

Using molecular and observational techniques to estimate the number and raiding patterns of crop-raiding elephants

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Summary

1. Conflict between humans and animals, generated by behaviours like crop raiding, can represent a major threat to the survival and conservation of protected species. Crop raiding is an example where the conflict is assumed to be attributable to a small number of habitually raiding animals. No studies have systematically tested this assumption on African elephants *Loxodonta africana*.
2. In the greater Amboseli basin, in southern Kenya, we determined the number of elephants that come into conflict with humans through crop raiding, their gender, and their patterns of raiding. We tracked footprints, and observed elephants after they raided farms, and genotyped DNA extracted from faeces collected from raided farms. Using these data, we estimated the number of raiders with asymptotic regression and count models.
3. We found that 241 elephants from several elephant populations in the Amboseli basin raided farms. Raiders were independent males; we detected no females raiding crops. Approximately 35% of the raiders were from the Amboseli elephant population, representing about 1/3 of the independent males in that population. Approximately 12% of raiders from the Amboseli elephant population were habitual and were responsible for 56% of elephant raiding events.
4. *Synthesis and applications.* Our results suggest that targeted elimination of habitual raiders could in theory reduce crop raiding. However, the large pool of occasional raiders, the availability of palatable crops in areas of conflict, and the link between crop-raiding and natural male foraging tactics, indicates great potential for recruitment of habitual raiders from this pool of occasional raiders. Furthermore, shooting of raiders as a strategy for reducing crop raiding carries a high risk of misidentifying habitual raiders. We suggest instead an ethical management strategy that uses remote monitoring of raiders as an early warning system for crop protection, and longitudinal studies to evaluate the development of habitual raiding.

Key-words: habitual behaviour, males, molecular censusing, wildlife–human conflict

Introduction

Conflict between humans and wildlife is a major conservation concern because many threatened species frequently depredate crops or livestock (Hoare 1999; Marker *et al.* 2003; Woodroffe & Frank 2005; Woodroffe *et al.* 2005; Basille *et al.* 2009; Hockings & Humle 2009). This can be a major cause of wildlife mortality, because farmers attempt to secure their crops or livestock from wildlife depredation by killing or injuring wildlife.

Mortality from conflict is accelerating the demise of populations that are already experiencing dramatic declines from habitat loss (Haigh *et al.* 1979; Andren *et al.* 2006).

The prevailing paradigm for the management of large protected mammals that come into conflict with humans is the selective culling or translocation of offending individuals (Linnell *et al.* 1999; Omondi, Bitok & Kagiri 2004). This approach assumes that a few habitual individuals cause most of the conflict (Sukumar 1991; Stahl *et al.* 2001). Although some evidence supports this in some populations of Asian elephant *Elephas maximus* (Sukumar 1995; Williams, Johnsingh &

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Krausman 2001) and carnivores (Linnell *et al.* 1999; Woodruffe & Frank 2005), this view has been challenged for the African elephant *L. africana* (Hoare 2001) and the Eurasian lynx *Lynx lynx* (Odden *et al.* 2002).

Crop raiding by elephants is recognized as a major challenge to elephant conservation (Sitati *et al.* 2003). However, very little is known about the number of raiders, their sex or the frequency of raiding in large free ranging elephant populations, because raiding is largely nocturnal (Graham *et al.* 2009). Furthermore, the size of source elephant populations is not usually precisely known, making it difficult to determine the proportions of raiders in these populations. Such data are important for inferring the ultimate drivers of raiding and for developing ethical and effective conflict management strategies to enhance species conservation and survival in human dominated landscapes.

Recent advances in non-invasive molecular censusing (Eggert, Eggert & Woodruff 2003; Guschanski *et al.* 2009) make it possible to estimate the number of elephants that are raiding crops. However, the costs associated with non-invasive molecular censusing can be high, mean recapture rates are often small, and the probability of capture is likely to vary non-randomly across individuals. Thus, molecular census data from crop-raiding elephants will have a capture probability bias, which poses problems for population estimation models because individuals that raid repeatedly will be over-represented in the census whereas those that raid rarely will be under-represented. When such bias is prevalent, the same data can fit more than one alternative statistical model even though each model predicts a substantially different population size estimate from the data (i.e. alternative models are non-identifiable, see Link 2003; Holzmann, Munk & Zucchini 2006). It may be difficult to choose the best model from these alternative models on the basis of their fit to the data, rendering conventional model selection such as Akaike Information Criteria (AIC) inappropriate.

Here, we use a combination of genetic and observational techniques to address four objectives concerning the numbers of crop-raiding elephants and their patterns of raiding in a well-studied population of elephants. The first objective was to estimate the total number of crop-raiding elephants in the Amboseli basin in Kenya. The second objective was to estimate the proportion of total raiders originating from a single elephant population in the Amboseli basin, namely the Amboseli elephant population (AEP), a population in which all individuals and their histories are known. Our third objective was to investigate the patterns of crop raiding by individually identified elephants and to test for habitual raiding behaviour. Finally, our fourth objective was to determine sex differences in raiding patterns.

Achieving these objectives required that we determine *a priori* a suitable model for estimating population size from data characterized by small mean recapture rates and heterogeneity in capture probabilities among individuals. To do this, we tested two classes of models through simulations: (1) three asymptotic models, specifically the negative exponential, the Michaelis–Menten and the Chessell models (examples: Kohn

et al. 1999; Eggert, Eggert & Woodruff 2003; Meijer *et al.* 2008), and (2) three count models known to be robust to heterogeneity in the probability of individual recaptures, specifically the finite Poisson-mixture, Zelterman and Chao models (examples; Chao 1987; Zelterman 1988; Böhning *et al.* 2005).

Materials and methods

STUDY AREA

We monitored crop raiding in three farming communities, Namelok, Isinet and Sompet, representing major agricultural areas surrounding Amboseli National Park (ANP). Two of these areas, Isinet and Sompet, were also in proximity to Chyulu, Tsavo and Kilimanjaro National Parks and Kimana Sanctuary (Fig. 1). Other larger tracts of neighbouring agricultural land were not monitored during this study (Fig. 1).

The Amboseli basin contains three contiguous elephant populations that use discrete core areas corresponding to specific protected areas: the AEP uses the ANP as a core area, the Chyulu–Tsavo population uses the Chyulu and Tsavo National Parks as core areas, and the Kilimanjaro elephant population uses Kilimanjaro National Park as a core area. The Kimana Sanctuary, because of its small size, does not maintain a discrete population but serves as a zone of overlap between the AEP and the Chyulu–Tsavo populations (Moss 2001). The AEP comprises *c.* 1400 elephants, the Kilimanjaro population comprises *c.* 793 elephants, and the Chyulu–Tsavo population comprises *c.* 10 397 elephants estimated from a total aerial count (Blanc *et al.* 2007).

The AEP has been studied since 1972 by the Amboseli Elephant Research Project but the other populations are not well studied. All elephants born into the AEP are individually known and recognizable from pinnae, tusk, and body characteristics (Lee & Moss 1995). This enabled us to identify raiders from the AEP with certainty. All AEP elephants are assigned a birth month and year (Moss 2001), allowing us to examine raiding behaviour in relation to age. Genotyping has been completed for 251 out of a total of 471 adult females and 110 out of a total of 275 adult males representing about 50% of adult elephants in this population (Archie *et al.* 2008; this study). This genetic data base allowed us to assign genotypes of raiders to known AEP elephants.

FIELD RECOGNITION OF RAIDERS AND FAECAL SAMPLE COLLECTION

We monitored elephant incursions into Namelok, Isinet and Sompet between September 2005 and December 2007 on a daily basis whenever crops were available. Our team monitored farms during the day in order to detect raiding events from the previous night. Specifically, we followed elephant tracks from raided farms to locate and identify elephants that were involved in raiding. When tracking led us directly to elephants, we determined their sex and took photos of their ears for identification so that we could classify raiders as AEP elephants, or as non-AEP elephants (i.e. as originating from the Kilimanjaro or Chyulu–Tsavo populations), using the photo identification data base.

When tracks did not lead us directly to raiders, we collected faecal samples from raided farms. Faecal collection was opportunistic because raiders did not always defecate in crop fields when they raided. When elephants did deposit dung, multiple dung piles were present for some raiders. To minimize the collection of duplicate

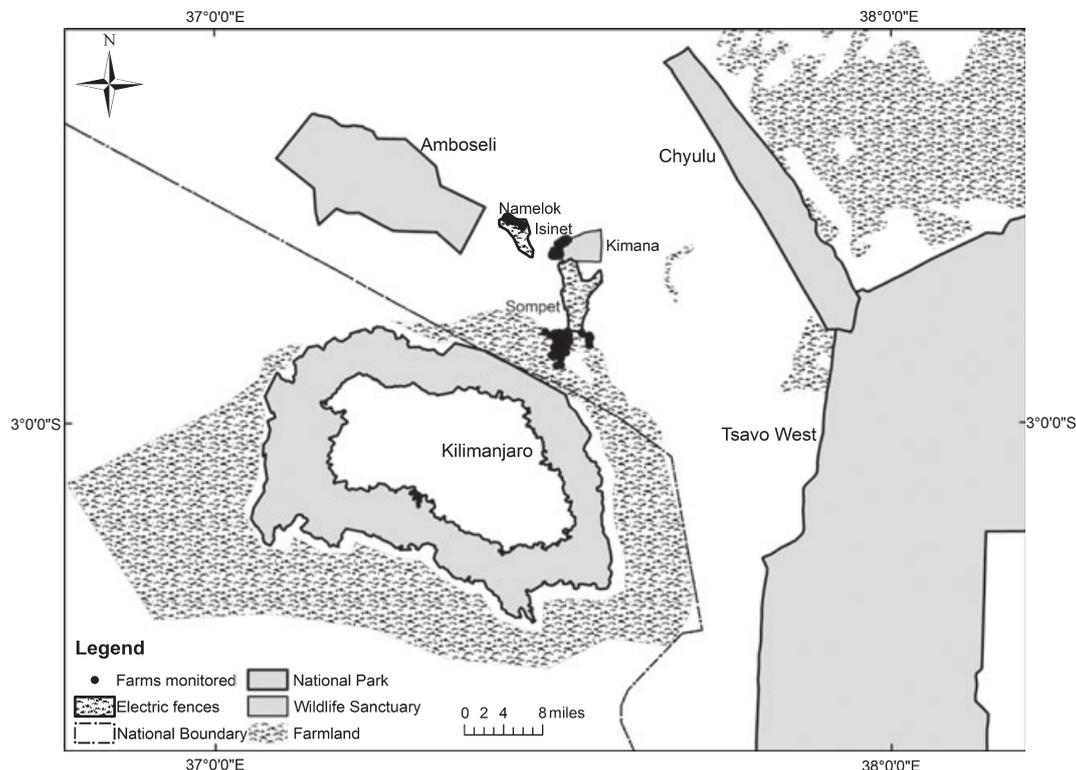


Fig. 1. Map showing protected areas (grey) that represent core areas used by the three major elephant populations in this study; Amboseli elephant population (AEP), Kilimanjaro, and the Chyulu–Tsavo elephant populations. Stippled areas indicate the farming communities near these protected areas and the black dots indicate the locations where we monitored crop-raiding elephants (see map legend).

samples and increase the chance of collecting dung from as many different individuals as possible, we identified two types of elephant trails at entry or exit points to crop fields. First, we located trails that were used by single individuals (based on number of footprints), collected one dung sample and assumed that all the dung on each track was deposited by a single elephant. Secondly, we located trails used by multiple elephants, and collected multiple dung samples from these trails, assuming that any two dung piles on the same trail were from different individuals if the dung bolus sizes, consistency and composition were different. We collected a sample from the outer layer of faeces (rich in mucus and dead cells) into a 15-ml plastic capped tube containing 95% ethanol, 6–24 h after defecation. We kept these faecal tubes at ambient temperature in the field for 6–12 months and at -80°C once in the laboratory.

IDENTIFICATION OF RAIDERS FROM DNA GENOTYPING

We extracted DNA from 175 faecal samples using a QIAamp DNA Stool Mini Kit (Qiagen, Germantown, Maryland, USA) following a modified Qiagen DNA extraction protocol (Archie, Moss & Alberts 2003). We amplified and genotyped 112 of 175 faecal samples at between 5 and 9 loci using the polymerase chain reaction (PCR) protocols detailed in Archie, Moss & Alberts (2003) to amplify target loci. These loci included one dinucleotide locus (LAFMSO2; Nyakana & Arctander 1998), and eight tetranucleotide loci (LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18 and LaT24; Archie, Moss & Alberts 2003). We used the 3730XL DNA Analyzer and GENEMAPPER v.3.7 (Applied Biosystems, Beverly, Massachusetts, USA) to generate genotypes at these loci, and scored alleles using GENE MARKER v.1.6. (SoftGenetics, State College, Pennsylvania, USA).

To minimize error due to allelic dropout or spurious alleles, 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.

Genotype matching involved two stages. First, we identified unique genotypes from all raiders by examining genotypes from all faecal samples collected from raided farms and matching the identical ones to obtain a set of unique genotypes from raided farms. Secondly, we determined whether any of these unique genotypes matched known genotypes from the AEP.

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 did this by calculating the probability of identity (PI), i.e. the probability that a pair of animals will match at a specified number of loci. Previous studies have identified a PI threshold of 0.0001 as sufficient for discriminating between genotypes of different individuals (Waits, Luikart & Taberlet 2001; Creel *et al.* 2003), we therefore sought to identify the number of loci that would provide a similar threshold for our study population. We calculated the PI from allele frequency using the formula provided by Waits, Luikart & Taberlet (2001). This formula is based on a theoretical expectation of Hardy–Weinberg equilibrium. From calculated PI values, genotyping four loci (i.e. $\text{PI} = 0.00004$) was sufficient for individual identification (Table S1, Supporting information). We therefore treated two genotype samples as coming from the same individual if four or more loci were identical. We also allowed for a mismatch at a maximum of one additional locus for pairs that were identical at all other loci that we typed to further minimize possible genotyping error (see Appendix S1, Supporting information). Using this criterion, we matched similar genotypes using the CERVUS software (Marshall *et al.* 1998; Kalinowski, Taper & Marshall 2007).

ESTIMATION OF THE NUMBER OF RAIDERS

We estimated the number of raiders independently from observation counts and from genotype counts because we could not consolidate these data sources for two reasons. First, we lacked genetic samples for some individuals from AEP that we knew to be crop-raiders from observations: dung from these individuals may have occurred in our samples of dung from unknown individuals, but we could not confirm this. Consequently, we expected to detect approximately half of the raiders from AEP using genotype counts because we had known genotypes from 50% of the adult AEP. Secondly, genotype counts were obtained from a wide area of farmland representing areas used by elephants from the three populations: AEP, Chyulu–Tsavo and Kilimanjaro. Counts of raiders from direct observations on the other hand were obtained in areas closer to the core area (ANP) used by the AEP than to core areas used by other elephant populations in the Amboseli basin (Fig. 1).

For each type of data, we therefore estimated the total number of raiders in the Amboseli basin, and more specifically the number of raiders originating from the AEP. We used two classes of models to estimate the total number of raiders; count models and asymptotic regression models.

For count models, we fitted a finite Poisson mixture model (equation 1, below), and Zelterman’s model (equation 2, below), to the observed counts and genotype counts of raiders. We estimated the total number of raiders from these counts using the Horvitz-Thompson formulation: ($N = n/(1-P_o)$), where N is the total number of raiding elephants, n is the number of individuals that were detected raiding, and P_o is the probability that some raiders were not detected. For the finite Poisson mixture model, P_o is the exponent of lambda ($e^{-\lambda}$) where λ is estimated by a nonparametric maximum likelihood procedure using the Expectation-Maximization (EM) algorithm (Böhning & Schön 2005). With this procedure, several Poisson models (ranging from a simple one parameter Poisson model to models with a mixture of two or more Poisson parameters) are sequentially fitted to the data and the number of raiders is estimated for each model. We selected the Poisson models with the best fit using Bayesian Information Criteria (BIC) where the best model has the smallest BIC value, as recommended by Kuhnert *et al.* (2008).

$$N = \frac{n}{1 - \sum_{j=1}^k e^{(-\lambda_j)q_j}}, \tag{eqn 1}$$

Here, q_j represents weights of j th λ component in the model (where $q \geq 0$ and $\sum q = 1$) and k is the number of λ components in the mixture model. For the Zelterman’s model (equation 2), $\lambda_1 = 2f_2/f_1$, where f_1 , and f_2 , are the number of unique individuals or genotypes counted once or twice respectively (Zelterman 1988).

$$N_Z = \frac{n}{1 - e^{-\lambda_1}}, \tag{eqn 2}$$

The total number of raiders was estimated using another count model, Chao’s model ($N_C = n + f_1^2/2f_2$) (Chao 1987). In this model, N_C is the total number of raiders and f_1 , and f_2 are defined as in the Zelterman’s model above.

The 95% confidence interval for the estimated number of raiders using the finite Poisson mixture model was calculated using the 2.5 and 97.5 percentiles from 1000 parametric bootstrap samples (Böhning *et al.* 2005). The 95% confidence interval for the estimated number of raiders using the Zelterman’s and Chao’s models were determined using the equations 3 to 5 for variance (Var) and standard error (SE) shown below (Böhning 2008) where f_1 and f_2 are defined as for equation 2.

$$\widehat{\text{Var}}_{(\lambda|n)(\bar{N}_Z)} = nG(\lambda) \left[1 + nG(\lambda)\lambda^2 \left(\frac{1}{f_1 + f_2} \right) \right], \tag{eqn 3}$$

$$\text{and } nG(\lambda) = \frac{\exp(-\lambda)}{(1 - \exp(-\lambda))^2}$$

$$\widehat{\text{Var}}(\lambda|n)(\bar{N}_C) = \frac{1f_1^2}{2f_2} \left(1 - \frac{f_1^2}{2f_2n + f_1^2} \right) + \frac{f_1^3}{f_2^2} \left(1 + \frac{1f_1}{4f_2} \left(1 - \frac{f_2}{n} \right) \right) \tag{eqn 4}$$

$$\text{SE} = \sqrt{\widehat{\text{Var}}_{(\lambda|n)(\bar{N}_C \text{ or } Z)}} \tag{eqn 5}$$

The estimates and confidence intervals for the number of raiders from count models were implemented using the Computer-Assisted Mixture Model Analysis for Capture–Recapture count data (CAMCR) (Kuhnert & Bohning 2009).

We also used three regression models, namely a negative exponential model ($y = a(1 - \exp(-bx))$) (Eggert, Eggert & Woodruff 2003), a Michaelis–Menten model ($y = ax/(b + x)$) (Kohn *et al.* 1999) and a Chessel model ($y = a - a(1 - (1/a)^x)$) (Valiere 2002) to estimate the number of crop-raiders. These models, estimate the number of crop raiders from an asymptote of the accumulation curve of unique individuals with sample size. In these models, 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 were estimated by iterative nonlinear least squares function in R (R Development Core Team 2010). 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 parameters a and b per iteration. We then calculated the mean, median and the 2.5 and 97.5 percentiles of the mean from these iterations. These analyses were carried using R.

We selected the best model for our data by testing the accuracy and precision of each of the asymptotic regression and count models on simulated data. Specifically, we generated data for a population of known size, with a small recapture mean and a high variance in recapture probability across individuals. These simulated data enabled us to compare the population size estimates from the different models with the true value that they are estimating (Table S2 and Fig. S1, Supporting information).

HABITUAL RAIDERS

To determine the presence of habitual raiders and their number, we fitted the frequency distribution of elephants by number of raiding incidents to a truncated finite Poisson mixture using equation 1. We conducted separate analyses for all raiders using genotype data, and for Amboseli elephants using observational data. For each analysis, we fitted several models ranging from a simple one parameter Poisson model to a mixture of two or more parameters and we selected the model with the smallest BIC value as the best fit to our data. We predicted that the distribution of raiding frequencies across individuals would fit a simple (one parameter) Poisson distribution model if (1) we had no habitual raiders, (2) if all elephants were raiding with equal probability, and (3) if variation among individuals was predicted by chance. However, if some individuals were raiding more frequently than predicted compared to others, we expected the distribution of raiding frequencies across individuals to fit a mixture of two or more Poisson distributions.

To estimate the number of raiding elephants that were habitual raiders, we used the weight (q) of the largest parameter component of λ (equation 1) from our Poisson mixture model to estimate the proportion of habitual raiders in the population (where q represents the proportion of raiders in the population).

Results

OBSERVATIONAL AND MOLECULAR SAMPLE COUNTS

We observed 130 elephants during 37 raiding events in Sompet and Namelok during the 2005–2007 growing seasons. We did not follow elephants raiding Isinet because they always entered Kimana Wildlife Sanctuary after leaving the farms, where thick vegetation precluded tracking. We were able to determine, for 107 of the 130 elephants we observed, whether they were AEP or non-AEP elephants. Because some individuals raided multiple times, these 107 elephants included 50 unique individuals (42 AEP elephants and eight non-AEP elephants).

We collected 175 samples during 68 raiding events from Namelok, Sompet and Isinet farms during the 2005 and 2006 growing seasons. We successfully amplified and genotyped 112 dung samples representing 67 unique genotypes. Twenty unique genotypes matched known genotypes of Amboseli elephants whereas 47 unique genotypes did not match any known genotypes of Amboseli elephants.

These unique individuals and genotypes were detected in specific farming areas; few unique individuals or genotypes were shared by all the three farming areas that we monitored (Fig. 2a,b). However, Namelok farms shared 60% of the unique genotypes with Isinet farms, whereas 74% of the unique genotypes sampled in Isinet farms were not detected elsewhere.

ESTIMATED NUMBER OF RAIDERS

Our simulations showed that the best performing models when recapture probability significantly varied non-randomly among individuals were the Zelterman and the Michaelis–Menten models (Fig. S1, Table S2 and Appendix S2, Support-

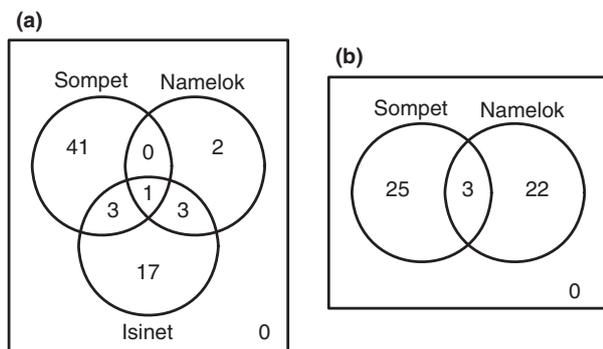


Fig. 2. Venn diagrams showing the spatial distribution of unique genotypes (a) and individuals from observations (b). Circles represent sampled farming areas (Sompet, Namelok and Isinet). The integers inside the circles indicate the number of unique genotypes/individuals observed to raid in a farming area; the overlap of two or more circles shows the number of unique genotypes/individuals observed to raid in the two or more farming areas indicated by the circles.

ing information). We focus on the results from the Zelterman model in the rest of the paper but show estimates from other models in Table 1.

Our population estimate of AEP raiders from direct observations was $N = 84$, twice as large as our estimate of AEP raiders obtained from genetic data, $N = 41$ (Table 1). This result was expected because we had genotypes for only a half of the AEP population.

The population size estimate of raiders from the three populations obtained from genetic data, $N = 241$, was approximately twice the magnitude of the population size estimate obtained from observational data, $N = 108$ (Table 1). This difference in estimates obtained from observational and genetic data reveals that we were much more likely to detect raiders from AEP through observations than we were to detect raiders from other populations (see Discussion), whereas genetic data represented all three populations in the study area (Fig. 2a, see Discussion). In fact our estimates from observational data, using counts of all individuals (i.e. AEP elephants and non-AEP elephants) yielded a population size estimate that was close to the estimate derived using counts of known AEP elephants only (Table 1). This further supports our conclusion that our observations of raiders were strongly biased towards detecting AEP raiders.

HABITUAL RAIDERS

The distribution of crop raiding frequency across genotypes best fitted a mixture model with two Poisson distributions ($\lambda_1 = 0.24$, $\lambda_2 = 3.15$, BIC = 139.3). There was some support for a mixture model of three Poisson distributions ($\lambda_1 = 0.0001$, $\lambda_2 = 1.414$, $\lambda_3 = 5.23$, BIC = 141.6, Fig. 3a) but not for a single Poisson distribution model ($\lambda = 1.00$, BIC = 157.5). Similarly the distribution of crop raiding across AEP elephants that were identified from direct observations best fitted a model consisting of a mixture of two Poisson distributions ($\lambda_1 = 1.03$, $\lambda_2 = 6.91$, BIC = 133.5) but not a simple Poisson distribution ($\lambda = 1.935$, BIC = 157.4) or a model with three Poisson mixtures ($\lambda_1 = 1.740$, $\lambda_2 = 7.99$, $\lambda_3 = 0.039$, BIC = 136.0, Fig. 3b).

Twelve per cent of raiding elephants from AEP, as estimated from observation counts, were classified as habitual raiders, whereas 88% were classified as occasional raiders ($\lambda_1 = 1.03$, $q_1 = 0.88$; $\lambda_2 = 6.91$, $q_2 = 0.12$). For raiding elephants from all of the populations, as estimated from genotype data, 21% of raiders were classified as habitual raiders whereas 79% were occasional raiders ($\lambda_1 = 0.24$, $q_{1t} = 0.79$; $\lambda_2 = 3.15$, $q_2 = 0.21$). Further, these 12% of habitual raiders from AEP (10 individuals) were involved in 56% of the total elephant raiding events attributed to this population. Two individuals with the most raids contributed to 10% and 9.5% of the total observed elephant raiding events.

SEX OF RAIDERS

We documented a total of 61 specific individual raiders of known identity and source population, using both observations

Table 1. Estimates of the number of raiders from the Amboseli elephant population (AEP) and from all populations in the Amboseli basin combined (all raiders) determined from direct observations and from genotype counts of raiders

Model	Estimates from observations		Estimates from genotypes	
	Mean (95% CI)	Median	Mean (95% CI)	Median
AEP 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
Negative 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 (112–9.3 × 10 ⁵)	331
Asymptotic models				
Michaelis–Menten	106 (79–162)	101	222 (144–448)	199
Negative exponential	67 (55–95)	65	129 (91–241)	117
Chessel	55 (48–62)	55	98 (84–114)	97

The number of all raiders from direct observations was estimated using 107 sightings of raiders involving 50 individuals whereas the number of raiders from AEP was estimated from 95 sightings of raiders involving 42 individuals. The number of all raiders estimated from genotype counts was determined using 106 genotype samples consisting of 67 individuals whereas the estimated numbers for AEP raiders were obtained from 32 genotypes from 20 individuals. Estimates from six models are shown but the most reliable results according to simulations are estimates obtained using the Zelterman model, indicated in bold. AEP, Amboseli elephant population.

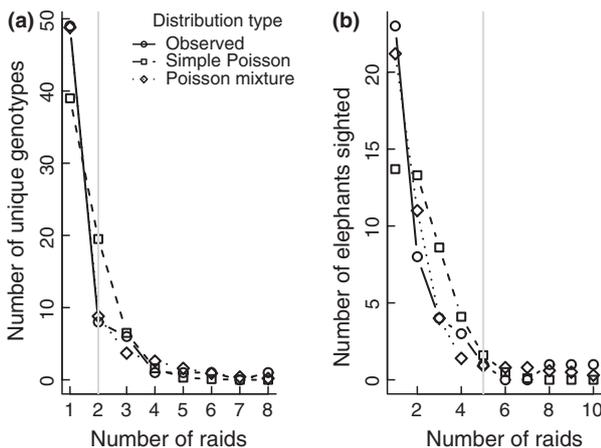


Fig. 3. The observed distribution of number of raids across individual elephants using data from unique genotypes detected (a) and data from elephants sighted (b) showing the best fit to a two component mixture of Poisson distributions and less fit to a simple poisson. Vertical light grey lines approximately demarcate habitual (to the right) and occasional raiders (to the left). We used data from 106 genotypes distributed among 67 unique genotypes and 95 elephant sightings distributed among 42 individuals.

and genotypes. Fifty-two were known AEP males, and nine were non-AEP males. All were independent males; no females were among the identified raiders. These data

strongly suggest that all raiding was done by males. The estimated 84 raiders from ANP represent approximately one-third of the 275 independent males in that population.

Discussion

NUMBER OF RAIDERS

The number of raiders in our study area is large (c. 241) and drawn from several elephant populations in the Amboseli basin. AEP elephants comprise about 35% of these raiders while the rest come from the Chyulu–Tsavo and Kilimanjaro populations.

Our observational data detected raiders from the AEP more than from other populations in the basin. In particular, 84% of the raiders we detected through observations were AEP elephants. This was because we saw raiders only when they stayed in woodland refuges between Sompot and Namelok farms and ANP, which represents a core area used by AEP elephants and not other populations. In fact the number of all raiders (i.e. raiders originating from the AEP and other non-AEP populations) and of AEP raiders alone that we estimated using data from direct observations were very similar, suggesting that the estimated number of raiders from observational data consisted of largely habituated (through research and tourism) and easy to detect elephants from the AEP.

In contrast, our genotype data provided a representative sample of raiders over a wide area of the Amboseli basin (i.e. the farming communities of Sompet, Namelok and Isinet). Genotype data showed that 60% of individuals who raided Namelok also raided Isinet, but that 74% of the individuals that raided Isinet were not detected raiding in other places. Most raiders in Isinet came from Kimana Sanctuary, an area where the AEP and the Chyulu–Tsavo elephants overlap (Moss 2001). Because of the care we took in genotyping and processing our genotype data, 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 chance that a genotype from a single animal was 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).

These results indicate that molecular censusing has an advantage over observational censusing for obtaining spatially unbiased counts of raiders. Observational censusing has inherent biases associated with the challenge of observing elephants during or after raiding. These challenges are not easy to overcome because they result from difficulties of tracking elephants in thick vegetation, from the generally nocturnal nature of raiding, and from the observer's inability to predict where elephants are going to raid. Similarly, in areas where elephant core habitats are near raided farms, it may be difficult to differentiate raiders from non-raiders because raiders will retreat to the safety of core areas where they are likely to mix with non-raiders before they are detected. The major disadvantage of molecular censusing is that genotypes must be linked to known individuals in order for this information to be useful for management. However, for the purposes of estimating population sizes, when individual identities are not an issue, molecular censusing will be superior to observational censusing.

HABITUAL RAIDING

Our results support previous studies showing that elephants that are habitual raiders account for a substantial amount of crop damage; we estimated 50 habitual raiders and 10 of these were from the well-studied AEP. Furthermore, these AEP raiders contributed to 56% of all raiding events by elephants from that population. Two of the top habitual raiders from AEP contributed to *c.* 20% of all the raiding from this population. However, our study also revealed a large number of occasional raiders, *c.* 189 individuals in total and 74 specifically from AEP, that contributed to many raiding events. These findings on habitual raiding are comparable to results from a study of Asian elephants (Sukumar 1995) in which two bulls caused nearly 30% of the total raiding incidences by elephants; 70% of raiding events involved less frequent raiders.

SEX DIFFERENCES IN CROP RAIDING

In this study only males were detected 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 vervet monkeys *Chlorocebus aethiops* (Saj, Sicotte & Paterson 1999), Asian elephants *Elephas maximus* (Sukumar & Gadgil 1988), chimpanzees *Pan troglodytes* (Wilson, Hauser & Wrangham 2007), and olive baboons *Papio anubis* (Forthman-Quick 1986). Sex differences may result from differences in raiding costs and benefits for males and females that stem from differences in intra-sexual competition. Because males in polygynous social systems have a larger variance in reproductive success than females, sexual selection is expected to enhance behaviours 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; Poole 1989; Hollister-Smith *et al.* 2007), which are in turn dependent on age and nutritional state (Poole 1989; Sukumar 2003). Sexual selection should therefore favour males adopting foraging strategies for maximizing nutrient gains that can be allocated for growth and maintenance of musth. Females are likely to incur higher risks of raiding than males, because of dependent offspring, and raiding gains may not offset these risks.

These high-risk and high-gain foraging strategies are consistent with observations of natural foraging behaviour in male sexually dimorphic mammals. For example males foraging in the wild seek more abundant or high quality forage at the risk of predation, whereas females may sacrifice forage abundance to minimize predation risk when there is a positive correlation between food abundance and predation risk (Bleich, Terry & Wehausen 1997; Apollonio, Ciuti & Luccarini 2005; MacFarlane & Coulson 2007; Hay, Cross & Funston 2008). We conclude that raiding is a manifestation of natural high-risk, high-gain foraging strategies commonly observed in males of many polygynous mammals.

MANAGEMENT IMPLICATIONS

A large number of males from different populations in the Amboseli basin raided farmlands surrounding the ANP, and some elephants raided habitually. Raiding in areas around ANP occurred in spite of the fact that the elephant populations in the Amboseli basin still have relatively large tracts of natural range available, and supports the notion that raiding by male elephants does not reflect inadequate natural forage, but instead reflects a natural tendency for males to engage in high-risk, high-gain foraging behaviour.

These results have several implications. First, while they suggest that targeted elimination of habitual raiders can reduce raiding, they also indicate a great potential for replacement of habitual raiders from a large pool of occasional raiders. Although no longitudinal data currently exist to support the idea that occasional raiders can become habitual raiders, the potential for this to occur is high, given the large number of

occasional raiders demonstrated by our findings, the natural tendency of males to indulge in risky foraging behaviour, and the ready availability of crops in areas of conflict. This potential means that control shooting may not be a sustainable strategy for managing conflict and for conserving elephant populations.

Even when the potential for replacement of habitual raiders is low, control shooting of raiders as a strategy for reducing crop raiding carries a high risk of misidentifying habitual raiders. This is because even when detailed long term records are available to identify habitual raiders, as in this study, wildlife managers are likely to make decisions about shooting elephants without the time-consuming consultation that is required to confirm individual identification. This risk is higher than might have been anticipated before our study, which revealed that the number of habitual raiders is small relative to the number of occasional raiders.

A more ethical alternative for managing conflict in elephant populations with known habitual raiders, is to attach habitual raiders with Global System of Mobile communications (GSM) collars programmed to send text messages to mobile phones of farmers when they cross 'no go' locations programmed on to the collar. This method of remotely monitoring habitual raiders could provide an early warning system for crop protection from raiding elephants. Preliminary tests of this method conducted at the Ol Pejeta Nature Conservancy, Kenya, have shown success (Muchiri 2010).

Our study also highlights the value of molecular censusing for the estimation of patterns of individual animal involvement in the conflict with humans in elusive mammals.

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Supporting Information

Additional Supporting Information may be found in the online version of this article on page numbers indicated in the legend below.

Fig. S1. A box plot showing distribution statistics for estimates of population size using different models shown in Table S2.

Table S1. Results of predicted and observed probability of identity values for up to four different loci.

Table S2. Results of population estimates confidence intervals using data sets simulated for a populations of 100 individuals with different means and variances in recapture.

Appendix S1. Calculating the probability of identity from genetic data.

Appendix S2. Effect of mean and variance of recapture on population estimation.

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