Using camera traps to study the age-sex structure and behaviour of crop-using elephants in Udzungwa Mountains National Park, Tanzania

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ABSTRACT

Crop losses from elephants are one of the primary obstacles to the coexistence of elephants and people and one of the contributing causes to elephant population decline. Understanding if some individuals in an elephant population are more likely to forage on crops, and the temporal patterns of elephant visits to farms, is key to mitigating the negative impacts of elephants on farmers. We used camera traps as a novel technique to study elephant crop foraging behaviour in farmland adjacent to the Udzungwa Mountains National Park in southern Tanzania from October 2010 to August 2014. Camera traps placed on elephant trails into farmland captured elephants on 336 occasions over the four-year study period. We successfully identified individual elephants from camera trap images for 126 of these occasions. All individuals detected on the camera traps were independent males, and we identified 48 unique bulls aged between 10 and 29 years. Two-thirds of the bulls identified were detected only once by camera traps over the study period, a pattern that also held during the last year of study when camera trapping effort was continuous. Our findings are consistent with previous studies that found that adult males are more likely to adopt high-risk feeding behaviours such as crop foraging, though young males dispersing from maternal family units also consume crops in Udzungwa. Our study found a large number of occasional crop-users (32 of the 48 bulls identified) and a smaller number of repeat crop-users (16 out of 48), suggesting that lethal elimination of crop-using elephants is unlikely to be an effective long-term strategy for reducing crop losses from elephants.

KEYWORDS human-elephant coexistence, HEC, crop foraging, Problem Animal Control, PAC, Udzungwa Mountains, Tanzania

INTRODUCTION

The dramatic population decline of African elephants (*Loxodonta africana*) is one of the most pressing conservation issues currently facing sub-Saharan Africa (Maisels et al., 2014; Wittemyer et al., 2015; Chase et al., 2016). Another great challenge for elephant conservation in the long-term is coexistence with people, in particular where elephants consume or damage human crops (Hoare, 2012). As a taxon with large range requirements and long-distance movements (Graham et al., 2009), elephants spend considerable time outside of protected areas (Blanc et al. 2007; van Aarde & Jackson, 2007; Kikoti, 2009), where they are more likely to share and compete for space and resources with people. The impacts of elephants outside protected areas include loss of crops and reduced yields, damage to human property, death of livestock, human injury and in some cases, death (Thouless, 1994; Ngure, 1995; Kangwana, 1996; Lahm, 1996). These impacts of elephants on people's livelihoods can lead to retaliatory and legal killing of elephants under Problem Animal Control policies (Hoare, 2000; Hoare, 2012). In this context, understanding which elephants in a population are more likely to forage on crops, and investigating temporal patterns in crop foraging behaviour, are integral to developing effective strategies for reducing crop losses from elephants (Naughton-Treves, 1998).

Previous studies have highlighted a male bias in elephant crop foraging behaviour (Osborn, 1998; Hoare, 1999; Sitati et al., 2003; Graham et al., 2010; Chiyo et al., 2011; 2012; Ekanayaka et al., 2011). Crop foraging has been observed as a 'high-risk, high-gain' foraging strategy for male elephants to maximise nutrient intake while minimizing time spent and distance travelled while foraging (Sukumar & Gadgil, 1988; Chiyo & Cochrane, 2005), a behaviour that has also been documented in males from other polygamous species, including at least nine species of African primates (Trivers, 1985; Davenport et al., 2006; Wallace & Hill, 2012). In contrast, females might not show this behaviour as often as males owing to the potential risk incurred in agricultural landscapes by dependent offspring (Sukumar & Gadgil, 1988). This may not always be the case, as studies in south-eastern Tanzania and around Tsavo National Park, Kenya, found that mixed groups consisting of bulls, females, and calves were responsible for the majority of crop loss incidents (Smith & Kasiki, 2000; Malima et al., 2005). However, age and sex data from enumerator-based studies may be unreliable because they commonly rely on interviews with farmers who are usually not formally trained in sexing and ageing elephants (Smith & Kasiki, 2000).

Moreover, ‘repeat’ or ‘habitual’ crop use has previously been documented in African elephants (Hoare, 2001; Chiyo & Cochrane, 2005; Chiyo et al., 2011; 2012). A study in Amboseli, Kenya revealed considerable individual variation in crop use (Chiyo et al., 2011), with a small number of bulls feeding on crops relatively frequently and others sporadically. Bulls may also acquire crop foraging behaviour through social learning, and therefore the structure of male association networks may influence the tendency for crop foraging in bulls and drive differences in crop foraging behaviour between individuals (Chiyo et al., 2012).

Elephant crop foraging behaviour is difficult to study because incidents usually occur at night (Gunn et al., 2014), and thus direct observation in the field is often risky and hampered by poor visibility. Previous studies have employed indirect methods to assess the sex and age structure of crop-users, such as estimating elephant age from dung size and footprint diameter (Chiyo & Cochrane, 2005; Morrison et al., 2005). Others have studied elephant crop use at the individual level using genetic data collected from elephant dung (Chiyo et al., 2011). Camera traps have been widely implemented to identify individuals (Karanth & Nichols, 1998; Silver et al., 2004) and study animal behaviour that may be challenging to document using direct observations (Griffiths & van Schaik, 1993); however, until now, they have not been used to study crop foraging behaviour in elephants.

In this study, we used camera traps to investigate patterns of crop use and to establish the number and sex and age structure of crop-using elephants along the boundary between Udzungwa Mountains National Park and adjacent farmland in south-central Tanzania. We first assess whether elephants photographed on camera traps are likely to be foraging on crops. We then estimate the minimum number and the age and sex structure of crop-using elephants between October 2010 and August 2014. Finally, we discuss the implications of our results in the context of current policies for managing crop losses from elephants at our study site, in Tanzania, and more generally across Africa where elephants and people co-occur.

STUDY AREA

The study site is located in Njokomoni, a small area of farmland (approximately 2.5 km^2) directly adjacent to the Udzungwa Mountains National Park (UMNP) in south-central Tanzania. The Udzungwa Mountains encompass the largest and biologically richest forest blocks of the Eastern Arc Mountains (Burgess et al., 2007), and are home to a relatively young, recovering population of forest-using African savannah elephants (Nowak et al., 2009). After heavy poaching between the 1960s and 80s led to the near extinction of elephants in the Udzungwa Mountains, this elephant population – presumed to have taken refuge at high elevations (Jones & Nowak,

2015) – began to recover following the gazetting of the National Park in 1992 (Joram, 2011).

The Njokomoni area is farmed by villagers from two villages known as Man’gula A and Mang’ula B, both of which are located along the east-facing escarpment of the Udzungwa Mountains (Fig. 1). The vegetation along the eastern side of the National Park comprises lowland rainforest and miombo woodland, which extend to the Park boundary. Crop losses from elephants in the area emerged as a regular occurrence in 2008 (Joram, 2011) and appeared to be related to the blockage of elephant movements associated with the loss of wildlife corridors between the Udzungwa Mountains and the Selous Game Reserve (Jones et al. 2012).

The Njokomoni farmland holds over 120 farms, with individual farm size ranging from 0.25 to 2 ha. Over 30 different crops are cultivated in a mixed intercropping system (Joram, 2011). The wet season spans November to May, and the dry season June to October (Lovett et al., 2006). Farming activity occurs year-round, with rain-fed farming during the wet season and irrigation farming during the dry season enabled by perennial streams. Crop losses to elephants occur throughout the year, but are generally more frequent in the dry season, peaking in September when the irrigated maize crop matures. A 2010-2011 survey of six adjacent villages along the eastern boundary of the National Park identified Njokomoni as a hotspot of elephant crop use, as over 75% of verified reports of crop losses came from farmers in the Njokomoni farmland (Joram, 2011). The major reason for high levels of elephant activity in this area is the lack of a buffer zone between the National Park and adjacent farms (Joram, 2011).

METHODS

Camera trapping

Between October 2010 and August 2014, a total of 23 camera trap sites were monitored along an approximately 1 km stretch of the eastern boundary of Udzungwa Mountains National Park. Effort and coverage were variable over this period, with one to ten camera traps active each night from October 2010 to April 2012, one to three from August 2012 to January 2013, and ten from July 2013 to August 2014 (see Supplementary Material, Table S1). Heat and motion camera traps (Cuddeback Capture) were placed along current known elephant pathways going in and out of farms and were shifted according to elephant activity. More specifically, camera traps were removed from trails that became less frequently used by elephants and shifted to new trails with more observed elephant activity (as indicated by the presence of elephant dung and tracks). Due to a limited number of cameras, only one camera trap was placed per trail. In order to obtain suitable portrait photographs for individual identification, camera traps were mounted on a tree at a height of 3 meters and oriented downward to best capture the head, pinnae, and tusks of passing elephants. Camera traps were programmed to take colour photographs with an incandescent flash, and the trigger interval was set to 30 seconds (the minimum possible for the model). Batteries were replaced and SD cards downloaded every two weeks.

A database of all camera trap images of elephants was created, which included the site, date and time of capture, and the direction of elephant movement (into or out of the farmland area, i.e. back into the National Park). In addition, each image was classified according to whether or not it was suitable for individual identification. For those images that were deemed suitable, the elephant’s sex, and when possible, age, were determined and individual identifications made based on unique characteristics of individuals' pinnae and tusks (Moss, 1996). The sexing and ageing of elephants was carried out by one main researcher (J. Smit) following training at the Amboseli Elephant Research Project, Kenya on known-age elephants.

Monitoring crop losses from elephants

Monitoring of crop losses from elephants in this focal area has been carried out since 2010 following a modified protocol developed by the African Elephant Specialist Group of the International Union for Conservation of Nature (IUCN) (Parker et al., 2007). Two local enumerators employed by the Southern Tanzania Elephant Program (STEP) responded to calls from farmers reporting crop-loss incidents and surveyed farms within the study area six days a week for additional unreported incidents. They recorded the date and location of the crop-loss incident, the type(s) of crops and trees eaten or trampled, and the size of the area affected (Joram, 2011).

Data analysis

To account for inconsistent camera trapping effort, we considered two time periods over which different analyses were carried out: the entire study period (hereafter, "study period") and the last year of monitoring between July 2013 and August 2014 (hereafter, "last year"). We first ran a temporal analysis comparing the timing of camera trap captures of elephants observed to travel into or out of the farmland area. More specifically, we used a non-parametric Kolmogorov-Smirnov test to determine whether the distributions of timings of captures into and out of farmland were significantly different. To do this, we used data collected over the entire study period since temporal activity at the scale of a single night is unlikely to be affected by inconsistent camera trap effort. Image time stamps were classified into hourly bins (0-23), resulting in a frequency distribution spread over 24 hours.

We also tested for a significant association between the occurrence of an elephant detection on any of the camera traps in operation (absence = 0, presence = 1) and that of a crop-loss incident in the Njokomoni farmland recorded on the following day by enumerators (absence = 0, presence = 1) using data collected between July 2013 and August 2014. We arranged corresponding frequencies into a 2 by 2 contingency table and performed a Pearson's chi-square test of independence to investigate whether observed frequencies were more or less than expected by chance. We used data from the last year of monitoring to do this, as camera trap effort during this period was constant (10 cameras operating every night). In addition, to assess whether monthly patterns of camera trapping events served as a good indicator of crop-loss incidences, we correlated the proportion of days in the month for which at least one elephant picture was obtained and the proportion of days for which a crop-loss incident had been recorded by the enumerators.

In addition, we estimated the minimum number of elephants known to use the forest/farm boundary area over both the study period and the last year based on individuals identified from camera trap images. Identification photographs of two bulls detected multiple times by our camera traps are available as supplementary material (Fig. S2). We also assessed the number of nights that individual bulls had been detected by camera traps, and used this as an indicator of a bull's relative likelihood to visit the Njokomoni farmland area. We repeated this assessment using a subset of our data for which camera detections of elephants were positively associated with crop-loss incidents (see Supplementary Material). Lastly, we investigated the sex and age structure of individuals identified over the four-year study period. We classified elephants identified in camera trap photos into four age classes (Moss, 1996): 10-14, 15-19, 20-24 and 25-29 years old (we did not observe any individuals over 30 years old). As our cameras detected only male elephants, we relied primarily on head size and shape for ageing because these features change noticeably with age and are easily seen on camera trap photos. With age, the male head increases in size and takes on a pronounced hourglass shape around the age of 25 (Moss, 1996). We also used height and body size for ageing when we had full body photos of bulls. Images of bulls representative of the four age classes used in our study are provided as supplementary material (Fig. S1).

R v3.0.1 was used for all statistical analysis in this study (R Core Team 2014).

RESULTS

We obtained 443 elephant photographs over 5,314 trap-nights between October 2010 and August 2014, representing 336 independent events. We defined an event as the capture of a unique elephant at a unique date and time, as this best represented one visit by a single elephant. In cases where an event could not be defined by distinguishing between individual elephants, an arbitrary time threshold of 5 minutes between separate events was assumed. Elephants were photographed traveling into the farmland predominantly between 18:00 and 00:00 (median = 19:00) and back into the National Park between 00:00 and 07:00 (median = 04:00) (Kolmogorov-Smirnov test: D = 0.541, $p < 0.001$) (Fig. 2). We found a similar pattern in elephant movements into and out of farmland when we used a subset of the data for which camera detections of elephants were associated with crop-loss incidents (Fig. S3). During the last year of study, we found that camera trap data and crop-loss incidents as recorded by enumerators co-occurred more than expected by chance (n = 39, χ^2 = 13.6, df = 1, p < 0.001). Despite this, instances when crop losses were reported and no elephants were photographed remained high (n = 98), as were instances when cameras detected elephants but no crop losses were recorded (n = 118). We also found a positive, albeit non-significant, correlation between the proportion of days in the month for which we obtained camera trap images of elephants and that for which crop losses were reported (r^2 = 0.407, df = 10, p = 0.19; Fig. 3).

Of the 336 camera trap events, 37% (n = 126) were suitable for individual elephant identification. All of the elephants identified were males, representing a total of 48 individuals (Fig. 4). No females were observed in any of the camera trap images for which the sex of the individual could be assessed. Most of the bulls identified were detected only once by camera traps across the study period (66.7%, Fig. 5), a pattern that was also found during the last year of study when camera trapping effort was constant (70.6%, Fig. 5). A skew towards single detections was also found when we used only those camera detections of bulls associated with crop-loss incidents (Fig. S4).

Sixteen individuals were photographed multiple times over the entire study period (Fig. 5), with one individual detected over 30 times. Five of the 17 bulls identified in the last year of the study were captured multiple times on camera (Fig. 5). The 48 bulls identified from camera trap images over the study period were primarily between 25 and 29 years old. (Fig. 6). Bulls who were detected multiple times on the camera traps were also primarily 25-29 year olds, followed by younger bulls aged 10-14 and 15-19 years. The time between successive detections of individual bulls was highly variable (range 0-681 days, median 13.5 days), probably mostly because of the inconsistency of camera trap effort (although we cannot exclude the possibility that some of the bulls had breaks in visits to the study area). However, a conservative estimate is that 24% of re-captures occurred on two consecutive days, and 43% of re-captures occurred within 7 days.

DISCUSSION

We tested camera trapping as a tool to investigate the behaviour, number, and age and sex structure of crop-using elephants along the boundary between Udzungwa Mountains National Park and a small area (2.5 km^2) of adjacent farmland in south-central Tanzania. Camera trap images of elephants showed a distinct pattern of elephant activity, with elephants heading into farmland at night and returning to the National Park early in the morning along regular trails. This is consistent with previous studies that highlight elephant avoidance of farmers and a propensity for nocturnal crop foraging behaviour (Graham et al., 2010; Chiyo et al., 2012; Gunn et al., 2014; Smith & Kasiki, 2000). The evidence for elephants using these trails for the purpose of entering farms and consuming crops is strengthened by the significant pattern of co-occurrence between elephant visits captured on cameras and crop-loss incidents recorded by local enumerators.

However, we did not find a significant temporal correlation between recorded crop losses and camera detections of elephants. This could be because not every crop foraging attempt by a bull was successful, such that bulls photographed while heading to farmland did not always consume crops because of risk factors encountered there (such as the presence of farmers, fire, or dogs). This suggests that the frequency of elephant visits to farmland as detected by camera traps, and the extent of crop damage recorded by enumerators, may be independent measures of elephant crop foraging behaviour. Additionally, it may be that bulls occasionally used routes to farmland that were not sampled by our camera traps. Camera trapping may therefore not be suitable for studying temporal patterns in crop losses from elephants. Nevertheless, we view camera trapping and enumeration of crop losses as highly complementary indices with the potential to improve the reliability of data on elephant crop use if used jointly, especially in areas where elephants use well-established trails into farmland.

Using standard ways of identifying individual elephants on the basis of tusks and ears from camera trap photographs, we identified a minimum of 48 bulls in our study area over the period of four years. However, only about one-third of images from the study period were suitable for reliable individual identification. Future studies could increase the success rate of identification by increasing the number of camera traps active per night, and by using two opposite-facing camera traps per trail as is done in studies of large cats (Kelly et al., 2008; Harihar et al., 2010).

Most of the bulls identified in this study were aged 20-29 years (55%), followed by younger bulls aged 10-14 (34%) and 15-19 (11%) years; raising the possibility that older bulls are leading younger bulls into farms, or that they comprise a larger portion of the boundary-visiting population. The age structure of crop-using bulls in Udzungwa is consistent with previous studies carried out in Kibale, Uganda (Chiyo & Cochrane, 2005) and Amboseli, Kenya (Chiyo et al., 2012) (Table 1). Our results indicate that crop use in Udzungwa could be an example of a high-risk, high-gain foraging strategy linked to male life history milestones, including dispersal from the maternal family unit and the initiation of reproduction, with associated increases in energetic demands (Chiyo et al., 2012).

In Udzungwa, as in Kibale, the youngest bulls involved in crop foraging were 10-14 year olds, suggesting that crop use may be initiated during male dispersal (Chiyo & Cochrane, 2005). This is a time when males leave their natal groups and search for new feeding areas, and show greater exploratory and risk-taking behaviour thus increasing their chances of coming into contact with crops (Chiyo & Cochrane, 2005). In Amboseli, over 40% of crop-using bulls were aged over 30 years (Chiyo et al., 2012), while the present study in Udzungwa identified no bulls over the age of 30. This likely reflects the history of poaching experienced by the Udzungwa population, which typically leaves populations with few older bulls (Mondol et al., 2014) and a population structure biased towards younger age classes (Poole,1989; Nowak et al., 2009).

Our study suggests considerable variation in crop foraging behaviour between individual bulls, with camera traps detecting some bulls more frequently than others. Over two-thirds of the 48 bulls identified were detected only once on the camera traps over the study period, a pattern that also held for the 17 bulls identified in the last year of study. This suggests that a large number of bulls are ‘occasional’ crop-users. Sixteen bulls were detected multiple times (2-32) on camera over the study period suggesting these individuals may be ‘repeat’ crop-users. There was considerable variation in detection rates of the repeat crop-users, with one bull detected four times more frequently than any other repeat crop-user. Importantly, these are likely to be conservative numbers, and we acknowledge that a great number of elephants could have gone undetected owing to the small number of cameras available throughout our study, the large proportion of photos that were not conducive to individual identification, and the likelihood of cameras missing elephant visits.

Nevertheless, we highlight a large pool of occasional crop-users and a few repeat crop-users, a pattern also detected using genetic data in Amboseli, Kenya (Chiyo et al., 2011). Repeat crop use by certain individuals was also observed in a study of radio-tracked bull elephants in Muzarabani District in Zimbabwe (Hoare, 2001), and via the presence of crop remains in elephant dung on farms bordering Kibale National Park (Chiyo & Cochrane, 2005). Repeat crop use seems to be more common among older males in Udzungwa, as nearly half of the repeat crop-users were bulls aged 25-29 years. Studies in Kibale and Amboseli similarly found a positive correlation between age of the bull and the likelihood of repeat crop use (Chiyo & Cochrane, 2005; Chiyo et al., 2011).

The time between successive camera captures of bulls with multiple detections was highly variable (range 0-681 days, median 13.5 days). Though inconsistent camera trapping effort complicates the picture, it is possible that some of these potentially repeat crop-users had breaks in visits to our study area. For three of the bulls identified in this study, a year or longer passed between successive detections on the camera traps. These results bear some similarity to forest elephant visitation patterns to the Dzanga Bai in Dzanga-Ndoki National Park, Central African Republic (Turkalo et al., 2013). Long-term monitoring of the Dzanga Bai showed that individual visitation patterns were highly variable especially among males, some of whom were absent for years at a time (Turkalo et al., 2013).

Our study has important implications for strategies to mitigate crop losses from elephants, particularly the legal killing of animals considered to be ‘pests’ under Problem Animal Control policies. Such an approach has been applied across elephant range in Africa and Asia to in an attempt to reduce crop losses from elephants (Hoare, 2001). However, the persistence of crop foraging behaviour in areas where Problem Animal Control has been implemented in the long-term, such as in the Selous Game Reserve in Tanzania and Muzarabani District in Zimbabwe, has led to concerns regarding its effectiveness and motivation (Malima et al., 2005; Hoare, 2012). Although we found evidence for repeat crop use by elephants, the presence of a much larger pool of occasional crop-users argues against the killing of elephants as an effective crop loss reduction method in Udzungwa. Furthermore, the finding that a large number of bulls use a small area of farmland that is a hotspot of elephant crop use (Joram, 2011), suggests that high levels of crop losses at such hotspots do not result from the activity of a handful of habitual crop-users. Lethal elimination of crop-users carries the risk of misidentifying elephants, and can also be used as justification of elephant poaching or ivory accumulation under the pretext of Problem Animal Control (Masunzu, 1998; Malima et al., 2005). Removal of habitual crop-users may also create a gap or opportunity for new habitual crop-users to emerge (Hoare, 2012). Therefore, our study is in agreement with previous work questioning the effectiveness of killing elephants under Problem Animal Control policies for crop-loss mitigation.

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AUTHOR CONTRIBUTIONS

The study was conceptualized by T.J., K.N, and J.S. Data collection and processing were carried out by J.S., T.J. and K.N. Data were analysed by R.P, J.C, and J.S. All authors contributed to writing of the manuscript.

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BIOGRAPHICAL SKETCHES

Josephine Smit is a co-founder of STEP and manages its elephant monitoring programs in southern Tanzania. She is interested in incorporating elephant behavioural ecology into conservation strategies.

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TABLES

Table 1. Age structure of crop-using bull elephants at three different East African sites: Udzungwa Mountains National Park, Tanzania (this study), Kibale National Park, Uganda (Chiyo & Cochrane, 2005) and Amboseli National Park, Kenya (Chiyo et al. 2012).

Age class (years)	**Udzungwa** (% population)	**Kibale** (% dung piles)	**Amboseli** (% population**)**
5-9	0	6	0
10-14	34	22	0
15-19	11	32	7
20-24	15	27	-
25-29	40	13 (>25 years)	50 (20-30 years)
>30	0	-	43

FIGURES

Figure 1. Map of Njokomoni study area. a) inset map of the location of Udzungwa Mountains National Park (black rectangle) in south-eastern Tanzania. b) Njokomoni study area along the east-facing escarpment of the Udzungwa Mountains (grey) and village farmland (white). c) Njokomoni study site between the National Park (grey) and farmland (white) showing GPS location of camera traps (black dots). Due to the steep gradients of the Udzungwa Mountains, elephants use distinct trails into farms along

preferred slopes. Camera traps were placed on elephant trails and sampled an approximately 1km stretch of the National Park boundary.

Figure 2. Temporal patterns of elephant detections at camera traps placed along the eastern border of Udzungwa Mountains National Park. Black and grey bars represent frequencies of elephants going into and out of adjacent farmland, respectively.

Figure 3. Proportion of days in the month when crop-loss incidents (light grey bars) and camera trap images of elephants (dark grey bars) were reported and detected, respectively.

Figure 4. Camera trap detection rates for 48 identified bulls over the study period. The colour of each square represents the number of detections per month for a particular bull. The histogram at the top of the figure depicts sampling effort as measured by the number of trap-nights (the number of camera trap deployment days multiplied by the number of cameras) per month.

Figure 5. Frequency distributions of the number of nights identified bulls were detected on camera traps a) for the entire study period, and b) for the last year only.

Figure 6. Age structure of a) 40 of the 48 bulls identified over the entire study period, and b) for 14 of the 16 bulls who were detected multiple times over the study period for whom ageing was possible.

SUPPLEMENTARY MATERIALS

Table S1. Camera trapping effort over the study.

Figure S1. Photographs of bulls representative of the four age classes used in the study.

Figure S2. Camera trap photographs of two bulls (B03 and B01) detected multiple times over the study period.

Figure S3: Temporal patterns of elephant detections at camera traps placed along the eastern border of Udzungwa Mountains National Park, when a reduced dataset including the 35% (n=67) of camera trap detections associated with recorded crop-loss incidents is used. Black and grey bars represent frequencies of elephants going into and out of adjacent farmland, respectively. A Kolmogorov-Smirnov test on timings of detections of elephants moving into and out of farmland was not significant.

Figure S4: Frequency distributions of the number of nights identified bulls (n=21) were detected on camera traps a) for the entire study period, and b) for the last year only when a reduced dataset including only camera trap detections (n=67) associated with recorded crop-loss incidents is used. The stronger skew towards low detections in this figure likely results from a reduction in sample size, as only 28 (42%) of detections had photographs suitable for elephant identification.