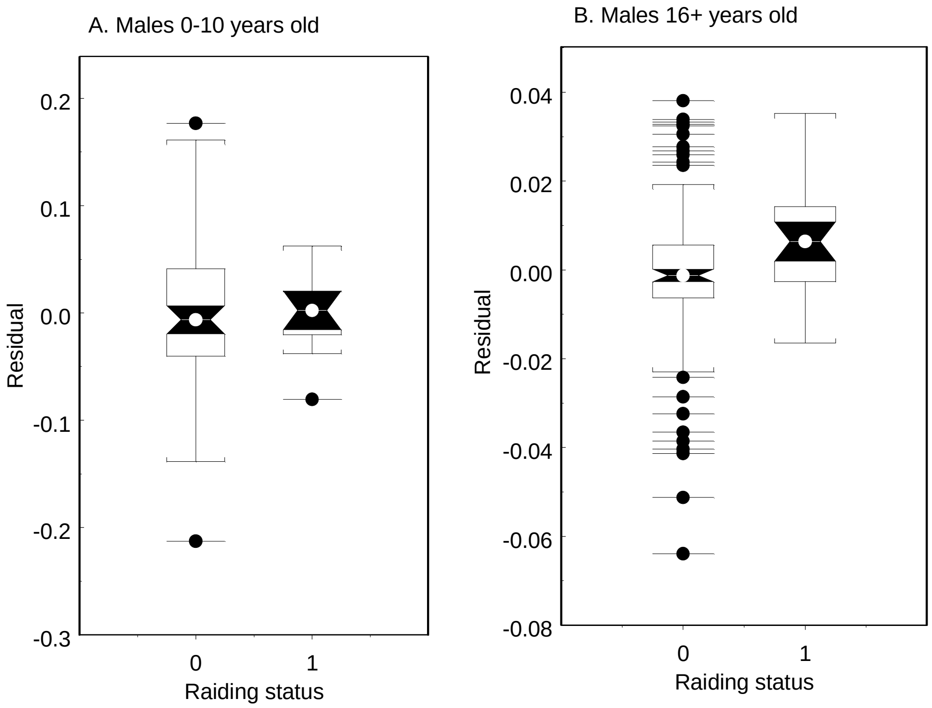


Figure 5: Effects of crop-raiding on size-for-age in (a) males 0-10 years of age and (b) males 16+ years of age showing that mean residuals of footprint size-for-age are not significantly different for males that eventually become crop raiders and those that do not become raiders (part a; t = 0.0588, d.f. = 21, p = 0.842). However for males 16+ years of age raiders were significantly larger than non-raiders (part b; t = -3.13, d.f. = 53, p = 0.0028). Box plots were constructed from mean residuals for non raiders (0) and raiders (1) obtained from the footprint size for age model.

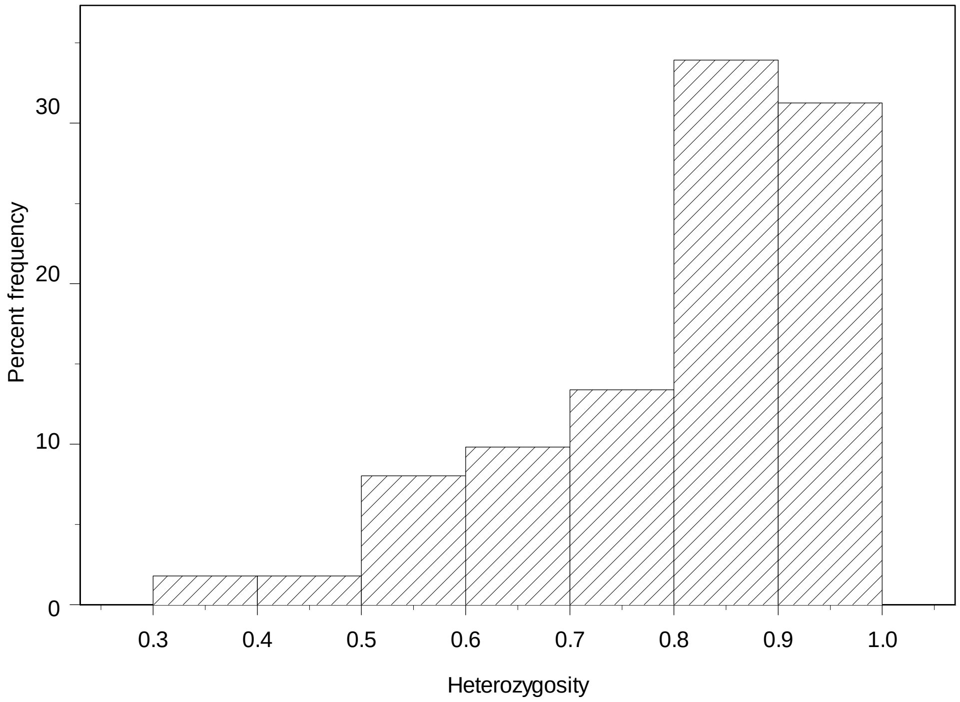


Figure 6: Distribution of mean multi-locus heterozygosity using microsatellites in male Amboseli elephants, showing that multilocus heterozygosity was generally high in this population. Heterozygosity was calculated as 1-(HL, homozygosity by loci) estimated using the method of Aparicio, et al (2006)

4. Association patterns of male African elephants: the role of age and genetic relatedness

4.1 Introduction

Mammals in fission-fusion social groups exhibit dynamic and complex associations that vary in strength and stability between individuals or groups. This variation results from groups repeatedly dividing and reforming in order to optimize the benefits of living in groups (Couzin & Laidre 2009). These benefits depend on the optimal group size, which varies in response to changes in predation pressure, resource availability and social interactions (Creel & Winnie 2005; Heithaus & Dill 2002; Mitchell et al. 1991; Wittemyer et al. 2005). Social structure, a population level representation of these associations, is vital for understanding the evolution of cooperation (Voelkl & Kasper 2009), kin selection (Krützen et al. 2003) and cognition (Dunbar & Shultz 2007). Social structure can profoundly influence the rate and pattern of transmission of disease and social information in populations (Hoare & Krause 2003; Perkins et al. 2009), thereby affecting the fitness of individuals (McDonald 2007).

Strong and relatively stable association patterns are a common feature of female social behavior in mammalian societies (Wrangham 1980) but strong associations are rare among male mammals. This is because male social behavior is influenced by strategies for controlling access to groups of females or gaining access to fertilization, and fertilizations are rarely shareable (Van Hooff & Van Schaik 1994). Male relationships are expected to be competitive. Most instances of male-male associations in mammals that have been described occur in species exhibiting male philopatry such as chimpanzees (Mitani et al. 2000) and hamadryas baboons (Kumer 1995), joint dispersal of male siblings such as lions (Packer & Pusey 1982), and occasionally in species with reduced sexual dimorphism such as bottlenose dolphins (Connor 2002; Tolley et al. 1995).

African male elephants do not exhibit male philopatry or joint dispersal of siblings. Elephants are strongly sexually dimorphic and male alliances have never been reported. These and other features of male elephant behavior indicate that intra-sexual competition is a major force in elephant evolution (Poole 1989b), and make it unlikely that males have strong and stable associations. Additionally, socio-ecological models based on predation, reproduction and feeding competition predict that male elephants should be mostly solitary or associate randomly with other males. For instance, male elephants disperse from family units when they are the size of adult females and are no longer vulnerable to predation by large carnivores, other than humans (Blake 2004; Joubert 2006; Loveridge et al. 2006; Ruggiero 1991). Male elephants are therefore not expected to display cooperative group defense that will require stable male associations seen in female elephant groups. Male elephants are predicted to forage solitarily, to reduce feeding interference and competition and to maximize forage intake (Shannon et al. 2006). Maximizing forage intake should consequently improve body condition, musth duration (Sukumar 2003) and male reproductive dominance (Poole 1989a). Social structure in male elephants is therefore speculated to be rudimentary, with no strong or stable associations (Croze 1974).

There are, however, aspects of male behavior in some fission-fusion social systems, particularly in elephants and certain ungulates, that suggest that males may form stable or even strong relationships with other males. For example males in some ungulate species segregate from females to form bachelor herds. This segregation into bachelor groups provides opportunities for males to form stable and strong associations with other males and for potential benefits to accrue from these associations. These potential benefits include foraging, access to sparring partners, and access to social and ecological knowledge from older individuals.

When males in fission-fusion societies join bachelor groups, they may regain body condition after loss of condition following a rut, or avoid the harassment by reproductive males that they encounter when they are in mixed groups (Dunham & Murray 1982; Jarman ; Komers et al. 1992; Prins 1989; Turner et al. 2005). Consequently some studies have shown that when there is spatial segregation between sexes, areas occupied by males tend to be rich foraging patches that are often inaccessible to females because they are riskier (Hay et al. 2008) or have steep topography that is costly to navigate for females with calves (Kabigumila 1993; Wall et al. 2006). Competitive feeding interactions among males in these bull areas can create a pattern of male-male associations that favors kin based alliances. For example dominant males associating with relatives can maximize indirect fitness benefits by tolerating and sharing forage with relatives while excluding and supplanting nonrelatives.

Males in bachelor groups may also benefit from access to a large pool of associates to spar with. Sparring, a play behavior that is frequent among males, is hypothesized to be relevant for honing fighting skills needed during male-male competition for estrous females (Miller & Byers 1998). Similarly, males frequently spar with others close in age to themselves rather than with males with a large age disparity (Croze 1974; Kabigumila 1993). Sparring is thought to be vital for male's to assess their own strength (Lee & Moss 1999), a skill necessary for minimizing conflict during the establishment of dominance hierarchies. But there is no reason to expect these associations to be stable, unless sparring poses a risk of escalation to a fight when done with unfamiliar individuals. Because sparring may involve self handicapping (Pereira & Preisser 1998), individuals compromise their guard while sparring and put themselves in a vulnerable position. If honing of fighting skills and strength assessment are important for male reproductive success, we predict that male elephants should have stable associations with age peers with whom they frequently spar.

In long lived species with complex social behaviors and a large disparity in ecological and social knowledge between young and old individuals, living in stable social groups can allow young individuals to benefit from the experience gained by older individuals regarding appropriate responses to the dynamic social and ecological environment. In elephant family groups, older females are leaders and repositories of social and ecological knowledge (Foley et al. 2008; McComb et al. 2001; McComb et al. 2000). Males usually have separate ranges from females, and range more widely than females. Males, like females, therefore require ecological knowledge on forage and water distribution over large areas. Male ranging behavior also brings them in contact with humans (Galanti et al. 2006) and humans are one of the major causes of injury and death for male elephants (Moss 2001; Obanda et al. 2008). By associating with older males, younger males may benefit from knowledge on navigating human dominated landscapes rich in forage while avoiding contact with humans.

Very little is known regarding the social roles of individuals in male elephant social groups. We expect that, like females, older males are repositories of social and ecological knowledge in bull society. We therefore predict that young elephants will have strong associations with older individuals. However, if younger males and older males will both prefer to associate with age mates, but if younger males will also prefer to associate with older males, then the tendency of younger males to associate with age mates as well as with older males will be difficult to detect. One approach for detecting the tendency for young males to associate with age mates as well as with older males is to group males into age classes and examine attraction between the classes of young and older males (e.g., Pepper et al. 1999). Using this approach, we expect the age class with a strong within class as well as between class attractions will appear to have a random association if the two forces of attraction are equal.

In this paper we tested several predictions. First we tested the prediction that male elephants have stable or nonrandom association clusters or communities of closely associating members. Secondly, we tested the hypotheses that male elephants will associate with genetically related individuals and with age peers more than expected by chance. Lastly we examined whether older males play a pivotal role in elephant associations as sources of social knowledge by testing the hypothesis that the class of younger males are strongly attracted to the class of older male elephants.

4.2 Materials and methods

4.2.1 Study area and study population

This study focused on the Amboseli elephant population, currently consisting of ~1,400 elephants. This population has been intensively studied since 1972 by the Amboseli Elephant Research Project (AERP). All elephants born to the Amboseli population are individually known and are identified using natural tears, notches, holes and vein patterns on ear pinnae. Elephants are also identified from tusk characteristics (size, shape and configuration, one tusked, broken or intact), natural body marks and body shape. We used a photo ID database, initiated and maintained by AERP and expanded by P.I. Chiyo, on all Amboseli males to confirm individual identities in the field. This population is free ranging and occupies nearly 3000 km^2 of Masai group ranches and Amboseli National Park (Moss 2001). This population is contiguous with elephants from Kimana, Tsavo and Chyulu, in Kenya to the east, and the Kilimanjaro and Longido controlled hunting areas in Tanzania, in the south and southwest (Douglas-Hamilton et al. 2005; Moss 2001). All known Amboseli elephants have ages assigned to them; elephants born since 1975 have their ages estimated to within 2 weeks, those born between 1972 and 1974 have ages estimated to within a few months, and elephants born between 1969-1971 have ages estimated to within one year. However, ages for elephants born before 1969 are estimated to within 5 years using measurements of shoulder height, hind footprint length and body shape (Lee & Moss 1995).

4.2.2 Estimation of male association patterns

We collected association data from June to December of 2005-7. We did this opportunistically because sightings were unpredictable. We searched for male elephants daily by driving to areas where elephants were likely to be sighted. When we sighted elephants, we recorded the time, their location using a Global Positioning System (GPS), and the size and type of group they were encountered in. We defined three types of elephant groups as, a bachelor group if it consisted of only male elephants, or as a mixed group if it consisted of both male and female elephants. For each sighting of a mixed group, we identified all males that were 15 years of age or older, and for bachelor groups, we identified all individuals irrespective of age. We defined an elephant group as a spatially cohesive and behaviorally coordinated aggregation of two or more elephants. We considered a group of elephants as spatially cohesive if they were orientated towards the same direction and clustered within a radius of 100 meters. Elephants were considered to be behaviorally coordinated if they had similar activity patterns or interacted during a 10-30 minute observation window. For the analyses on male association patterns, we used only sightings from bachelor groups and chose only individuals for whom we had a minimum of 15 sightings during the study period. Consequently, we restricted our analyses to 47 individuals which met three criteria. First we choose individuals for whom we had a minimum of 15 sightings (population averages; mean=45, mode=46, median=39, maximum=107). Second, we choose individuals who were sighted in the same groups as others for whom we had at least 15 sightings. Individuals observed at least 15 times but who were only sighted grouping with other individuals seen less than 15 times were removed from the analyses. Last, we only considered genotyped individuals. From these data we estimated pairwise associations for all dyadic combinations using a simple association ratio (Association Index, AI). We defined AI as $AI=N_{AB}/(N_A+N_B+N_{AB})$, where N_{AB} is the number of times individual A and B are sighted in the same group, and N_A and N_B is the number of times individuals A and B are sighted in different groups in the absence of the other.

4.2.3 Detecting non-random association

In order to test whether male elephants associated non-randomly, we compared the standard deviation obtained from the observed AI for each pair with the standard deviations derived from 1000 AI generated by randomizing elephant sightings data. To generate randomized sightings data, we used the contingency table randomization algorithm of Patefield (1981), implemented using the R software package VEGAN (Oksanen et al. 2009). The contingency table randomization technique randomly assigns individuals to different sightings or groups while maintaining the number of groups an animal was observed in and the group size for every sighting. We generated 1,000 randomized datasets and then calculated AI from these data and estimated the Standard Deviation (SD) of these AIs. When a pair of individuals have a social preference for each other or avoid each other, the SD of their observed AI will be significantly higher than that estimated from randomized data. The probability for the deviation of the observed AI from randomized sightings data due to avoidance or preference was determined as the proportion of randomized datasets with a SD greater that the SD obtained from observed AI. We ruled out the possibility of obtaining spurious results from this test as a result of the turnover of sampled individuals over time, by performing a temporal pattern analysis of associations (see Appendix B).

4.2.4 Determining the social role of older individuals in male elephant societies

To determine whether older elephants play a pivotal role in elephant social network, we tested two sets of predictions. The first set of predictions focused on individual level analyses and the second set focused on age class level analyses.

At the individual level, we tested two predictions. First we tested the prediction that older males have significantly higher association strengths than younger males (sum of AIs of each male with all other males). Second, we tested the prediction that older males have a high eigenvector centrality (eigenvalue of AI), a composite measure of how connected each male is in the network through associations. An individual is highly connected if they have high association strength or they have a large number of associates and if those associates are connected as well. To test the first prediction, we estimated the association strength, the eigenvector centrality, and the number of associates each individual had using SOCPROG. We then performed partial correlation analyses between age and association strength, eigenvector centrality, number of associates and total number of groups an individual was sighted in because all these covariates can be correlated. These correlations were performed using the R software.

At the class level, we tested the prediction that younger male classes should have significantly stronger associations with older age classes than expected by chance. To test this, we divided elephants into three age classes; 10-19 years, 20-29 years, and 30+ years and conducted an association analysis between classes. We used this age classification because these age classes coincide with important aspects of elephant life history. Ages 10-19 coincide with the transition period to independence from maternal units. Elephants in this social class also spend a significant proportion of their time in mixed sex groups. Age class 20-29 years covers the age range when all males are fully independent and experience their first musth, and some become reproductively active for the first time. Age 30+ years marks the period when all males are reproductively competitive. We estimated the mean association index within each age class and between age classes. We performed randomization tests on elephant AIs in order to generate expected mean AIs between and within classes under the null hypothesis, that all classes are equivalent in their association patterns. These randomizations were conducted by repeatedly reshuffling individuals across classes, while retaining class size and individual AI values. We performed 6 sets of randomizations, each generating the null distribution of means from 10,000 randomization runs within male classes, 10-19, 20-29, and 30+ and between male classes 10-19 and 20-29, 10-19 and 30+ and lastly 20-29 and 30+. We finally calculated the probability that the observed values were either larger or smaller than expected by estimating the ratio of mean values from randomized data greater or lesser than the observed.

4.2.5. Genetic sample collection and microsatellite genotyping

We collected dung samples from males that were not previously genotyped. We extracted DNA from these dung samples using a QIAamp DNA Stool Mini Kit (Qiagen™) following a modified Qiagen™ protocol (Archie et al. 2003). All individuals were genotyped at a minimum of 8 loci and up to 11 loci including one dinucleotide loci; LAFMS02 (Nyakaana and Arctander 1998), and ten tetranuclotide loci; LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18, LaT24, LaT25 and LaT26 (Archie et al. 2003). We used the PCR protocols detailed in Archie et al. (2003) to amplify DNA from the loci of interest and the PCR products were separated using Applied Biosystems 3730XL DNA Analyzer and run on Genemapper v.3.7 Applied Biosystems. Microsatellites alleles were scored using Gene Marker v.1.6. (SoftGenetics). We ran PCR for each sample and genotyped it twice if the initial PCR product was scored as a heterozygote and three to four times if it was a homozygote. We tested all genotyped loci for Hardy-Weinberg equilibrium and for the presence of null alleles (non amplifying alleles) using CERVUS software before estimating relatedness (Kalinowski et al. 2007; Marshall et al. 1998).

4.2.6 Estimation of pairwise genetic relatedness

Genetic relatedness r, for all pairwise combinations of individuals males were estimated using RELATEDNESS 5.0.8 (Goodnight 2006). RELATEDNESS employs a regression estimator of r developed by Queller and Goodnight (1989) to estimate pairwise r values. This estimator has been demonstrated to perform better than other relatedness estimators such as the estimators of Wang (2002), Li et al (1993) and Lynch & Ritland (1999) for this study population using the same markers (Archie et al. 2007). We used allele frequencies from 585 individuals typed from previous studies as well as this study for the estimation of pairwise r values. We also determined the reliability and accuracy of our pairwise r estimates for these additional genetic data by comparing the mean pairwise r estimates for known pairs of known kinship relationships with the theoretical expectation. These comparisons (see Appendix A) suggest that our pairwise r values were reliable and comparable to values found for similar studies (Archie et al. 2006; Van Horn et al. 2008).

4.2.7 Correlations between age, relatedness and AIs

In order to test whether age similarity and genetic relatedness influence association patterns in male elephants, we carried out correlations between AI matrix with either absolute dyadic age difference or genetic relatedness. Because dyadic measures are not independent, conventional tests for evaluating the probability that the correlation is significantly different from zero could not be employed. Instead we used Mantel tests, which assess the statistical significance of these correlations by comparing the observed r coefficient with the distribution of r values calculated from randomized data using Monte Carlo simulations (Mantel 1967). We used one tailed probability values. These values were determined by the proportion of r values from the randomized data greater than or lesser than the observed r coefficient for hypotheses for which we predicted a positive or negative relationships respectively (Manly 2007). Because previous genetic analyses on elephants of both sexes in this population showed that elephants were more related to individuals in their age cohort than to other age cohorts (Archie et al. 2007), we carried out partial mantel tests to control for the effect of age or genetic relatedness on the relationship between AI and genetic relatedness and AI and age respectively (Castellano et al. 2002; Smouse et al. 1986). All tests were carried out using XLSTAT (Addinsoft 2009).

4.3 Results

4.3.1 Association patterns of male elephants: influence of age and relatedness

The standard deviation (SD) and coefficient of variation (CV) of observed AI were significantly larger than AI calculated from randomized data (observed AI: mean=0.028, SD=0.040 CV=1.429; randomized AI: mean=0.027; SD=0.0196, CV=0.731, p=0.001) indicating that male associations were not random.

Male associations were weakly but highly significantly correlated with pairwise relatedness (r=0.0789, P=0.0095, Mantel test; Figure 7). Specifically, males that were strongly associated were more likely to be genetically related than expected by chance. Similarly, male associations were weakly but significantly correlated with age differences such that individuals with strong associations were more likely to be close in age than individuals that did not associate (r=-0.1019, p=0.0003, mantel test; Fig.8). Age difference and relatedness were negatively correlated but this correlation was not statistically significant (r=-0.045, p=0.140, mantel test). This indicates that it was somewhat uncommon to encounter pairs of male elephants that were age peers and that had high pairwise r values. In addition, it indicates that the relationship between (1) association and relatedness (r=0.0741, p=0.0165, partial mantel test) and (2) association and age difference (r=-0.0983, p=0.0011, partial mantel test) were not inflated by an association between age difference and relatedness.

4.3.2 Association patterns of male elephants: the role of older males

Older elephants had a higher association strength than younger males after controlling for confounding factors such as the number of sightings per male (r= 0.457, p=0.00066) or the number of times an individual male was sighted as well as the number of male association partners an individual had (r =0.290, p=0.0470). Older males were also more connected (measured using eigenvector centrality) than younger males after controlling for the number of sightings (r= 0.414, p=0.0026). However, this relationship became weak and less significant when we controlled for the number of association partners (r =0.179, p=0.23245). This is because older individuals also had more association partners than younger individuals (r=0.395, p= 0.0043). These results indicate that the number of association partners was strongly correlated with eigen-value centrality (r=0.815, p< 0.0001) and was the major metric influencing this composite measure of connectedness.

Males in the age class 20-29 were associated with males 30+ years more than expected by chance, indicating that males 20-29 years old were attracted to older males (30+ years of age). Within age classes, males10-19 years and males 20-29 years old associated among themselves as expected by chance, whereas males 30+ associated among themselves more than expected by chance. Further, males aged 10-19 were associated with males 20-29 years as expected by chance but were associated significantly less than expected by chance with males 30+ years old (Table 5). These results indicate that younger males 10-19 years were equally attracted to males 20-29 and to males their own age, but avoided older males (30+ years of age).

4.4 Discussion

Male elephant associations in Amboseli were significantly non-random, but weak compared to findings on female associations (mean group AI = 0.637, range = 0.196-0.993; Archie et al. 2006). These weak male associations result from males asynchronously alternating between being solitary, in a bachelor group or in a mixed group. Long term data from the Amboseli elephant population show that males 15-60 years old spend 57% of their time in mixed groups, 30.5% in bachelor groups and 12.5% being solitary (Lee et al. In press.).

In this study, males preferred to associate with individuals to whom they were more genetically related. These results are in agreement with findings on female elephants (Archie et al. 2006; Moss & Poole 1983; Wittemyer et al. 2009). In female elephant groups, association patterns are correlated with pairwise genetic relatedness such that closely related individuals spent more time together than with unrelated individuals. The positive correlation between association and genetic relatedness in males therefore highlights the importance of kin selection and suggests there may be indirect fitness benefits of association in bachelor groups. We speculate that these benefits may include tolerance towards relatives during foraging, defense benefits when in human dominated landscapes and helping behavior towards injured individuals (Buss 1990).

Males also associated with individuals to whom they were close in age. This result is consistent with findings from studies on elephants elsewhere showing that young adult males of similar age spend a lot of their social time sparring. This in turn suggests that age matched association is important in assessment and establishment of male dominance hierarchies (Evans & Harris 2008; Kabigumila 1993). Sparring could provide a mechanism for horning fighting skills necessary during male-male competition for estrous females.

Findings from this study also suggest that old males play a pivotal role in elephant male societies. Old males were more socially connected; they had a higher eigenvector centrality, and larger association strength due to a large number of association partners compared to young males. Males 30+ years of age also associated with males in the 20-29 year old age class but not with males in the 10-19 age class, presumably because males 10-19 years of age spent less time in bachelor groups and more time in mixed groups or with their family (Evans & Harris 2008; Lee et al. In press.), and these analyses focused on males in only bachelor groups. Possibly, younger males 10-19 years old can increase their association with other males while in mixed groups as observed by other studies (Evans & Harris 2008). The central role older males' play in male social networks suggest that they are sources of ecological and social knowledge in male societies. Males like females likely utilize the skills of older males on where to find forage and water during periods of scarcity. For example young males have been observed to prod older individuals when confronted with unfamiliar risk situations (Croze 1974), presumably as a way to elicit the older males response to impending risk.

The apparently weak association patterns and the weak correlations between AI and age or genetic relatedness reflect the complexity of optimizing the benefits from the diverse social relationships necessary for male survival and reproductive success. For example, individual males may be constrained to associate with age peers, relatives, or older males, at a time when with other males. This association constraint results from two sources. First the lack of a strong correlation between age and relatedness means that most individuals have to choose between either associating with a relative or with an age peer. Secondly, although time spent with other males increases with age (Lee et al. In press.), adult males come to musth asynchnously every year for a period of 2-4 months (Poole & Moss 1981). The increase in time spent in bachelor groups with age enhances associations between age peers but the corresponding increase in time spent in musth as males grow old reduces the strength of association among age peers.

Our results highlight the complexity of male social behavior and the role of kin selection and dominance assessment in male associations. Lastly, our results also highlight the role older males play in male elephant social groups, and suggests that the removal of older males in the population through poaching or culling can destabilize the social core and knowledge base of male elephant societies.

Table 5: Observed mean association index within and between three age classes compared with corresponding randomized mean association index within and between age classes in male elephants. Also shown are the upper and lower confidence limits for the mean estimated from the randomized AI and the probability values for the difference between the observed and randomized means.

Age class (years)	Observed mean AI	Randomized mean AI	lower CL for randomized mean AI	Upper CL for randomized mean AI	Probability value
Between age class					
20-29 & 30+	0.03772	0.02789	0.02253	0.033236	0.005
10-19 & 20-29	0.02301	0.02792	0.02267	0.033027	0.0638
10-19 & 30+	0.01435	0.02791	0.02253	0.033262	0.003
Within age class					
10-19	0.02695	0.02786	0.02018	0.038073	0.9085
20-29	0.03645	0.02788	0.02024	0.038093	0.0854
30+	0.04473	0.02791	0.01975	0.038778	0.0064

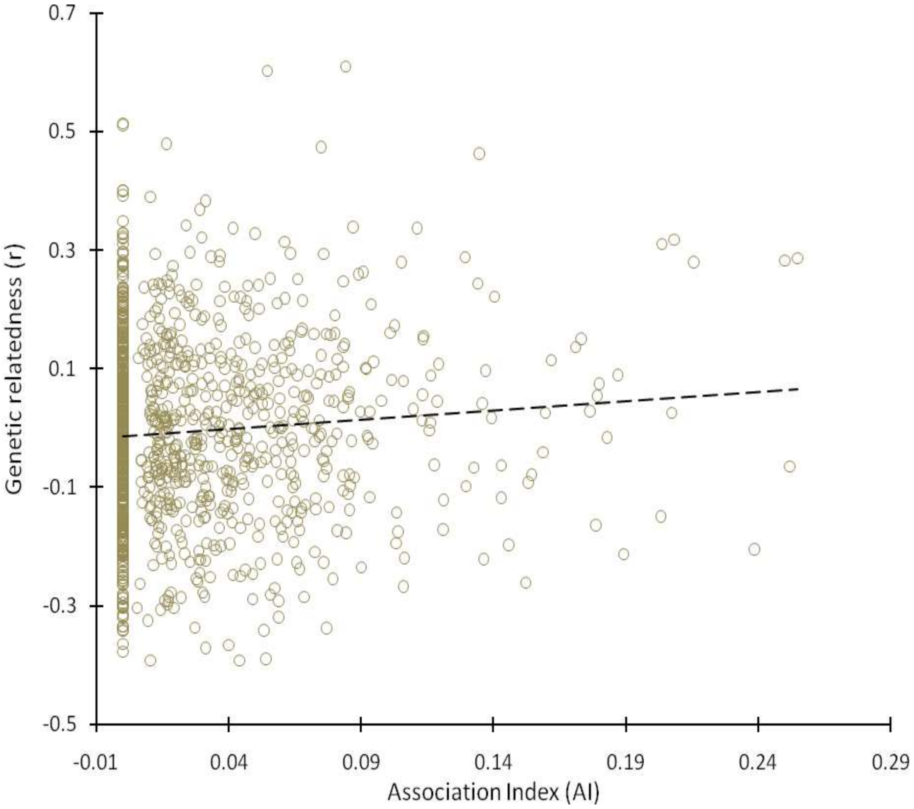


Figure 7: The relationships between pairwise association indices and pairwise genetic relatedness for all possible dyadic relationships of 47 individual male Amboseli elephants. Pairwise genetic relatedness was determined using Queller and Goodnights' r estimator

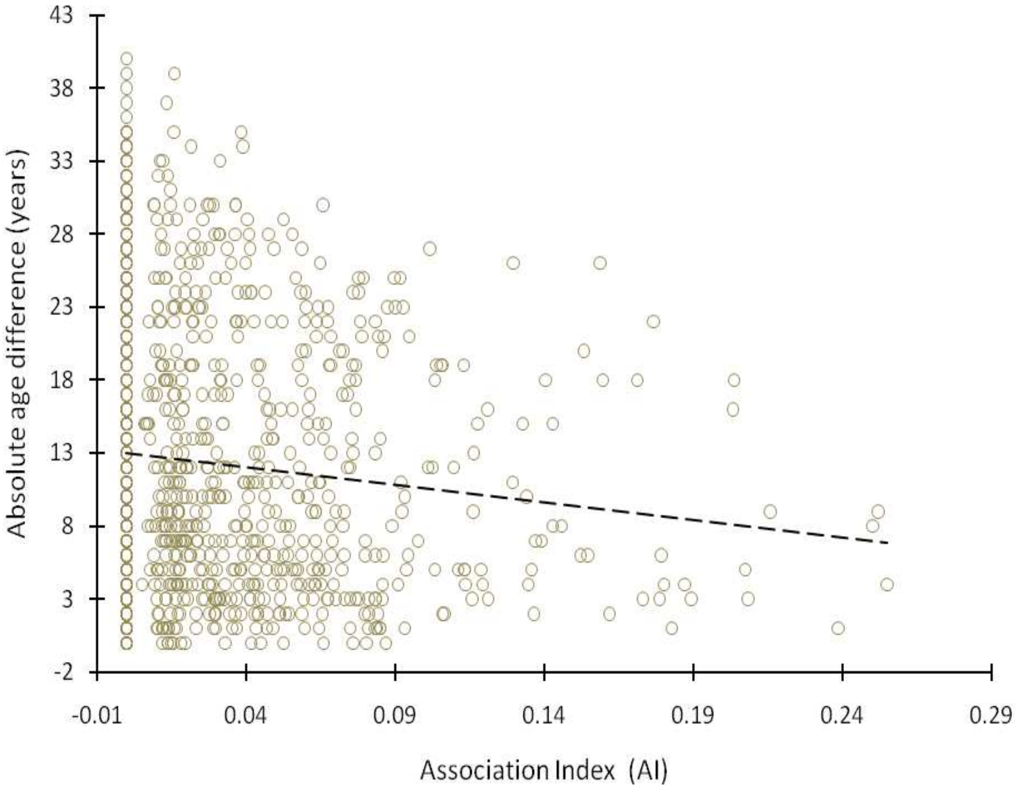


Figure 8: The relationships between pairwise association indices and absolute pairwise age differences among all possible male dyads from 47 individuals. Age for all individuals was calculated for August 2007.

5. The influence of life-history milestones and social networks on crop-raiding behavior in African elephants

5.1 Introduction

Life-history milestones such as age at dispersal, age when growth is accelerated, age of first reproduction and age of attainment of reproductive peak are accompanied by major changes in physiology and behavior (Beehner et al. 2009; Gesquiere et al. 2005). Changes in energy demands resulting in these major developmental milestones in animals can provide motivations for the acquisition and adoption of behaviors that may be adaptive during specific life history stages (Holekamp & Smale 1998). The spread and maintenance of such adaptive behavior in populations can be influenced by the complexity of the behavior and by social networks in these populations (Hoare & Krause 2003). Social networks can dictate the conditions and the social environments that are favorable to or impede social learning (Centola et al. 2007; Centola & Macy 2007; Gronlund & Holme 2005). The contexts under which social learning occurs have been the focus of numerous experimental and theoretical studies (Kendal et al. 2004; Webster & Laland 2008). It is uncommon for studies to examine the joint role of life history milestones and social networks on the acquisition and spread of complex behavior in natural populations.

Here we investigate the role of life-history and social networks on a complex behavior; crop-raiding. Crop raiding is a high-risk and high-gain foraging behavior in African elephants that requires dynamic assessment of risk by the raiding animal. Crop raiding is a high-risk foraging behavior, because farmers try to defend their crops from elephants whenever they detect them raiding. Studies on mortality and injuries in wild free ranging elephants show that a significant proportion of male elephant deaths and injuries are caused by humans (Moss 2001; Obanda et al. 2008) and most of these deaths and injuries are linked to human elephant conflicts (Obanda et al. 2008). However, human crops may offer nutrient-rich food sources that motivate elephants to take this risk (Sukumar 1990). Although elephants forage for 16-18 hours daily, foraging on crops usually occurs at night; particularly during moonless nights (Barnes et al. 2007) probably to minimize risks by avoiding detection by farmers. Elephants also appear to adjust the time in which they visit farmland depending on the risk. In places where farms are not guarded, elephants have been seen to raid during the day whereas in areas where farms are protected, elephants are known to come late at night when the farmers are likely to be sleeping. Crop raiding is undertaken by a few individuals in some populations (Sukumar 1995) and as many as one third of males in the Amboseli population (Chapter 2). Some raiders may raid a few times per year and others adopt raiding as a major foraging strategy (Sukumar 1995). In most mammals, mothers greatly influence the diets of their offspring (Mazur & Seher 2008; Sargeant & Mann 2009). In the case of crop raiding elephants mothers are likely to have a very limited or no role in teaching their sons to raid because female elephants rarely raid, including in the study population (Chapter 2).

Life history theory predicts that when behaviors that enhance current reproductive success are associated with risks to survival, males in their reproductive prime or with a high current reproductive potential should engage in risky behaviors that enhance reproduction (Candolin 1998; Grignolio et al. 2007). On the other hand young males with a low current reproductive value and high future reproductive potential should reduce adopting risk behaviors that compromise survival. Crop-raiding in elephants differs between the sexes (Sukumar & Gadgil 1988); males appear to raid much more than females (Bhima 1998; Chiyo & Cochrane 2005; Hoare 1999). This male bias in risk taking is common in polygynous social systems because the potential benefits of high risk behavior are greater for males than for females. A male taking risks to improve his reproductive competitiveness can potentially sire more offspring in a single breeding season than a female can in her lifetime. This suggests that risky behavior such as crop-raiding contribute to male reproductive tactics and also suggests a role of life history in raiding behavior. In male elephants, reproductive success is greatly influenced by social dominance and the onset and duration of musth, which are in turn dependent on age and nutritional state (Poole 1989). It is therefore postulated that sexual selection should favor bulls that adopt foraging strategies that maximize nutrient gains. These nutrient gains can then be allocated for growth and maintenance of musth. Male elephants, unlike many large mammals, continue to grow for most of their lifespan. With continuous growth, and with increasing musth duration with age, energetic and nutrient demands are likely to increase with age in elephants.

Two aspects of social learning are relevant to understanding the acquisition and spread of behavior in natural population. One of these is knowledge on when animals should acquire behaviors socially rather than through exploratory learning and from whom. Second is knowledge of the network structure of the population and how this structure may affect the propagation of complex socially acquired behaviors.

Social learning theory predicts that individual animals should use public information or learn from others when the cost of generating personal information through trial and error or exploratory learning is high and when public information is reliable (Dall et al. 2005; Galef & Laland 2005). Crop raiding is a high risk behavior and making errors could be costly. Animals are expected to learn from reliable sources such as experienced, older, or familiar individuals (Duffy et al. 2009; Laland 2004). Animals can also assess the reliability of behavior by observing multiple incidences of behavior from several demonstrators (Ward et al. 2008). Crop-raiding behavior is a common post-dispersal behavior among males in some elephant populations (Chiyo & Cochrane 2005), and we speculate that males learn to raid from conspecifics or through a combination of learning from conspecifics and exploratory learning (van Bergen et al. 2004). That social learning may be involved in the development of crop-raiding behavior is suggested by the fact that young elephants frequently sample food items eaten by conspecifics (Lee & Moss 1999).

Social network theory of contagion and propagation of complex behaviors in social networks predicts that social structure can impede the distribution and spread of behavior in the entire network. This is because, in theory, individuals adopt a behavior only if they have had contact with multiple sources of the behavior or repeated contact from a single source of the behavior. This requires a critical threshold number of demonstrators for the behavior to spread or critical association strength between demonstrators and naïve individuals. Crop-raiding wherever it has been documented is said to be undertaken by a small fragment of the adult male population (Sukumar 1991). How males acquire crop-raiding behavior and why some males never adopt raiding even when they range in proximity to crops is not known. Theoretical models for the propagation of information in social networks when social learning is involved predict that individuals raiding crops should be more associated among themselves than they are with the rest of the population if the population is structured into distinct subunits

(Centola et al. 2007). We predicted that young male elephants may learn to crop-raid from older associates.

In this paper, we tested three hypotheses. First we tested the hypothesis that life history milestones provide motivation for the acquisition and adoption of crop-raiding behavior. We did this by examining whether the probability of becoming a crop raider gradually increased as elephants became older because of the continuously increasing costs of reproduction and growth in a species with indeterminate growth. We predicted that elephants would begin their crop-raiding careers during the years of dispersal (10-19 years), when they gradually increase their time away from their natal family. Further, we predicted that the proportion of raiders should gradually increase with age, because of rising growth energy demands when males start to become reproductively active and are experiencing post pubertal growth (20-30 years) and/or when they reach their reproductive prime (45-50 years), a period when males experience protracted musth episodes (Hollister-Smith et al. 2007; Laws et al. 1975; Lee & Moss 1999; Owen-Smith 1988). We also tested whether the probability of being a raider was higher during specific life history stages. We predicted that most elephants would raid at 20-30 years when they are initiating reproduction and when they have accelerated growth.

Secondly we tested the hypothesis that the age and raiding status of a male elephant's associates influence his probability of becoming a crop raider. We tested this by simultaneously asking whether elephants copy a behavior practiced by the majority of their associates or whether they copy from older individuals or from the closest associates.

Lastly, we tested the hypothesis that raiders should occur in a limited set of male social units if the elephant population has a strong social structure, similar to female elephants. Specifically, although elephant females tend to have a strong social structure for fission-fusion systems, less is known about the social structure of male elephants, or how their structure affects raiding behavior. We predict that male elephants have a strong social structure and that raiders belong to social clusters that are composed of almost exclusively raiders.

5.2 Materials and methods

5.2.1 Study area and study population

This study focused on the Amboseli elephant population, currently consisting of ~1,400 elephants. This population has been intensely studied since 1972 by the Amboseli Elephant Research Project (AERP). All elephants born to the Amboseli population are individually known and are identified using natural tears, notches, holes and vein patterns on ear pinnae. Elephants are also identified from tusk characteristics (size, shape and configuration, one tusked, broken or intact), natural body marks and body shape. We used a photo ID database maintained by AERP on all Amboseli males to confirm individual identities in the field. This population is free ranging and occupies nearly 3000 km2 of Masai group ranches and Amboseli National Park (Moss 2001). This population is contiguous with elephants from Kimana, Tsavo and Chyulu to the east and the Kilimanjaro and Longido controlled hunting area in the south and southwest (Douglas-Hamilton et al. 2005; Moss 2001). All known Amboseli elephants have ages assigned to them; elephants born since 1975 have their ages estimated to within 2 weeks, those born between 1972 and 1974 have ages estimated to within a few months, and elephants born between 1969-1971 have ages estimated to within one year. However, ages for elephants born before 1969 are estimated to within 5 years using measurements of shoulder height, hind footprint length and body shape (Lee & Moss 1995).

5.2.2 Estimation of male associations

We collected association data from 2005-2007, and we did it opportunistically because sightings were unpredictable. We searched for male elephants daily by driving until we located them. When we sighted elephants, we recorded the time, their location using a Global Positioning System (GPS), the size and type of group they were encountered in (whether a bachelor group, consisting of males; a mixed sex group, consisting of males and females or solitary). For each sighting of a mixed group, we identified all males that were 15 years of age or older, and for solitary individuals and bachelor groups, we identified all individuals irrespective of age. We defined an elephant group as a spatially cohesive and behaviorally coordinated aggregation of two or more elephants. We considered a group of elephants as spatially cohesive if they were orientated towards the same direction and clustered within a radius of 100 meters. Elephants were considered to be behaviorally coordinated if they had similar activity patterns or interacted during a 10-30 minute observation window. For the analyses on male association patterns, we used only sightings from bachelor groups and choose only individuals for whom we had a minimum of 15 sightings during the study period. Consequently, we restricted our analyses to 58 individuals for whom we had a mean of 40 sightings each (minimum=15, mode=46, mean=36, median=18, maximum=107) and who were mostly sighted in groups of other individuals for whom we had at least 15 times or more. Individuals sighted 15 or more times but in groups of individuals seen in less than 15 times were removed from the analyses as well.

From these data we estimated the association of dyads using a simple association ratio or Association Index (AI), where $AI=N_{AB}/(N_A+N_B+N_{AB})$. N_{AB} is the number of times individual A and B are sighted in the same group, and N_A and N_B are the number of times individuals A and B are sighted in different groups in absence of the other respectively.

From these association indices, we chose the 10 individuals with whom each male was most frequently associated and ranked them from 1 to 10, with 1 being the male most frequently associated with the focal male and 10 as the least frequently associated with the focal male. From the association index data we calculated the average association index for the top ten associates ranked 1-10 (Figure 9).

5.2.3 Detecting male social units by maximizing the modularity of associations

In order to determine whether male elephant's social network is divided into social units of individuals that are more associated than they are with the rest of the population, we conducted two analyses. First, we conducted a hierarchical agglomerative cluster analysis that grouped males according to their association indices into nested groups of closely associated males. Secondly we conducted modularity analysis at different levels of group nesting of male associations produced using hierarchical clustering. We then delineated elephant communities using a point of nesting that produced maximum modularity (Q).

Hierarchical agglomerative clustering proceeds by joining two individuals with the smallest distance (distance is defined as 1-AI) or largest association in the population. Subsequent groups or individuals are joined in order of increasing distance, until all individuals and groups have been successfully joined into one cluster by applying the Unweighted Pair-Group Method using Arithmetic average (UPGMA). We used the UPGMA method for linking individuals and groups instead of complete linkage, single linkage, or Ward's methods because UPGMA produced a correlation between AI and the cluster dendrogram that was equal to or greater than 0.8; this is a recommended measure for an acceptable level of concordance between AI and the cluster dendrogram (Legendre & Legendre 1998). Modularity was defined as the difference between the proportion of total AI within clusters (first term in the equation) and the expected proportion of AI (second term).

$$Q = \frac{\sum_{I,J} \alpha_{IJ} \delta(c_I, c_J)}{\sum_{I,J} \alpha_{IJ}} - \frac{\sum_{I,J} \hat{\alpha}_{IJ} \delta(c_I, c_J)}{\sum_{I,J} \hat{\alpha}_{IJ}} \qquad \text{(Newman 2004)}$$

Where α_{IJ} is the AI between individuals I and J, $\hat{\alpha}_{IJ}$ is the expected value for α_{IJ}. $\delta(c_I, c_J)$=1 if I and J are members of the same cluster or $\delta(c_I, c_J)$=0 if I and J are members of different clusters.

Although there are different ways of determining the expected value of $\hat{\alpha}_{IJ}$ from AI (Whitehead 2008), in this study, $\hat{\alpha}_{IJ}$ was estimated as a product of association strength of individuals I and J ($\hat{\alpha}_{IJ} = \frac{S_I S_J}{2m}$), where SI and SJ are the strength of associations of individual I and J ($\text{For example, } S_I = \sum \alpha_{I,J}$) and m is the sum of all dyadic AI, i.e. $m = \sum \frac{S_I}{2}$ (Newman 2004; Whitehead 2008).

Cluster analysis and estimation of modularity were all implemented using SOCPROG (Whitehead 2009).

Populations with a strong community structure or consisting of discrete non interacting social units have modularity of 1, whereas populations with no social structure or with social clustering predicted by random expectation have a modularity of zero. However, because some random networks are known to produce communities with high modularity values (Guimerà et al. 2004), we estimated whether Q could arise by chance by comparing the value of Q estimated using real data with Q estimated from randomized data. Q from real data was then considered statistically significant if it was in the top 5 % or less of Q estimated from randomized data (Croft et al. 2008; Wolf et al. 2007).

5.2.4 Identification of crop-raiders

Identification of crop raiders was a multi-step process (see chapter 2). In the field we either identified crop raiders by tracking elephants for several hours following a farm raid or, when we were not able track raiders, by collecting their dung from raided farms. For elephants that we tracked and located, we identified them as known members of the Amboseli elephant population as opposed to other populations in the ecosystem (chapter 2). In cases where we were not immediately able to ascertain their identities, we took photos and later matched these photos with photos from a database of all Amboseli-born males. Dung collected from raided farms was preserved in 95% ethanol in the field and later brought to the lab at Duke University. In the lab, we extracted and genotyped DNA from the dung of these unknown crop raiders that we collected from raided farms. We then compared the genotypes of crop-raiding elephants collected over a period of two years with genotypes of 586 known individuals. We matched a raiding sample to a known individual in the database if four or more loci matched between the two. We used 4 loci because our data indicated that a dyad would match by chance at 4 loci with a probability of 0.00004 (this represents the probability of identity, PI; Waits et al. 2001). We allowed for one mismatch to account for potential genotyping errors such as allelic drop out. All matching of fecal samples with similar genotypes and genotype assignments to known individuals was carried out using the software CERVUS. Because we detected most raiders and because all individuals used in these analyses were seen frequently and have genotypes, the separation of individuals as raiders or non-raiders is highly accurate. We were able to individually identify 43 of an estimated 84 raiders originating from Amboseli National Park.

5.2.5 Statistical analyses

We analyzed the influence of life history separately from the analysis on the influence of association patterns and social networks on the probability of being a raider because we had a different data set for each analysis. We used a dataset for the entire population of 365 Amboseli elephants that were 10 years and above by August 2007 to test the influence of life history on raiding. To test the influence of association patterns and social networks, we used data on male association for 58 elephants collected between 2005 and 2007. In order to test the combined effects of life history and association, we used the subset of data from 58 individuals after establishing that a life history effect was detectable in this smaller dataset.

To examine the role of life history on raiding, we tested the hypothesis that the probability of being a raider gradually increased as a continuous function of age because of the rising costs of reproduction and growth with age in a species with indeterminate growth. For this hypothesis, we ran a logistic regression model with raiding status of the individual as the independent variable and age as a quantitative covariate. To test the test the alternative hypothesis that a specific life history stage influences the probability of being a raider, we grouped elephants into age classes corresponding with major life history phases and then performed a logistic regression on the raiding status of the individual elephant and the age class they belonged to as a categorical variable. This assumes that life history influences crop raiding in a stepwise manner and enables us to detect whether specific life history stage has a disproportionately large effect on crop raiding behavior. To test this hypothesis, we grouped males into five age classes associated with major life-history milestones in male elephants: 10-14 years, 15-19 years (these two age classes correspond to early and late dispersal phase respectively, Lee & Moss in press), 20-30 years corresponding to a period of post pubertal growth, 31-44 years (a period of rapid rise to a reproductive peak) and 45 years and above (corresponding to the attainment of a peak in a male's probability of siring an offspring).

To examine the role of association patterns in the acquisition of crop raiding behavior, we tested three alternative hypotheses. These hypotheses implicate specific social learning strategies that elephants might use for learning to crop raid from others. First, we tested the hypothesis that for a given individual, its' probability of being a raider increased with a rise in the number of its five closest associates who were crop raiders. Second, we tested the hypothesis that the probability of being a crop raider was higher if an animal's top associate was also a crop raider. Third, we tested whether elephants that associated with older raiders were more likely to become raiders than individuals that associated with age cohort members or younger raiders. For all these analyses, we used logistic regression with raiding status (raider =1, non raider=0) of an individual as a dependent variable. As covariates, we used (1) the raiding status of the first, second, third, fourth and fifth closest associate for each focal male, (2) the number of the top five associates of each focal male that were raiders and (3) whether these associates were older than the focal or not. For these and subsequent analyses we used data on 58 focal male elephants for which we had association data.

In order to identify, a combination of life history and social factors that could be used to predict the raiding status of an individual, we ran a multiple logistic regression using covariates from the life history and social learning models. Specifically we examined the effects of age class of the focal male, the crop raiding status of his top two associates and the age difference between him and his top associates on the probability that he is a raider. With regard to age difference between the focal male and his associates, we classified associates as either older or not older than the focal male. First we examined our data for the multi-collinearity of covariates by estimating of their correlations and the associated variance inflation factor in the models. This enabled us to use alternative evaluations of model fit.

Finally, we examined the influence of social structure on crop raiding by testing the hypothesis that male elephants have a strong social structure, and raiders are expected to form their own social clusters or clusters that are nearly exclusively composed of raiders. To test this, hypothesis, we estimated the social clusters of elephants by maximizing the modularity of associations in the population. We then assigned elephants to social clusters and ran a logistic regression of raiding status as a dependent variable and cluster ID as a covariate.

For the analyses where we wanted to compare several alternative models for a given hypothesis, we selected the best model using Aikake Information Criteria (AIC).

We also performed alternative model evaluation tools such as R^2 and Area Under the receiver operating characteristics Curve (AUC). AUC corresponds to the probability of success (or being a raider in this case) as predicted by the model is higher than the probability of failure (not being a raider). A model with AUC=1 predicts a success without error whereas a model with AUC=0.5 is random or an extremely poor predictor of a success. A model with AUC higher than 0.7 is generally considered to good whereas a model with AUC between 0.87 and 0.9 is considered excellent in terms of discriminating a success or minimizing false positives.

Covariates were evaluated using probability values for the coefficients are greater than zero and secondly by using the odds ratios. The odds are the probability that an event occurs divided by the probability that it does not occur. In other words the odds ratio of 1 means that an event is equally likely to occur or fail to occur. An odds ratio is the ratio between two odds and odds ratio greater than one means an event is more likely to happen than to fail.

5.3 Results

5.3.1 The influence of age on the crop raiding behavior

When we examined the effect of age on crop raiding, the model for the influence of age as a categorical variable had a substantially lower AIC and a higher R^2 value from the model in which age was treated as a continuous variable (Table 6). This suggests that crop raiding does not have a smooth and continuously increasing relationship with age but that life history stages influence crop raiding in a stepwise manner (Table 7). Both models for the influence of age on raiding had a large unexplained variance suggested by the low R^2 (Table 6).

5.3.2 Effect of raiding status, age and rank of associates on crop raiding behavior

The probability of being a raider was influenced by a male’s two closest associates’ raiding status such that associates of raiders were more likely to be raiders as well (Table 8, Figure 10). The raiding status of the third, fourth, and fifth ranked associates did not influence the probability that a focal male was a raider. Similarly, the number of the top five associates who were crop raiders did not strongly influence the probability that a focal male was a raider. The best model for the effect of association (assessed using AIC), for predicting the raiding status of an individual male was a model that included the raiding status of his two closest associates and the interaction between relative age of the second closest associate and his status (Table 8). In other words an elephant was likely to be a raider if his two closest associates were raiders. However, age of the associates was only important for the second closest associate such that a male was more likely to be a raider if his second closest associate was a raider older than him. The relative age of the top associate had little influence on the probability of a focal male’s raiding status.

5.3.3 A combined life history and social network model for predicting crop raiders

The most parsimonious model for predicting whether a male was a crop raider was a model incorporating three covariates: two of the three significant covariates from association analyses and one covariate from life history analyses (R^2=0.779, AUC=0.91, AIC= 43.2017, X^2=13.546, P=0.035). These covariates were age class of the focal individual (life history), the raiding status of his top associate and the interaction between age (older or not) and raiding status of his second closest associate (association). Although a model that included all four covariates (that were significant from association analyses (3) and a covariate from life history analyses), had a similar predictive accuracy to a parsimonious model, it was not statistically significant (R^2=0.798, AUC=0.91, AIC= 41.286, X^2=11.546, P=0.105). The lack of significance in the full model was caused by collinearity. Raiding status of the second associate had modest correlations with raiding status of the closest associate and age class of the focal individual. Consequently, these correlations produced high variance inflation factors in the four a model with four covariates (age of focal male: 1.22, raiding status of top associate: 1.97, raiding status of second closest associate: 3.22, interaction between age and raiding status of second closest associate: 3.29) but less inflation in the model with three covariates (age of focal male : 1.09, raiding status of top associate: 1.17, interaction between age and raiding status of second closest associate:1.10).

5.3.4 Social structure and distribution of raiders among male social units

Associations among male elephants showed a low but statistically significant modularity (Q_m=0.362, P=0.001; Figure 10), indicating that while social units were detectable, individuals among these units greatly associated. The elephants were grouped into 6 social units based on how closely associated members of a group were to each other relative to individuals from other groups. Crop raiders did not cluster into any particular social units, but were distributed across all six social units (Figure 10). No social units had raiders more than expected by chance (X^2=9.541, d.f.=5, P=0.089)

5.4 Discussion

Our results supported a model of crop raiding by which energetic costs of reproduction and growth lead to a stepwise increase in the proportion of males becoming crop raiders as they go through major life history milestones. Crop raiding is considered as a high risk and high gain foraging strategy. Raiders may gain from this behavior by improving body condition or growing larger for their age (see chapter 3). This model suggests a stepwise increase in energetic costs associated with dispersal, post pubertal growth, phase of rapid ascent to age of reproductive peak and attainment of reproductive peak. This increasing energy needs may provide males the motivation to initiate crop raiding behavior themselves or learn it from others.

Our results also provide support for a model in which social learning plays an important role in the acquisition of crop raiding behavior by male elephants. Results showed that elephants associating with older raiders were more likely to be raiders compared to elephants associating with age peers or younger individuals who are raiders. This result supports findings from theoretical and experimental studies on social learning.

Theoretical studies on social learning suggest that when individuals differ in quality or relevance of information they provide, animals are expected to bias their selection of demonstrators towards individuals that are older, larger, of a higher dominance rank, more experienced or familiar conspecifics. Accordingly, several experimental and a few studies of natural populations have confirmed this. Alternatively animals should adopt a behavior they have seen practiced by several demonstrators (Ward et al. 2008). For example young female guppies copy mate preferences from older females but older females do not copy from younger females (Dugatkin & Godin 1993). A study of social learning of foraging behavior in the nine-spinned sticklebacks showed that individuals are predisposed to coping foraging information from larger demonstrators more than they copy from younger demonstrators (Duffy et al. 2009). Other studies have demonstrated "bayesian" learning where individuals update their behaviors based on their immediate experience as well as prior public information (van Bergen et al. 2004). The number of the top five associates who were raiders was not a good predictor of whether a male would be a raider. This result suggests that elephants do not use quorum to decide whether to adopt a behavior or not. The most likely explanation for the lack of quorum decision making by male elephants is because the adoption of complex and risky behavior such as crop raiding, may require demonstrations of raiding from reliable sources such as from closer associates or older demonstrators.

Although a model for a shared spatial environment could allow associates to adopt a similar foraging behavior through independent exploratory learning by individual animals irrespective of social learning, two major reasons make this a very unlikely explanation for the pattern we observed. First elephants are not territorial and are capable of walking long distance in a day. Areas with crops in Amboseli are within 20 km of Amboseli NP, well within a day's elephant ranging distance (Douglas-Hamilton 1998). Clearly, all male elephants can easily access crops, but only one third of males in Amboseli are known to raid crops. If exploratory learning is involved then we do not expected raiders to be always closely associated. Second, theoretical models predict that when trial and error or exploratory learning is associated with significant costs, or social learning is associated with substantive benefits, copying from more experienced individuals may be adaptive (Laland 2004). Learning to crop raid through trial and error could be costly for males and raiding has substantial nutritional benefits for males (Rode et al. 2006; Sukumar 1990). Our results suggest a social process of crop forage acquisition, where individual learning by trial and error is costly as individuals risk injury or even death from angry farmers protecting their crops. In these circumstances elephants are therefore expected to learn from others and to be choosy from whom they learn, because, individuals with raiding experience may have knowledge on how to avoid detection. For example they can avoid detection by raiding late in the night or on moonless nights, or use some cues for detecting protected farms.

Although the elephant social network showed that individuals were clustered into weak but significantly distinct social units based on modularity, raiders did not form distinct social clusters as predicted for socially modular societies. We suggest that a combination of two factors working in tandem influenced the pattern we observed. First the acquisition of raiding through social learning appears to be restricted to only two of the top associates. Secondly, the elephant male social network was sparse with a low modularity as well as a low clustering coefficient. This means that the probability of connectedness among individuals within a social unit was low. This was demonstrated by the rapid decay in association index among closely associated males. This low clustering can impede the spread of complex behavior within a cluster as well as between clusters.

These results have implications for understanding the spread of complex and risky behaviors in natural populations and specifically for understanding the spread of crop raiding behavior in elephant populations. These results also demonstrate that energetic costs associated with a male's life history strategy can drive foraging innovation and learning in males. They also demonstrate the value of incorporating life history stages in models for the spread of adaptive behaviors in populations.

Table 6: Comparison of an "age class" model (with males grouped into age classes corresponding to life-history milestones) with a model using age as a continuous variable showing that the age class model had a better fit to the data.

Model	*Chi-square*	*P-value*	*AIC*	R^2	*AUC*
Age Class	18.553	0.001	216.552	0.285	0.771
Age	27.975	< 0.001	240.175	0.146	0.771

Table 7: Comparison of the coefficients and odds ratios for being a raider across age classes, showing that the probability of being a raider increased with increasing age class

Coefficient	*Value*	*S.E*	*Chi-Square*	*P-value*	*Odds ratio*
Intercept	-5.209	1.426	13.349	0.000	
10-14	0.000	0.000			
15-19	2.099	1.528	1.887	0.170	8.159
20-30	3.703	1.445	6.568	0.010	40.566
31-44	4.111	1.464	7.890	0.005	61.000
45+	4.340	1.504	8.329	0.004	76.742

Table 8: A comparison of several models showing the influence of associates' rank (indicated by A1, for top the most associate and A5 for fifth associate respectively), their raiding status (RS) and their ages (Age1, Age2 for ages of associates ranked 1 and 2 respectively) on the probability of raiding by focal individuals. The best model (indicated by the lowest AIC) was that incorporating the raiding status of the topmost and second topmost associates and the interaction of age and raiding status for the second topmost associate. Models were evaluated using AIC; the smaller the AIC the better the model. AUC and R^2 also presented as alternative evaluation tools for model fit (The larger the AUC and the larger R^2, the better the model). In model specification (,) indicate a list of covariates used without interaction, (+) indicates that we run a model after summing the covariates and (*) indicates interaction of covariates in the model

Model	*Chi-Square*	*P-value*	*R^2*	*AIC*	*AUC*
RS-A1+RS-A2+RS-A2*Age-A2	11.658	0.0201	0.695	6.860	0.860
RS-A1 +RS-A2 +RS-A1*Age-A1 + RSA2*Age-A2	11.696	0.0691	0.733	47.541	0.876
RS-A1, RS-A2	13.687	0.0011	0.511	56.856	0.758
RS-A1+RS-A2	15.349	0.0005	0.411	61.272	0.750
RS-A1	11.498	0.0007	0.298	65.713	0.588
RS-A2	12.368	0.0004	0.296	65.790	0.658
RS-A1+RS-A2+RS-A3+RS-A4+RS-A5	9.664	0.0019	0.251	68.202	0.745
RS-A4	2.266	0.1322	0.054	77.588	0.474
RS-A5	1.210	0.2714	0.028	8.729	0.409
RS-A3	0.273	0.6013	0.006	9.661	0.387

Table 9: A comparison of the coefficients and odds ratios showing that a male's associates' raiding status and their relative age significantly influenced his probability of being a raider

Coefficient	*Value*	*Standard error*	*Chi-Square*	*P-value*	*Odds ratio*
Intercept	*-1.099*	*0.584*	*3.535*	*0.060*	
Top associate is a raider	*4.018*	*1.595*	*6.351*	*0.012*	*55.612*
Second top associate is a raider	*-2.308*	*1.796*	*1.651*	*0.199*	*0.099*
Second top associate is not a raiders and he is older	*-2.447*	*1.494*	*2.684*	*0.101*	*0.087*
Second top associate is a raiders and he is older	*4.018*	*1.812*	*4.920*	*0.027*	*55.616*

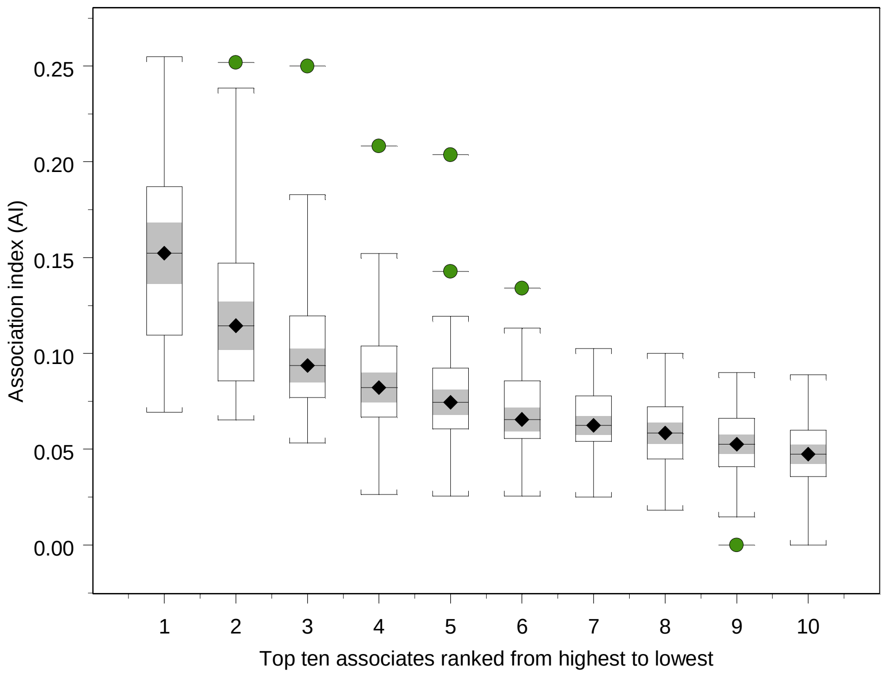


Figure 9: Mean Association Index values (with median, quartiles and outliers) for associates of different ranks, pooled across 58 focal male elephants. Associates of rank 1 are the most frequent associates, those of rank 10 the least frequent of the top ten.

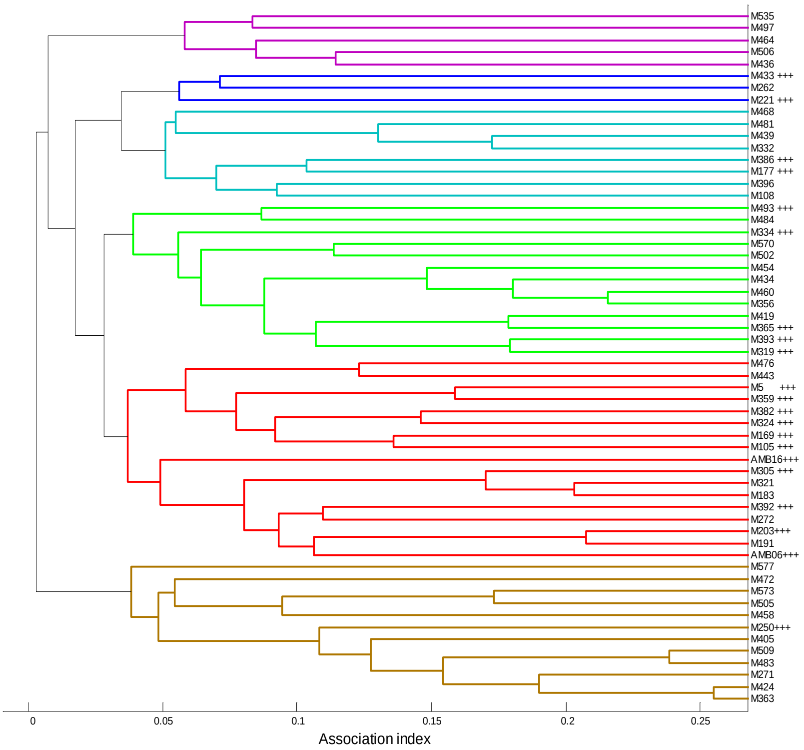


Figure 10: A cluster dendrogram showing that (1) crop raiders (indicated by +++) tended to have raiders among their top two associates and (2) crop raiders did not appear to form distinct social units (indicated by the different colors) but raiders were instead scattered among clusters. The dendrogram was determined from a hierarchical cluster analysis using the UPGMA method with a cophenetic correlation of 0.82. Clusters were delineated using a point on the association index where modularity was at its maximum (Q_m=0.362, AI=0.0346).

6. Conclusions and research directions

In chapter two, our results indicated that there is a large pool of crop-raiders in any population and that this can constitute up to one third of the entire adult male population. Our results in this chapter also indicated that females did raid or raided so infrequently that we could not detect. It is not clear at the moment whether the proportion of raiders in a population is influenced by environmental factors or by demographic patterns (e.g sex ratio, age structure e.t.c.). Similar studies are required in other elephant populations with different demographic patterns and living in diverse habitats. This will enable us to determine demographic and environmental influences on population levels patterns of raiding. In some elephant populations, females are known to raid. Circumstances influencing patterns of raiding by females are less understood and need to be explored.

In chapter three our results demonstrated that risk-taking pays off for males. These results suggest that risk-foraging behavior can evolve as a result of strong sexual selection for large size and condition dependent mating success in males. However reproductive success is also influenced by longevity particularly in elephants where male reproductive peak is attained at age 45 years. Risky foraging may compromise longevity as males may suffer injuries or risk being killed while raiding. Further research is therefore required to determine actual risk costs and to explore the potential trade-off between risk-taking and longevity on male reproductive success.

In chapter four, we demonstrated the complexity of male social relationships and the influence of kin selection and age on association patterns of male elephants. Specifically we showed that male associations although weak, were nonrandom and were positively correlated with genetic relatedness, suggesting a role of kin selection in the cohesion of male elephant social groups. Male associations were also negatively associated with age disparity, suggesting that males associate with familiar males of similar age with whom they may test their strength. Finally we found that older males had high centrality and strength in social networks, suggesting their possible role as sources of social and ecological knowledge. In this chapter we speculated foraging competition among males to promote kin based associations. There is a need to explicitly test this hypothesis.

In chapter five, we provided evidence for social learning (through association patterns) and life-history (through age effects) on the probability of raiding. We specifically found that in male elephants, the probability that an individual male is a raider increased as a function of its age, such that older males were more likely to be raiders than young males. Similarly, the probability that an individual male is a crop raider was greatest when his two closest associates were raiders and when his second closest associate was older than him. These results indicate that males choose models for behaviors before copying them, probably because these behaviors involve high risks. Raiders did not cluster into separate social units from non-raiders. These results suggest that differences in population age structure and social structure can greatly influence patterns of raiding in elephant populations. These results also suggest that, in populations where females raid crops, patterns of spread of crop raiding behavior will be different due to a difference in social structure between males and female social groups.

Appendix A

Table 10: Mean pairwise R values (±SD) observed from this study compared with expected theoretical kinship R values and observed kinship values from previous studies. N is the number of dyads used for estimating the observed R.

Kinship relationship	*Theoretical R*	*Observed R (this study)*	*Observed R (Archie et al. 2006)*	*Observed R (Wittemyer et al. 2009)*
Mother offspring	0.5	0.490 ± 0.100 (n=28)	0.47±0.01 (n=96)	0.490±0.088 (n=121)
Maternal siblings	0.25	0.284 ± 0.169 (n=9)	0.28±0.020 (n=58)	0.284±0.117 (n=81)

Appendix B

Detecting non-random association and temporal stability of associates

Temporal patterns of association are useful for characterizing the temporal dynamics of fission-fusion social systems. Here we assessed the temporal stability of associations following the method of Whitehead (1995). This method is implemented by the SOCPROG software (Whitehead 2009) and computes lagged and null association rates that are then compared to test whether elephants have stable or random associates through time. The lagged association rate is the probability that two individuals are associated after a previous association. This is then generalized for the entire population. The lagged association rate individual X has with Y in time lag τ or between sampling period j and k $g(\tau)$ is calculated from the association between X and Y in period j, $a_j(X,Y)$ and k, $a_k(X,Y)$ if X was identified in period k, $a_k(X,X)$. Associations and identification take the form of 1 if X and Y are associated or X is identified and zero otherwise.

$$g(\tau) = \frac{\sum_{j,k|(tk-tj)=\tau} \sum_X \sum_{Y \neq X} a_j(X,Y) \times a_k(X,Y)}{\sum_{j,k|(tk-tj)=\tau} \sum_X \sum_{y \neq x} a_j(X,Y) \times a_k(X,X)} \qquad \text{(Whitehead 2008)}$$

The null association rate $\hat{g}(\tau)$ is the probability that two individuals will be associated after a previous association by chance alone. It is calculated from the mean number of associates (m) and the number of potential associates (p) of individual X during time interval τ.

$$\hat{g}(\tau) = \frac{m}{p} \qquad \text{(Whitehead 1995)}$$

We then fitted several exponential models to lagged association rates using maximum likelihood. We evaluated the fit of these models to the observed lagged association rates using Quasi-AIC because of over dispersion in association rate data. We used lags in months smoothed over 1250 observations as this would reduce any effects of unequal sampling over time. Non fission-fusion groups with permanent companions have a lagged association rate of 1 and a null association rate of zero whereas randomly associating fission-fusion groups will have a lagged association rate overlapping with the null association rate. Fission-fusion groups with stable companions have associations rates lower than 1 but higher than the null association rates, and may consist of either permanent or ephemeral but predictable companions or both with the later being characterized by occasional temporal overlap of the lagged association rate with the null association rate when conditions for grouping aren't favorable.

Association rates across group or monthly lags were generally low and mostly non-random. Analyses of lagged association rates, using groups or months as lag units were similar and fitted models for temporal association rates that suggest two levels of casual acquaintances or ephemeral companions associating at different rates or time intervals perhaps dictated by some environmental or ecological factors (Fig. 2; Table1). We could not estimate time durations for which dyads are associated or dissociated from these models because time intervals for which association data was collected were discontinuous, with a period of 5-7 months of continuous data collection and a similar interval during which data wasn't collected each year.

Male elephant association patterns were non random and temporally stable and predicted to have different association patterns probably reflecting resource availability patterns as would be expected for dynamic fission-fusion social systems. It is in fact interesting to note that the period when stability of association collapsed to random coincides with the 2005 drought in the Amboseli region. 2006 and 2007 were wet and associations were higher and more stable.

Table 11: Models of temporal patterns of association from association rates estimated from monthly rates as well as rates of association using groups.

Model explanation	Models for lagged association rate $g(\tau)$	Parameter estimates ± standard error	QAIC
Two levels of acquaintances	a3*exp(-a1* τ) +(1-a3)*exp(-a2* τ)	a1=2.386±4.353 a2=-0.079±4.131 a3=0.0924±1.443	**2752.3**
Rapid dissociation with two levels of acquaintances	a3*exp(-a1* τ) +a4*exp(-a2* τ)	a1=-0.080±3.252 a2=2.285±6.269 a3=0.075±0.790 a4=0.838±64.591	2754.2
Cyclical association	a2+a3*exp(-a1* τ)	1a=0.044±0.026 2a=1.058±0.364 3a=0.130±0.021	2757.0
Rapid dissociation with constant companions & casual acquaintances	a2+a3*exp(-a1* τ)	a1=8.782±2.517 a2=0.116±0.028 a3=327.071±973.426	2769.0
Rapid dissociation & constant companions	a1	a1=0.130±0.024	2780.1
Casual acquaintances	exp(-a1*τ)	a1=0.617±0.170	4136.6
Rapid dissociation & casual acquaintances	a2*exp(-a1* τ)	a1=-0.013±0.047 a2=0.123±0.042	2781.4
Constant companions & casual acquaintances	a2+(1-a2)*exp(-a1* τ)	a1=2.901±1.491 a2=0.116±0.028	2767.5

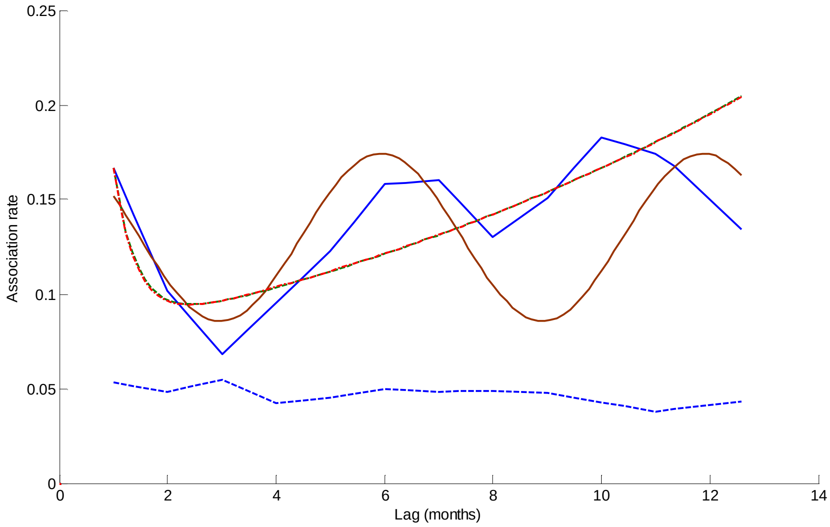


Figure 11: Comparison of three exponential models of temporal association patterns estimated from the observed lagged association rate in months (blue solid line). The exponential models include the model for two levels of casual acquaintances (red broken line) or rapid dissociation and two levels of causal acquaintance (Green broken line) and a cyclical association (brown solid line). These three models had some support from the observed data. We used a moving average of 1250 AI which was the median number of pairwise association observed each month. The null association rate (Blue broken line) or association rate from random expectation is shown.

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Biography

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PROFESSIONAL PREPARATION

1996-99: M.Sc. Zoology, Department of Zoology, Makerere University.

1991-94: BSc. Hons. (Major: Zoology), Makerere University, Departments of Botany & Zoology.

APPOINTMENTS

Jul 2001-Jan 2002. Research scholar, Department of Zoology, University of Florida (Prof. Colin A. Chapman's Lab.).

Dec 1998- Jun 2001. Consultancy on Problem Animal management with Kibale and Semuliki Conservation and Development Project (IUCN Project, funded by the Royal Dutch Government. Project Manager: Mr. Patrick Kidya).

May 1995-Sep 1996. Master of Science Research Fellow, Institute of Environment and Natural Resources, Makerere University, Uganda (Supervisor: Dr. Isabirye Basuta).

PUBLICATIONS

Wasser S, Poole J, Lee P, Lindsay K, Dobson A, Hart J, Douglas-Hamilton I, Wittemyer G, Granli P, Morgan B, Gunn J, Alberts S, Beyers R, **Chiyo P**, Croze H, Estes R,

Gobush K, Joram P, Kikoti A, Kingdon J, King L, Macdonald D, Moss C, Mutayoba B, Njumbi S, Omondi P, Nowak K. 2010. Elephants, ivory, and trade**.** *Science*, 327**(**5971): 1331-1332

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Chiyo, P.I., 2000. Elephant ecology and crop depredation in Kibale National Park, Uganda. *M.Sc. Thesis,* Makerere University, Kampala.

RESEARCH GRANTS AND AWARDS

2006: USFWS, African Elephant Conservation Fund. Awarded US $28,000 for dissertation research on "elephant socio-ecology and crop raiding in Amboseli ecosystem, Kenya"

1998: Pittsburgh Zoo, USA. Awarded US $2,000 for research on "Capsicain based elephant repellents and community based elephant deterrents"

1996: African Ele-Fund, Bristol UK. Awarded US $8,000 for M.Sc. thesis research on "Elephant ecology and crop depredation in Kibale National Park, Uganda"

1996: Foundation for Wildlife Conservation, Milwaukee, USA. Awarded US $2,000 for M.Sc. thesis research on "Elephant ecology and crop depredation in Kibale National Park Uganda"

1995: Makerere University Institute of Environment and Natural resources and USAID, M.Sc. Research Fellowships.