A stepwise approach to understanding and effectively mitigating human-wildlife interactions

A thesis submitted for the degree of Doctor of Philosophy
by
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Abstract

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The study of conflicts in conservation (also known as human-wildlife conflicts) is a growing field of research in areas where people and wildlife interact, because of the negative impacts each can have on the other. Addressing conflicts is certainly challenging because of the complexities of considering diverse interests from numerous stakeholders and the specific ecological and socio-economic characteristics of a given study system. No matter how complex the system under study is, the aim is in all cases to find effective and sustainable mitigation strategies for local people, as well as for wildlife conservation and local authorities. In this thesis, I look at two of the preliminary steps required to address conservation conflicts and develop efficient long-lasting management solutions: the gathering of ecological data and the assessment of mitigation strategies in the field. To do this, I use two case studies: crop-foraging by African elephants (*Loxodonta africana*) in northern Botswana, and selective hunting of the red deer (*Cervus elaphus*) population on the Isle of Rum in Scotland. In Chapter 2, I built a baseline for the level of conflict in the Okavango Delta Panhandle (Botswana) using temporal trends of crop-foraging by elephants as an index of the level of conflict, and subsequently looked at how this relates to trends in agricultural land allocated in the study area, as well as with trends in human and elephant population size. In Chapter 3, I mapped the distribution of the local population of elephants and assessed its interaction with landscape features and sites where crop-foraging events had been recorded. In both chapters (2 & 3) I found that -in general- the number of elephants was not a determinant of the level of conflict in the study area, but that the spatiotemporal distribution of the species as well as the spatial and temporal scales considered were. In the second half of my thesis, I assessed the effects of two common conflict mitigation methods: the use of deterrents (Chapter 4) and lethal control (Chapter 5). I first evaluated the effectiveness of chilli-briquettes in deterring elephants and secondly, I used a modelling approach to predict the demographic effects of increasing levels of selective hunting in a male red deer population. I found that both mitigation methods showed unexpected results, which would not have been detected had I not tested for them. This thesis highlights the advantages of applying methods that are based on informed decisions in areas of conflict, as well as the value of sharing results in conservation management. My findings contribute towards a better understanding of the negative impacts of human-wildlife interactions, which often lead to conservation conflicts, as well as contributing protocols and methodologies that can be adapted and applied elsewhere.

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RP formulated the research question in collaboration with TC. ACS, GM and AS helped with guidance of data collection. RP collected data, performed data analysis and wrote the manuscript. All co-authors contributed to the interpretation of results and commented on the manuscript.

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Chapter 6

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Contents

Chapter 1

Introduction

The exponential growth of the human population has been the greatest threat to biodiversity in recent decades. At the current growth rate, the global population is expected to increase the percentage of known species that are at threat of extinction from 7% in 2020 to 14% in 2050 (McKee et al. 2003). The reason for this is that as the number of people alive increases, so too does their requirement for land. Human expansion inevitably results in habitat loss for wildlife, with species becoming restricted to protected areas.

As the human population expands and consequently encroaches into more habitats more intensively, the interaction between people and wildlife has inevitably increased and in some cases has developed into competition for resources, ultimately leading to conflicts. Conflicts in conservation occur when ‘parties clash over differences in their objectives and when one party asserts, or at least is perceived to assert, its interests at the expense of another’ (Redpath et al. 2013, 2015). Classic examples include negative interactions between people and: lions in Africa (Bauer et al. 2010), grey wolves in North

America (Bangs et al. 2005) and crop-raiding elephants in Asia (Sukumar 1990). In addition, despite often representing (or perceived to represent) a threat to people's lives or livelihoods, species involved in conflicts are sometimes afforded a certain degree of protection (e.g. threatened species listed under the IUNC red list, CITES protected species). This makes conflict resolution more complex because local people or stakeholders resort to illegally killing these species in retaliation for wildlife impacts (Woodroffe et al. 2005), thereby intensifying conservation concerns.

Conflicts in conservation are a major challenge for modern conservation science and practitioners (Woodroffe et al. 2005; Sillero-Zubiri et al. 2007), not only because they have become more numerous and diverse in recent decades but also because of the multi-faceted and complex nature of the interaction between people and wildlife. To illustrate the complexities of conflicts in conservation a good example is the conflict between jaguar conservation and people, which started with the introduction of domestic livestock to South America (Arnold 1968). The killing of cattle by jaguars has been well documented, however research found that poor husbandry practices is the main factor in predisposing livestock to jaguar predation (Schaller 1983) and that although losses of cattle to this species are minimal compared with disease and depredation by other carnivores, jaguars are often blamed (Fernandez 1995; Rabinowitz 2005). Although jaguars are protected, considered a mythical animal and there are no records of man-eating jaguars, they are still feared and hunted by people (Rabinowitz 2005). The future of jaguars is uncertain because free-ranging cattle practices are still widespread, and the Government has not provided any support to local rangers to coexist with the species (Rabinowitz 2005). As a result, people in the Pantanal have developed negative attitudes towards jaguars. This example shows that in the case of jaguars, the problem is not exclusively that of local communities and conservation organisations, but also involves Governmental agencies, national parks and the cultural background of local communities.

Tackling conservation conflicts is challenging because of the multidisciplinary approach required to understand both the human and wildlife dimensions of the problem. To find solutions, ideally one would have to gather data on the ecological, economic, socio-political and anthropological characteristics of the system under study before decision-making and conservation management can take place. However, this is not always possible because those engaged in the conflict often need rapid solutions. Therefore, the inclusion of an adaptive management framework that interconnects these processes: gathering data and applied management, is an integral part of developing effective solutions (Holling 1978; Milner-Gulland and Rowcliffe 2007). Adaptive management incorporates a continuous process of learning, adaptation and consultation involving different stakeholders in the field, which then contribute towards long-lasting solutions for conflicts in conservation.

This thesis contributes towards the process of finding solutions for conservation conflicts. The first part (Chapters 2 and 3) highlights the importance of gathering ecological data before decision-making occurs. The second part (Chapters 4 and 5) focuses on the value of testing and assessing the consequences of conservation management actions before their application in the field. All research chapters are individually introduced here to emphasise the key questions behind them, before guiding the reader to the general discussion on the complexities of conflict resolution.

What can we learn from historical trends in human-wildlife interactions? (Chapter 2)

History gives us information about the specific conservation conflict we aim to tackle as well as contextualising the current status and future trends of human-wildlife interactions. Comparing past data with the existing status of a system (i.e. a baseline) has become a critical component of the process of conservation (Bull et al. 2014), and in the field of conflicts it is crucial to understand people and environmental change as well as how the society we live in now came into being (Lambert 2015). For instance, references about people's past and current perceptions of wildlife can help us to raise awareness and change people's behaviour in the future. Similarly, when working with endangered species, accounting for population trends in the long-term can drastically change the success or failure of conservation interventions depending on the temporal scale used. Therefore, setting appropriate frames of reference is key to appropriate decision-making and to developing effective conservation management (Alagona 2012; Bull et al. 2014).

The use of baselines in conservation is relatively new and not necessarily well applied. Pauly (1995) was the first to introduce the concept of 'shifting baseline syndrome', which refers to the fact that each conservationist sets extant biodiversity during their early years as their own personal baseline, which may mask longer term biodiversity decline (Bull et al. 2014). Certainly, historical data provide the why and the how of environmental change and conflicts (Lambert 2015), however the impacts of conflicts can be the consequence of long and short-term processes. Therefore, we must be open in determining objective but flexible criteria to look back at different temporal and spatial scales to then develop feasible conservation managements that can be assessed accurately in the future. This was my motivation for Chapter 2, in which I investigated historical trends in the number of reported African elephant (*Loxodonta africana*) crop-raiding incidents in Botswana's Eastern Okavango Delta Panhandle. I used the number of incidents as an indicator of the level of human-wildlife impact, and I assessed its relationship to long-term trends in human and elephant population sizes, as well as to long and short-term trends in agricultural land-use in the study area. My findings suggest that the level of conflict due to elephant crop-raiding events in the Eastern Panhandle has decreased in the last years primarily because of the decline in agricultural land allocated to local communities, as well as that inferences regarding the drivers of conflicts and predictions for the future are dependent on the time span of the data used.

Assessing spatio-temporal interactions between people and wildlife (Chapter 3)

Conflicts in conservation can arise for numerous reasons, which in most cases involve mobility (Barua et al. 2013). The displacement and expansion of people into areas occupied by wildlife have also had spatial effects on species migrating from areas dominated by people, or, conversely, using people's settlements to exploit new resources. Animals moving outside of protected areas, translocations and regular migrations are just a few examples of spatio-temporal changes in wildlife distribution that can alter the level of overlap with human activities and develop into conflicts. Therefore, it seems that without a clear understanding of the distribution of both wildlife and people in space and time, preventing and making decisions in conflict situations is extremely challenging.

In particular, the emergence of new technologies to monitor wildlife has been a revolutionary tool in conservation, and a step forward towards increasing understanding of the whereabouts of populations in the wild (Pimm et al. 2015). The use of satellite collars, pin tags, camera-traps and drones has enormously increased data collection and precision, representing a great source of information with which to study human-wildlife impacts (for examples see Sitati et al. 2003; Goswami and Vasudev 2017). Although current tracking data capabilities only provide information on a subset of sites occupied by a species (Rondinini et al. 2006), the use of movement models has offered new opportunities to analyse species occurrence (Jetz et al. 2012) and build systematic evidence-based conservation decisions (Guisan et al. 2013). In Chapter 3, I use data from 20 satellite-collared elephants in the Eastern Okavango Delta Panhandle (Botswana) to look at individual and population-level space-use across the dry, wet and crop-raiding seasons. I found that while collared elephant distribution was determined by the availability of water sources and the presence of elephant corridors, predicting clear patterns in population space use was challenging. This was specifically the case during the crop-raiding season when I found the spatio-temporal relationship between crop-raiding events and elephant distribution not to be linear.

Evaluating the effectiveness of mitigation methods (Chapter 4)

Finding solutions in conservation is hard, especially solutions that will be effective over longer periods of time (Mace 2015). Conservation conflicts are especially difficult to manage because of the multiple social, economic and political sensitivities involved. Thus, if each component is not carefully assessed it is extremely easy to create irreversible consequences from poorly planned mitigation managements. Webber et al. (2007) documented a good example of a failure in conflict mitigation practices because of lack of evaluation. In order to decrease primate crop-raiding in villages around the Budongo Forest Reserve (Uganda), a conservation organisation set up live-traps to identify crop-raiding individuals. However, the intervention was not evaluated and stakeholders not identified and involved, which resulted in poor trap maintenance, with local farmers not accepting responsibility for them. The traps did not decrease the level of conflict between people and wildlife, and instead the method created a hostile environment for conservation organisations because people were reluctant to collaborate in future conservation projects.

It is essential to evaluate conflict mitigation strategies before they are implemented in the field. Nevertheless, evidence-based measures are rare, and – as in other fields of conservation – in many cases implementation is based on anecdotes and myths (Sutherland et al. 2004). The problem with this is that although some untested management strategies can result in positive outcomes for conflicts, failure to evaluate can lead to acceptance of dogma that can be wrong (Sutherland et al. 2004), preventing managers from adopting efficient practices in the future (Pullin et al. 2004). Assessing the effectiveness of conflict mitigation methods is fundamental to changing how conservation conflicts are tackled and fostering co-existence between people and wildlife. This was my incentive to test in Chapter 4 one of the most popular methods to deter crop-raiding elephants from people's fields: chilli-pepper briquettes. I used a replicated and randomised experimental design to assess the effectiveness of chilli-briquettes in altering elephant space-use in the Eastern Okavango Delta Panhandle (Botswana). I found that elephants modified their temporal behaviour towards the daytime in areas where chilli briquettes were being burned, but that the number of individuals crossing experimental sites did not change.

Modelling the consequences of mitigation management (Chapter 5)

In my last research chapter, I explore the use of modelling to deal with conflicts in conservation when long-term data are available and – for example – the testing of conservation management strategies is not feasible in the field.

Modelling has been widely used in conservation because it is extremely versatile. Models enable us to represent how the real world works and to modify specific components in our study systems to provide simplistic outcomes of complex natural processes. In addition, models can also give accurate means for testing how systems may respond to different drivers in the present, and assess the likely responses of the same system to alternative future managements (Frederiksen et al. 2001; Bunnefeld et al. 2011; Heinonen and Travis 2015). Similarly, modelling conservation conflicts has also allowed us to predict and simulate natural systems when data is scarce, for instance when working with threatened species. Last but not least, modelling can incorporate many different kinds of data, from social to ecological or economical, as well as theoretical and empirical; and of course a combination of all them. Although modelling management options in the context of conservation conflicts is extremely valuable, there are some limitations due to the unpredictability and variation of some conflict components (Heinonen and Travis 2015) that increase the uncertainty and credibility of model outcomes. Nevertheless, because models can be adapted to new situations, they are excellent for understanding dynamic systems and what can happen to them under different conflict interventions. They thus represent a key component of the adaptive management framework.

In Chapter 5, I estimated the consequences of selective hunting on the male component of red deer (*Cervus elaphus*) population from the Isle of Rum National Nature Reserve (Scotland). I used integral projection models to assess the relationship between antler length and demographic processes at different intensities of harvesting regimes. I found that as mortality due to simulated hunting increased to 50%, the effects of selective removal of individuals from the population became evident on mean antler size and reproduction.

Closing remarks

This thesis is presented in four stand-alone manuscripts. Each chapter has its own supporting information section and bibliography. Although the last research chapter of this thesis (Chapter 5) has been published in a peer-reviewed journal, I have reformatted all manuscripts following a conventional thesis format, and thus all figures and tables are integrated in the text and not at the end of each chapter. Lastly, in the appendix section I have included two papers on which I am a co-author, and that I worked during the time of my DPhil. The first paper documents elephant crop-raiding behaviour in Udzungwa Mountains National Park (Tanzania), and the second investigates the demographic consequences of illegal killing across multiple Tanzanian elephant populations. Both papers represent the most relevant sources of conflicts and conservation threats for elephants, and therefore they reinforce the motivation behind this thesis for looking at solutions to conservation conflicts.

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Chapter 2

Determining baselines for human-elephant conflict: a matter of time

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Temporal trends of human-elephant impacts

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Determining baselines for human-elephant conflict: a matter of time

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Abstract

Elephant crop raiding is one of the most relevant forms of human-elephant conflict (HEC) in Africa. Northern Botswana holds the largest population of African elephants in the world, and in the eastern Okavango Panhandle, 16,000 people share and compete for resources with more than 18,000 elephants. Hence, it is not surprising this area represents a HEC 'hotspot' in the region. Crop-raiding impacts lead to negative perceptions of elephants by local communities, which can strongly undermine conservation efforts. Therefore, assessing trends in conflict levels is essential to developing successful management strategies. In this context, we investigated the trend in the number of reported raiding incidents (RRI) as one of the indicators of the level of HEC, and assessed its relationship to trends in human and elephant population size, as well as land-use in the study area. For each of these factors, we considered data spanning historical (since the 1970s) and contemporary (2008-2015) time frames, with the aim of comparing subsequent inferences on the drivers of crop raiding and predictions for the future. We find that the level of RRI by elephants in the eastern Panhandle appears to have decreased since 2008, which seems to be related to the reduction in agricultural land allocated to people in recent years, more than with human and elephant populations size. However, we did not find clear patterns when RRI are compared to historical population trends. We show that inferences regarding the drivers of HEC and predictions for the future are dependent on the time span of the data used. Although our study represents a first step in developing a HEC baseline in the eastern Panhandle, it highlights the need for additional

multi-scale analyses that consider progress in conservation conflict to better understand and predict drivers of HEC in the region.

Introduction

Elephant crop raiding (i.e. the foraging and/or damage of crops) is currently one of the most prevalent forms of conflict between humans and elephants worldwide (Lahm 1996; Sitati et al. 2003, 2005). The on-going expansion of human settlements and activities, in addition to growing elephant populations outside of protected areas in some localities (Blanc et al. 2007; Hoare 1999; Chase et al. 2016), has resulted in increased levels of interaction between people and elephants (Hoare 1999a; Hoare and du Toit 1999). Crop-raiding in particular has direct impacts on human livelihoods, through the destruction of agricultural crops and nearby properties, as well as injuries to people and in some instances, death (Barnes et al. 1995; Hillman-Smith et al. 1995; Hoare 2000; Hoare and du Toit 1999; Lahm 1996; Lee and Graham 2006; Naughton-Treves 1998; van Aarde et al. 2007). Such impacts lead to negative perceptions of elephants by local communities, which in many cases strongly undermine conservation efforts targeted at elephant populations (Naughton-Treves 2001; Osborn and Hill 2005; Strum 1994).

Assessing trends in human-elephant conflict (HEC) impacts (see Redpath et al. 2013) is essential to identifying key drivers and devising successful management strategies. However, in order to identify changes in HEC patterns, we first need to understand past and present trends. To do this, effective monitoring and evaluation systems are needed in areas of interaction between people and elephants. Monitoring programs provide a means of evaluating progress made towards wildlife conservation (Nichols and Williams 2006; Stem et al. 2005), and one monitoring strategy in elephant conservation is to count and assess crop-raiding incidents reported in affected areas. Nevertheless, the interpretation of observed trends can be dependent on the time frame over which they are measured, which may be constrained by the availability of historical data (Alagona et al. 2012). A consequence of this is that the reference point against which the current state of HEC impacts is compared, i.e. a baseline, may be arbitrary. Determining a baseline before conservation implementation starts is a key step in the conservation evidence framework (Sutherland et al. 2004; Bull et al. 2014). Lack of an appropriate "frame of reference" is a widespread issue in the evaluation of conservation actions worldwide (McDonald-Madden et al. 2009). This is particularly relevant to human-wildlife conflict studies (Treves et al. 2006) for which long-term data on impacts and potential drivers are scarce (although see Lukasik and Alexander 2011). In the case of HEC, not only does this affect our understanding of current impacts within a defined region, but it also limits our ability to make robust predictions for future trends.

Botswana holds the largest population of African elephants (*Loxodonta africana*) in the world (Blanc et al. 2007; Chase et al. 2016), and the Okavango Delta Panhandle represents a stronghold in terms of increasing elephant numbers and conservation in Africa. Approximately sixteen thousand people currently inhabit the eastern section of the Panhandle (CSO 2011), sharing and competing for resources with a population of more than eight thousand elephants (DWNP 2013; Songhurst 2016). Hence it is not surprising that this area also represents an HEC 'hotspot' in the region. Elephant crop-raiding is seasonal, with most incidents occurring throughout the crop-growing and harvesting months (Jackson et al. 2008; Songhurst 2012). Due to the presence of both artificial (e.g. veterinary fencing) and natural barriers (e.g. the permanent Okavango River) to elephant movement, elephant activity is concentrated within this area. Previous studies have suggested that crop-raiding incidents are associated with the spread of human populations, and particular agricultural encroachment into wild areas (Hoare and du Toit 1999; Sitati et al. 2003). It is also believed that an increasing elephant population leads to a higher incidence of crop-raiding events (Barnes et al. 1995; Sukumar 1991). Based on this, it can be expected that the incidence of crop-raiding will increase in the coming years in the eastern Panhandle, yet no study has attempted to verify this assertion by quantifying and predicting trends in human and elephant populations, as well as changes in land-use.

In this study, we first characterise temporal trends in the incidence of reported crop-raiding events by elephants occurring in the eastern Panhandle of Botswana's Okavango Delta. We then investigate trends in potential drivers of crop-raiding incidence, i.e. human and elephant population sizes, as well as the amount of agricultural land allocated, with the latter trends estimated using data collected over two temporal scales, historical (1970s - 2015) and contemporary (2008 - 2015). Thirdly, we assess the relationship between each of these drivers and reported crop raiding. Finally, we use the results from the previous steps to predict future levels of crop raiding, comparing the influence of historical and contemporary time scales on predictions.

Materials and Methods

Study area

The study area is located in the eastern Okavango Delta Panhandle in the Ngamiland District of northern Botswana. The Okavango Delta is formed from the Okavango River that originates in Angola, flows along the Caprivi Strip in Namibia and reaches a tectonic trough in the centre of the Kalahari. The 8,732km^2 non-protected area in the eastern Okavango is a mixture of agricultural land, people's settlements and savannah shrubland delimited by the Namibian border to the north, the Okavango River to the southwest and the northern buffalo fence on the south-eastern edge (Fig 1; Songhurst 2012). Deep Kalahari sands cover the majority of the region, with fertile soils near the Okavango River. Vegetation cover is represented mainly by mopane (*Colophospermum mopane*) woodland, *Terminalia sericea* sandveld, mixed marginal floodplain woodland (*Acacia nigrescens* and *Hyphaene petersiana*), acacia woodland (*Acacia erioloba, Acacia tortillis*) and perennial swamp woody communities (Roodt 1998). The Delta has a typical continental climate with annual rainfall of 360 – 500 mm, mostly concentrated during the wet season (November to April). Daily temperatures vary from 25 - 35°C during the day to an average of 8°C during the night (Ramberg et al. 2006). The hottest month of the year is October, at the end of the dry season (May to October).

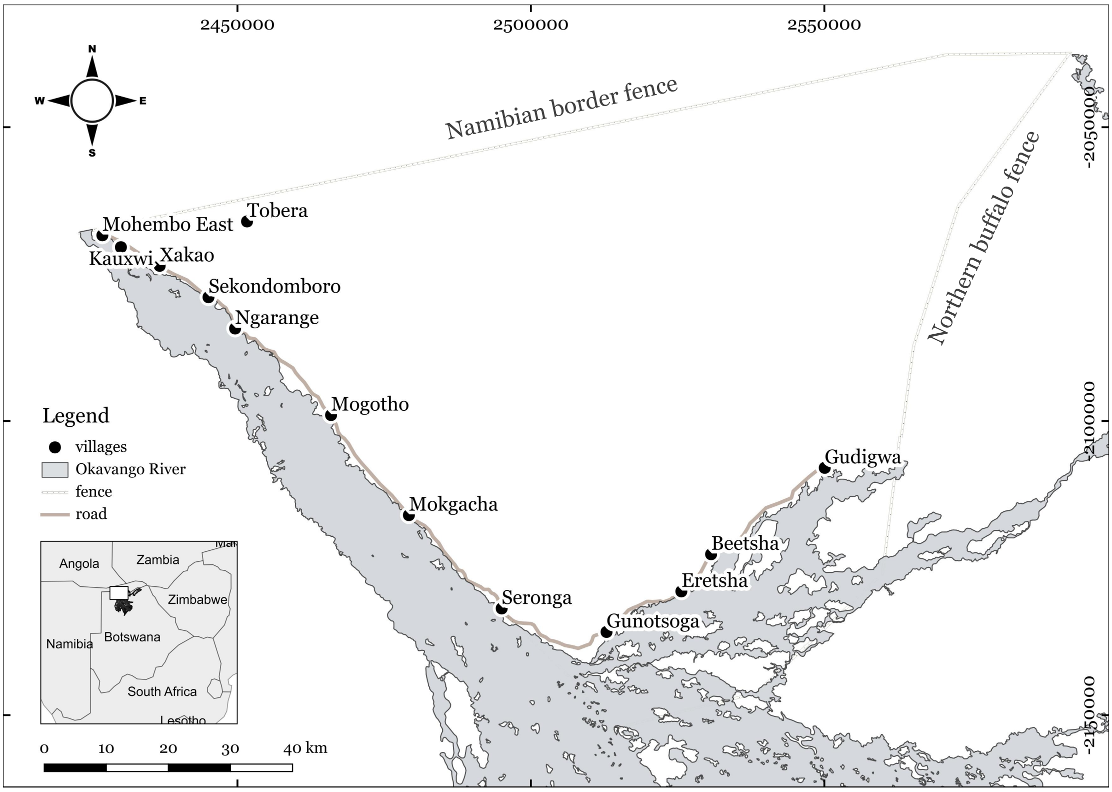

Fig 1. Location of villages in the eastern Okavango Delta Panhandle (Botswana). Circles represent the thirteen villages (i.e. Mohembo East, Kauxwi, Tobera, Xakao, Sekondomboro, Ngarange, Mogotho, Mokgacha, Seronga, Gunotsoga, Eretsha, Beetsha and Gudigwa) along the Okavango River. The small southern Africa inset map shows the location of the study area in northern Botswana in white.

More than 16,000 people live in thirteen villages along the Okavango River from Mohembo East to Gudigwa (Fig 1). The largest village is Seronga with 3,716 inhabitants (CSO 2011). Human livelihoods consist mainly of subsistence agriculture. Local farmers cultivate fields in areas from the river edge up to 14km inland. Ploughing takes place at the beginning of the wet season (November to April) and crops are harvested every year between March and June. The last estimated elephant population size within our study period (2008-2015) and area was 11,760 (DWNP 2013).

Data collection

In this study, we used data relating to three common determinants of elephant crop-raiding; i.e. the size of human and elephant populations, as well as the area of agricultural land allocated. Hoare (1999a) argued that crop-raiding events were more likely to occur at higher elephant densities, in areas where their range had shrunk as a result of human settlement expansion and land transformed for agriculture. None of these variables have been studied in the eastern Panhandle as determinants of the amount of HEC in the region. Population and land-use data had been previously collected in Botswana by the Department of Wildlife and National Parks (DWNP), the Central Statistical Office (CSO, Ministry of Finance and Development Planning), the Land Board Office (Ministry of Agriculture), and the Ecoexist Project. Our study uses data from elephant aerial surveys collected in the eastern Panhandle. These were performed either by the DWNP or by members of the Ecoexist Project. In both cases, the DWNP authorised the collection and use of the aerial survey data (for more details see DWNP 2013; Songhurst 2012). This project was under research permit EWT 8/36/4 XXVI (86) issued by the DWNP in May 2014, which allowed use and collection of data pertaining to the study area.

We used estimated elephant population sizes reported by the DWNP between 1991 and 2013. These were combined with independent aerial survey data collected across the study area by the Ecoexist Project (Table 1; Songhurst et al. 2015). In all aerial surveys (i.e. Governmental and independent) population size estimates were obtained using the Jolly Method II (Jolly 1969) for sampling blocks of unequal size and only dry season data was used.

Table 1. Human and elephant population size, agricultural land allocated (ALA) and number of reported raid incidents (RRI) from raw and predicted data.

Year	Elephant population			Human population		ALA (ha)			# RRI	
	Raw data	Predicted data	Source	Raw data	Predicted data	Raw data	Predicted data (historical)	Predicted data (contemporary)	Raw data	Predicted data
1971	-	-	-	2229	1592.6	-	-	-	-	-
1972	-	-	-	-	1784.4	-	-	-	-	-
1973	-	-	-	-	1996.7	-	-	-	-	-
1974	-	-	-	-	2230.7	-	-	-	-	-
1975	-	-	-	-	2487.9	47.2	1.5	-	-	-
1976	-	-	-	-	2769.5	62.7	3.6	-	-	-
1977	-	-	-	-	3076.8	97.4	8.8	-	-	-
1978	-	-	-	-	3410.6	84.8	21.3	-	-	-
1979	-	-	-	-	3771.6	11.7	50.2	-	-	-
1980	-	-	-	-	4159.9	126.4	113.5	-	-	-
1981	-	-	-	4598	4575.4	529.1	234.5	-	-	-
1982	-	-	-	-	5017.5	88.2	416.6	-	-	-
1983	-	-	-	-	5485	700.9	610.9	-	-	-
1984	-	-	-	-	5976.2	668.3	755.3	-	-	-
1985	-	-	-	-	6488.8	674.5	836.3	-	-	-
1986	-	-	-	-	7019.9	1704.1	874.7	-	-	-
1987	-	-	-	-	7566.1	1042.1	891.5	-	-	-
1988	-	-	-	-	8123.7	944.2	898.6	-	-	-
1989	-	-	-	-	8688.6	350	901.5	-	-	-
1990	-	2748.5		-	9256.3	617.6	902.7	-	-	-
1991	2412	2960.3	DWNP[a]	9032	9822.4	644.9	903.2	-	-	-
1992	-	3188.5		-	10382.5	1473.5	903.4	-	-	-
1993	1106	3434.2	DWNP	-	10932.4	1119.3	903.5	-	-	-
1994	4243	3698.9	DWNP	-	11468.2	661.1	903.5	-	-	-
1995	-	3983.9		-	11986.4	728.9	903.6	-	-	-
1996	3782	4291	DWNP	-	12484	717.3	903.6	-	-	-
1997	-	4621.6		-	12958.5	511.3	903.6	-	-	-
1998	-	4977.8		-	13408	937.1	903.6	-	-	-
1999	3886	5361.4	DWNP	-	13831.3	1359.6	903.6	-	-	-
2000	-	5774.6		-	14227.5	1248.9	903.6	-	-	-
2001	13173	6219.7	DWNP	15718	14596.2	706	903.6	-	-	-
2002	6660	6699	DWNP	-	14937.8	641.7	903.6	-	-	-
2003	5261	7215.3	DWNP	-	15252.6	368.2	903.6	-	-	-
2004	11870	7771.3	DWNP	-	15541.5	788.6	903.6	-	-	-
2005	5088	8370.3	DWNP	-	15805.6	1126.1	903.6	-	-	-
2006	9212	9015.3	DWNP	-	16046.1	622.8	903.6	-	-	-
2007	-	9710.1		-	16264.4	1021.4	903.6	-	-	-
2008	8905	10458.4	IS[b]	-	16462	1260.5	903.6	1330	405	318.6
2009	-	11264.4		-	16640.3	1345.9	903.6	1209.8	198	257.1
2010	15429	12132.6	IS	-	16800.8	1189.2	903.6	1089.7	185	207.4
2011	-	13067.6		16371	16945	755.9	903.6	969.5	-	167.4
2012	-	14074.7		-	17074.3	781.6	903.6	849.3	84	135
2013	11760	15159.4	DWNP	-	17189.9	844.5	903.6	729.2	-	109
2014	-	16327.6		-	17293.3	-	903.6	609	103	87.9
2015	-	17586		-	17385.5	-	903.6	488.8	102	70.9

[a] DWNP: Department of Wildlife and National Parks

[b] IS: Independent survey (Songhurst et al. 2015b)

Human population census data for the study area were obtained from the Central Statistical Office (CSO), Gaborone. Since 1966, Botswana has conducted decennial population and housing censuses. We therefore considered in our analysis the number of inhabitants per village available from 1971 through to 2011. We did not use human and elephant population densities as in previous studies (e.g. Hoare and du Toit 1999). This was because, although elephants distribute themselves throughout the study area (see Chapter 3), human settlements are exclusively clustered into areas close to the Okavango River (see Chapter 3; Songhurst 2012), and therefore calculating human population density throughout the eastern Panhandle would have given misguided estimates for areas where conflicts occur.

To quantify human land use in the study area, we collected data on the number and area of agricultural fields allocated and cultivated each year, both from the Land Board Office and the Ministry of Agriculture, respectively. In the Okavango's eastern Panhandle, the Land Board assigns fields exclusively for agricultural use to local farmers every year. Subsistence agriculture is the main source of livelihood in the study area, and so the majority of allocated fields are ploughed and harvested once assigned (Elizabeth Keabetswe - Head of Department of Agricultural Regional Office, Shakawe – *pers. comm.*). However, people in the eastern Panhandle move away from their houses and agricultural fields often and thus fields allocated in previous years are not necessarily cultivated every year in the same way as newly allocated fields (Elizabeth Keabetswe - Head of Department of Agricultural Regional Office, Shakawe – *pers. comm.*). Therefore, we decided to use the number of new fields allocated per year and not the cumulative number of fields per year in the study area. The latter measure would have not truthfully represented areas cultivated and with human activity each year during the harvesting season. In this way, we included in our analysis a conservative covariate, i.e. the minimum area used for agricultural purposes in our study site.

In the eastern Panhandle, each allocated field is measured before being given to farmers, and we used this information to calculate the total area allocated for agriculture each year. Since plots allocated are typically approximately rectangular or square, we estimated the area of each field by multiplying its width by its length. Ideally, our study should consider the area of agricultural land *cultivated* as a measure of human land use. However, this information was unavailable prior to 2008, and we therefore used the area of agricultural land *allocated* per year as a proxy. The latter, was found to be correlated with the area of land cultivated per year (Pearson' correlation r = 0.87; P = 0.024). In other words, the area of land allocated for agricultural purposes by the Land Board represents a similar proportion of the land cultivated by farmers in the eastern Panhandle, and both (land allocated and cultivated) change equivalently in our study area. We, therefore, consider the area of agricultural land allocated (ALA, hereafter) in a year as an indicator of human land use.

Lastly, we used the number of reported raiding incidents (i.e. RRI) per year collected by the Ecoexist Project as a measure of the level of conflict occurring between people and elephants in the study area. We are aware that HEC is a complex phenomenon and that the number of crop-raiding incidents per year represents only one way to quantify the level of interaction between people and elephants. We did not consider other causes of HEC because the aim our study was to develop a preliminary baseline to assess the interaction between three of the most popular variables to which conflict is attributed (i.e.

human and elephant population sizes and land use) given the overall levels of conflict in the region. Following the protocol of the International Union for the Conservation of Nature (IUCN 1999) for collection of primary data on HEC, local enumerators were selected and trained in consultation with the village Kgosi (chief) to identify and characterise elephant crop-raiding incidents in each village (for more details see IUCN 1999; Hoare 1999b; Songhurst and Coulson 2014). Enumerators lived throughout the year in one of the thirteen villages in our study area, and they visited raided fields following reports by farmers since 2008 when HEC data collection started. Consequently for this study, we used RRI data collected between January 2008 and April 2015. We used six years of data due to missing RRI reports for the years 2011 and 2013.

Statistical analysis

We performed our statistical analysis in three steps. We first investigated trends in HEC - here using the number of reported raiding incidents (RRI) as an indicator of the level of conflict between people and elephants -, and three HEC drivers, i.e. human and elephant population sizes, as well as the amount of agricultural land allocated. The latter trends were estimated using data collected over two temporal scales, historical (1970s - 2015) and contemporary (2008 - 2015). Secondly, we assessed the relationship between each of these drivers and the level of HEC in the study area. Finally, we used the results from the previous steps to predict future levels of HEC, and we compared both temporal scales: historical versus contemporary predictions.

Population and HEC trends

To investigate historical trends in elephant and human population sizes, as well as in ALA area in the eastern Panhandle, we fitted statistical models that reflected the underlying structure of each raw dataset. More specifically, we applied non-linear least square logistic models (nls) to the human population growth data and to the area of agricultural land allocated (ALA). We used nls because in both cases, the relationship between human population numbers and the area of ALA as a function of years - respectively - could not be linearized by traditional statistical transformations. For the elephant population data, we used a generalised linear model (GLM) with a Poisson error structure to account for count data and a non-normal error structure. We also investigated the trend in the area of ALA during the years in which conflict data were collected (2008 - 2015). To do this, we used a linear model (lm) to regress the area of ALA (2008 - 2015) as a function of year. This model yielded normally distributed residuals over this specific period of time. In all cases, model choice reflected assumptions about the underlying data. Finally, to better understand trends in the level of conflict observed in recent years, we studied the number of reported raided incidents (RRI) per year. We used a GLM with Poisson error structure because the number of RRI corresponds to count data.

Temporal interaction between RRI and HEC drivers

Using the above population and HEC models we then estimated temporal trends for (1) the number of RRI per person and per elephant, (2) the area of ALA (ha) per person and per elephant, and (3) RRI per hectare of ALA each year. The objective of this analysis was to determine the intensity of conflict experienced per person and agricultural field (ha), as well as the number of raiding incidents caused by elephants inhabiting the study area. We used the same two temporal scales (historical from the 1970s - 2015; and contemporary from 2008 - 2015) to test the effectiveness of using long and short-term area of ALA (ha) data in assessing trends in the level of HEC. All explanatory variables considered are annual, and therefore do not reflect changes within a given year.

Developing a model to predict future levels of HEC

We used generalised linear models with Gaussian error structures to identify which combination of the three explanatory variables considered in our analysis best described the level of conflict in the area. Human and elephant population sizes, in addition to the area of ALA (ha), were fitted as explanatory variables for the level of RRI at the historical and contemporary scales. In all cases model selection was based on corrected Akaike's Information Criterion (AICc) (Aikaike 1973), because of the small sample size of some of the datasets used in our study. The highest-ranked model (i.e. lowest AICc value) for each temporal scale was used to predict the area of agricultural land likely to be raided in the following ten years (from 2015 to 2025). For all statistical analysis in this study we used R v3.0.1 (R Core Team 2014).

Results

Population and HEC trends

Human and elephant populations showed increasing trends since the 1970s (Fig 2, Table 1). The number of people in the eastern Panhandle has shown a logistic growth since 1971 (Fig 2A, n=5). This curve reached an asymptote, and in 2015 our best model predicted a local population of 17,385 inhabitants (Table 1). The elephant population, in contrast, has increased exponentially in the study area, with the population model predicting a population size of 17,586 elephants in 2015 (Fig 2B, n=14). In contrast, the number of hectares of allocated agricultural land increased during the early 1970s in the eastern Panhandle before remaining stable from the 1980s onwards (Fig 2C, n=40). When considering contemporary data (2008 - 2015), we found that the area of ALA decreased significantly (Fig 3A). Lastly, the number of yearly RRI also showed a decreasing trend between 2008 and 2015 (Fig 3B, n=6).

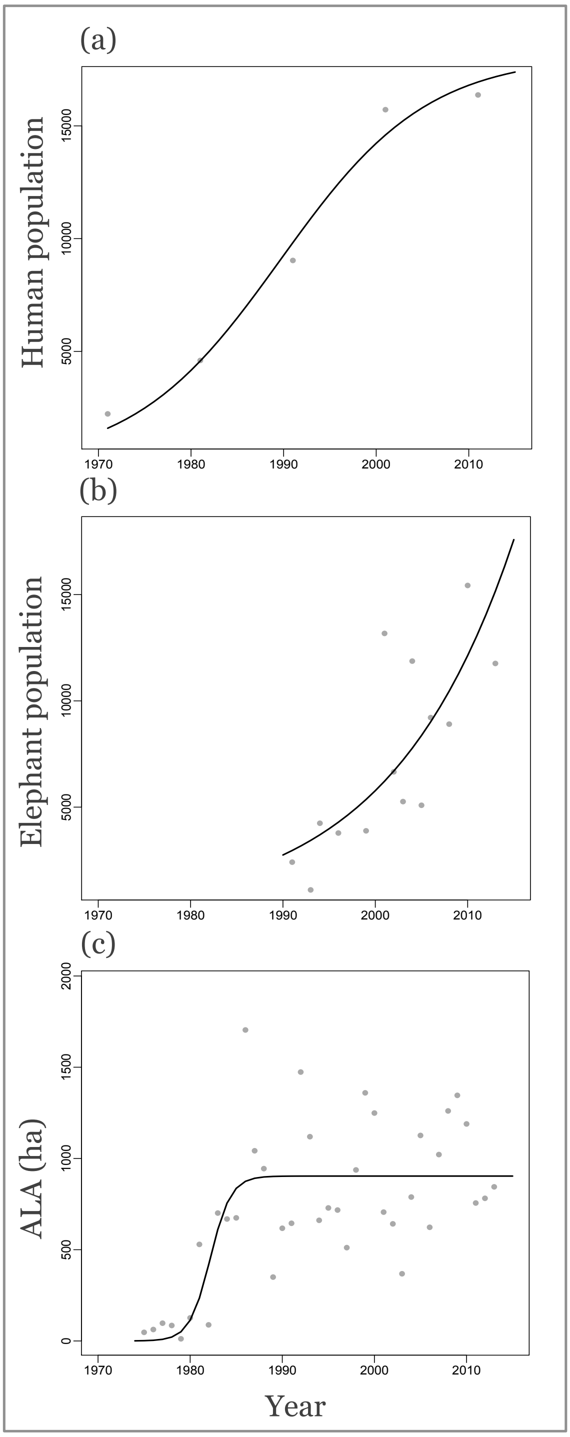

Figure 2. Historical trends for HEC drivers in the Eastern Panhandle. (a) corresponds to human population, (b) elephant population, and (c) agricultural land allocated (ALA) (ha) in the Grey dots and black lines represent raw data and the best fitted model, respectively.

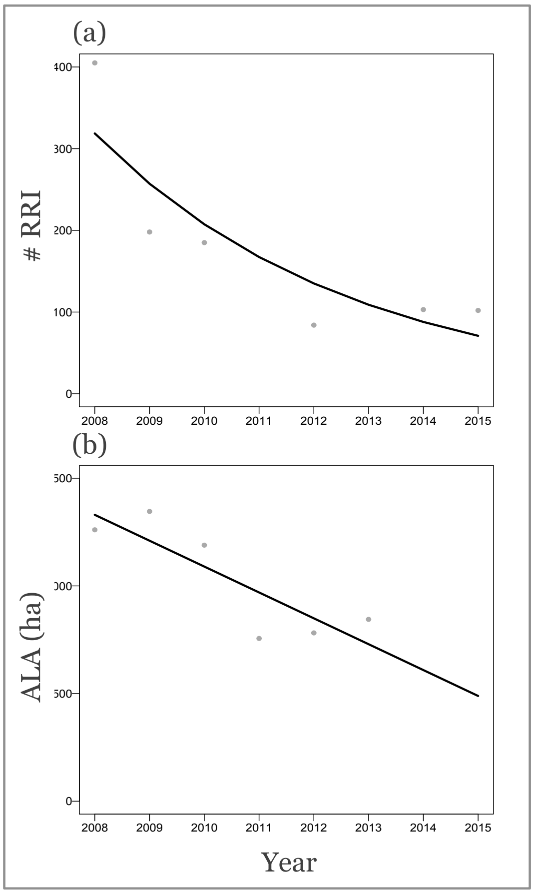

Figure 3. Contemporary trends for HEC drivers in the Eastern Panhandle. (a) corresponds to agricultural allocated land (ALA) (ha), and (b) number of reported of raid incidents (RRI) in the Eastern Panhandle. Grey dots and black lines represent raw data and the best fitted model, respectively.

Temporal interaction between RRI and HEC drivers

In accordance with the above results, the number of RRI per person and per elephant showed decreasing trends over the study period (Fig 4A). In 2008, our models predicted a number of raids per elephant of 0.03, which is in accordance with the 0.04 raids per elephant calculated from raw data. In both cases, the number of RRI decreased to 0.004 and 0.005 for fitted and raw data, respectively by 2015. A similar pattern was found for local people (Fig 4A), for which the number of RRI per person was 0.02 (from fitted values and raw data) in 2008; and in both cases respectively declined to 0.004 and 0.005 raids per person in 2015.

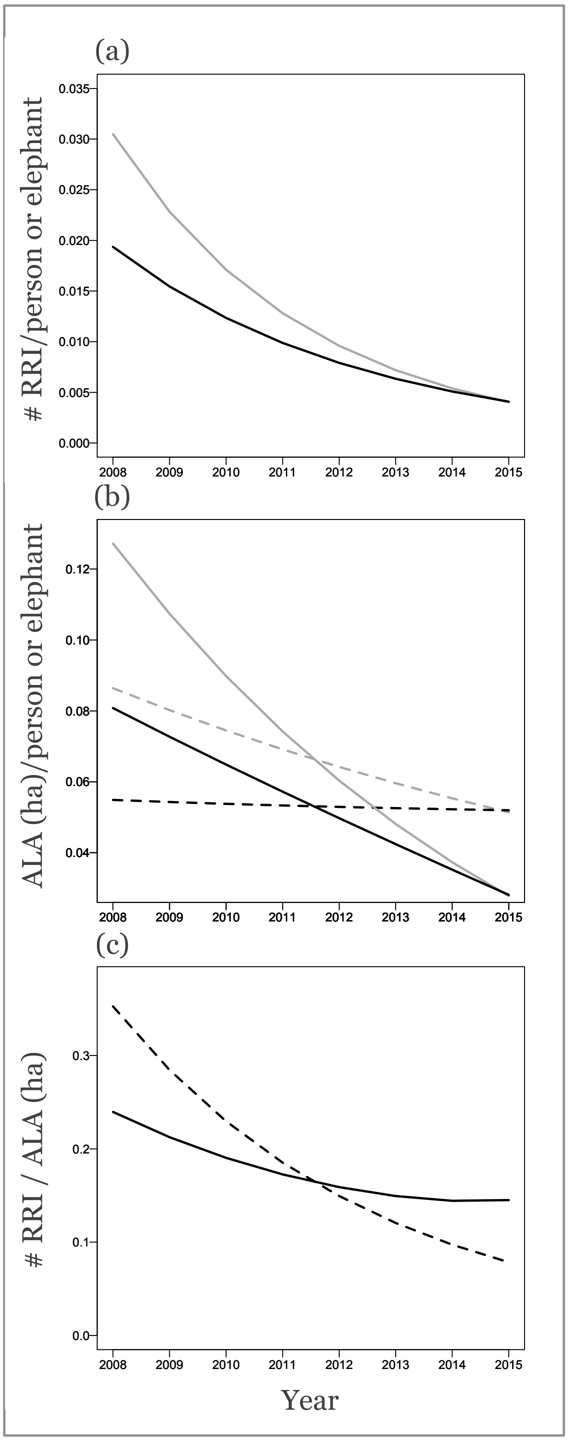

Figure 4. Temporal interaction between reported raid incidents and HEC drivers. (a) corresponds to the predicted number of reported raids incidents (RRI) per person (back) and per elephant (grey), (b) agricultural land allocated (ALA) per person (back) and elephant (grey); and (c) estimated raiding incidents per ha of agricultural allocated land (ALA). Dashed lines correspond to predictions from the historical model (1970s - 2015) and continuous lines to predictions from the contemporary model (2008 - 2015).

We detected contrasting trends for the area of ALA (ha) in the eastern Panhandle over the study period depending on which temporal scale was used. When historical data from the 1970s to the present day were used, allocated land over the study period (2008 - 2015) stayed constant (Fig 2C). However, when only contemporary data was considered, the trend was negative (Fig 3B). We therefore used predictions of yearly ALA from both models (historical and contemporary) to estimate: a) the hectares of ALA per person and elephant in the region, and b) the number of reported raiding incidents per ha of ALA per year. When the historical model was used to predict land-use, the number of hectares per person was found to remain constant from 0.055 in 2008 to 0.052 in 2015, but the ALA per elephant decreased from 0.087 ha in 2008 to 0.052 ha in 2015 (Fig 4B). In contrast, when the contemporary model was applied to predict land-use we observed a decreasing trend in ALA (ha) per person (from 0.08 to 0.03 ha of agricultural land (ha) per farmer) and per elephant (from 0.13 to 0.03 ha of agricultural land (ha) per elephant) (Fig 4B). Nevertheless, both models did predict a decrease in the total number of RRI per agricultural land from 2008 to 2015, albeit at different intensities (Fig 4C).

Developing a model to predict future levels of HEC: historical versus contemporary predictions

We used a multivariate analysis to identify explanatory variables that best explained the level of conflict in the study area at the historical and contemporary scales. Our results showed the best models to explain the amount of conflict included the additive effects of human and elephant population sizes in addition to ALA area for the historical (AICc = 47.2) the contemporary (AICc = 35.9) datasets (see Tables 2 and 3). However, because of the small sample size, we also considered models containing two explanatory variables. These models revealed that, for the historical approach, the additive effect of human and elephant population sizes were the most important predictors of conflict (AICc = 51.5), followed by the additive effect of human population and ALA (ha) (AICc = 59.3) (Table 2). In contrast, when contemporary trends where used, human population size in addition to ALA was the second best model to predict the level of conflict (AICc = 47.7), followed by the additive effects of human and elephant population sizes (AICc = 51.5) (Table 2). Independent GLMs for each explanatory variable showed human population size as the main factor affecting the trend in RRI at both temporal scales (AICc = 68.3). For both temporal scenarios, the number of people had a negative effect on the number of RRI in the region (Table 3). Similarly, RRI was negatively affected by increasing elephant population size (AICc = 84.6) at both temporal scales (Table 3). However, the area of ALA (ha) had a positive effect on the number of RRI for both, the historical (AICc = 91.7) and contemporary (AICc = 79.9) cases (Tables 2 and 3).

Table 2. Summary of model selection with corrected Akaike's Information Criterion (AICc). AICc used to evaluate relationships of the number of reported raid incidents with 3 explanatory variables: human (people) and elephant (elephants) population size as well as agricultural land allocated (ALA). Model selection was performed at two temporal scales, i.e. historical (1970s – 2015) and contemporary (2008 – 2015). The model and explanatory variables columns indicate specific combination of variables included in each function. Delta AIC (Δ AICc) shows the difference between each model and the best model selected for our analysis. The weight column represents the relative likelihood of each model.

Temporal scale	Model	Explanatory variables	AICc	Δ AICc	Weight
Historical (1970s-2015)	model 1	people + elephants + ALA	47.2	0	0.893
	model 2	people + elephants	51.5	4.3	0.105
	model 3	people + ALA	59.3	12.1	0.002
	model 4	people	68.3	21.1	0.000
	model 5	elephants	84.6	37.4	0.000
	model 6	ALA	91.7	44.5	0.000
	null	1	99.4	52.2	0.000
Contemporary (2008-2015)	model 1	people + elephants + ALA	35.9	0	0.997
	model 3	people + ALA	47.7	11.8	0.003
	model 2	people + elephants	51.5	15.6	0.000
	model 4	people	68.3	32.4	0.000
	model 5	ALA	79.9	44.0	0.000
	model 6	elephants	84.6	48.7	0.000
	null	1	99.4	63.5	0.000

Table 3. Summary of best historical and contemporary models. Best model coefficient estimates for the historical (1970s – 2015) and contemporary (2008 – 2015) analyses. The best model column corresponds to model number 1 in Table 2. Coefficient shows model intercept and explanatory variables included in the analysis: human (people) and elephant (elephants) population size, as well as agricultural land allocated (ALA). Estimate and standard error show the magnitude of each specific coefficient effect and the variation attributed to it, respectively. The t-value and Pr (>|t|) columns show the value of t-statistic and p-value for testing whether the corresponding coefficient is significantly different from 0.

Temporal scale	Best model	Coefficient	Estimate	Standard error	t value	Pr (>|t|)
Historical (1970s-2015)	model 1	intercept	1.90E+11	2.33E+10	8.156	0.00123
		people	-3.43E-01	8.84E-03	-38.836	2.63E-06
		elephants	-2.10E+08	2.57E+07	-8.156	0.00123
		ALA	1.24E-02	9.12E-04	13.553	0.000172
Contemporary (2008-2015)	model 1	intercept	1.70E+04	5.99E+02	28.36	9.19E-06
		people	-8.69E-01	2.72E-02	-31.96	5.72E-06
		elephants	-6.89E-02	5.18E-03	-13.28	0.000186
		ALA	-1.24E+00	7.34E-02	-16.93	7.13E-05

Finally, to assess the accuracy of our models we predicted the number of RRI per year with each of the best three above models (i.e. model 1 - 3, Table 2). In the short-term (2008 - 2015) the number of raids fitted did not differ significantly between both temporal scales (Fig 5A and C); however when the best model (from each temporal scale) was used to predict the level of conflict in the long-term we found contrasting trends (Fig 5B and D).

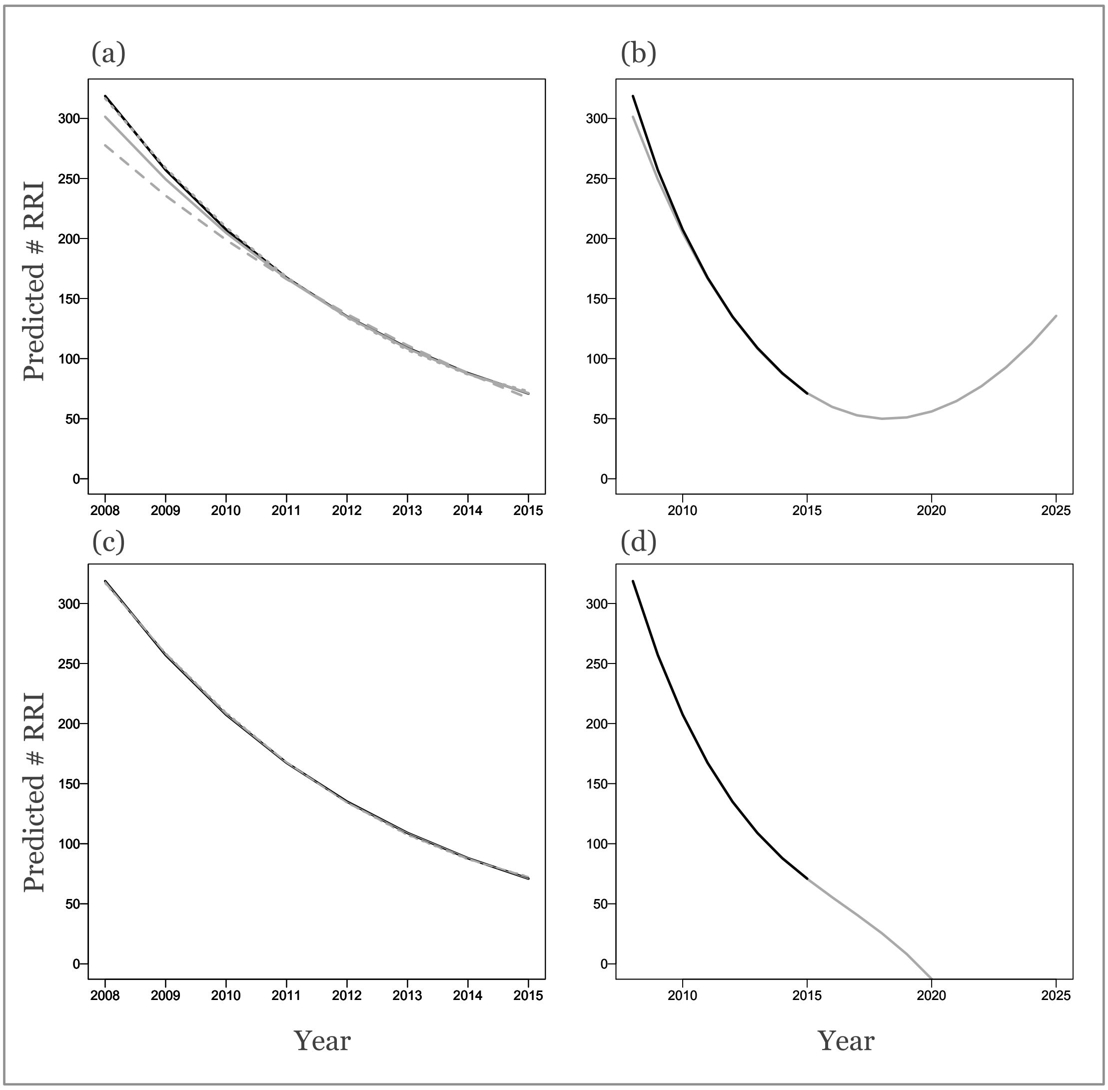

Figure 5. Temporal differences in predicted raiding incidents as derived from generalized linear models (GLMs). (a) and (c) show predicted reported raid incidents (RRI) from multivariate GLMs based on historical (a; 1970s – 2015) and contemporary (c; 2008 - 2015) data. In both graphs, grey lines represent model 1 (RRI ~ people + elephants + ALA), dotted lines model 2 (RRI ~ people + elephants), and dashed lines model 3 (RRI ~ people + ALA). (b) and (d) show RRI for the next 10 years (2015 - 2025) from the best GLMs (model 1) selected for historical (b) and contemporary (d) scales. Black lines correspond to raw number of RRI in all cases.

Discussion

This study shows that inferences regarding the drivers of HEC in the eastern Panhandle and predictions for future trends are dependent on the temporal resolution of the data used. The level of reported crop raiding events by elephants in the eastern Okavango Delta Panhandle has apparently decreased in recent years, which is unexpected given that both human and elephant populations were found to be growing in the region. Although our results are inferred from a relatively small dataset, they are in agreement with previous studies that have shown that the absolute numbers of people and elephants are not in themselves significant drivers of the conflict (Hoare 1999a; Songhurst et al. 2015). Rather, it is the use of space and competition for resources between people and elephants that likely determines the level of conflict (Sitati et al. 2003; Graham et al. 2009; Jackson et al. 2008). To this end, we investigated the relationship between the reported level of conflict and the area of land allocated for agriculture each year. Crucially, trends in the latter were estimated using data collected over both historical (since the 1970s) and contemporary (since 2008) timeframes, thus representing distinct data scenarios often encountered in practice (Pauly 1995).

When both temporal scales were considered independently our overview of the underlying processes of HEC changed, making it difficult to determine which were the most important factors contributing towards the level of conflict in the region. In line with this, the simultaneous reduction in the number of RRI and agricultural land observed since 2008 is indicative of the spatial nature of HEC (Jackson et al. 2008; Sitati et al. 2003; Songhurst and Coulson 2014), and suggests that both time and space are important in determining the likelihood of conflict (Hoare 1999a). The requirement for both people and elephants to share resources close to the Okavango River can be expected to result in conflict. However, our results suggest that negative interactions between humans and elephants can decrease with the amount of agricultural land used by people. Thus, based on the contemporary analysis, we would concur with previous research that has considered broad scale variables (i.e. number of people and elephants) to be inadequate predictors of the amount of expected conflict (Hoare and du Toit 1999), but land-use is a key factor determining the level of HEC, and would re-emphasise the importance of including appropriate land-use planning in conservation management (Graham et al. 2009). However, as previously mentioned, the contemporary model approach implemented was limited in terms of predicting conflict in the future probably as a consequence of the small dataset used here. We therefore also investigated the interaction between RRI and the area of land allocated to agriculture based on historical data.

When this historical approach was implemented the relationship between area of land allocated to agriculture and the number of RRI became unclear. With an increasing elephant population in the study area and an unchanging allocation of land for agriculture, a decrease in the number of RRI was observed. This could be a consequence of less land allocated being cultivated, or assuming all elephants forage crops when they are available, of a switch to less palatable crops for elephants. However, we know that in the short-term the area of cultivated land has decreased at the same rate as the area of land allocated (see Supporting Information), and that, although elephants are more likely to forage fields with pumpkins, the variety and proportion of crop species planted have not drastically changed in the region, with millet being the predominant crop grown since 2008 (Songhurst 2012). Alternatively, changes in elephant behaviour such as moving under the cover of trees, foraging predominantly during the night, and the use of pathways (Douglas-Hamilton et al. 2005; Galanti et al. 2005; Graham et al. 2009; Songhurst 2012; Songhurst et al. 2015b; Von Gerhardt et al. 2014), could help explain the decrease in HEC when trends in land-use are estimated from historical data. However, although we acknowledge the importance of behavioural components – which we did not include in our study – we argue it is more likely that the trend in RRI observed within the last decade is a reflection of population and land-use factors acting in the short term, which may be different to those acting over longer time-scales.

It is interesting to highlight that the use of different time scales when determining the area of land allocated for agriculture did not impact the estimation of temporal trends in conflict in the short-term. In contrast, disparities were found when predicting in the long-term. In both cases, the number of RRI per person, elephant and agricultural land (ha) decreased between 2008 and 2015. Accordingly, our multivariate analysis predicted minor dissimilarities between temporal scales, both of which resulted in an estimated decrease in the level of conflict. However, when the same models were applied to predict HEC in future years (2015 - 2025) we found opposite patterns between the two temporal scales. Such a result is likely due to the variation across different time scales as well as the number of observations considered in both analyses. Which, in other words, represents the changing trends of land-use at different time scales, and therefore we think these contrasting outcomes are a good example of the 'shifting baseline syndrome'. This concept was first introduced by Pauly (1995), who described how each generation of scientists set a baseline that started at the beginning of their careers, and used it to evaluate changes in the future. However, so-called shifting baselines masked longer-term changes. In our case, analyses based on land-use estimates derived from 2008 predicted an end to the conflict by 2020. However, when long-term data were considered, HEC was predicted to increase in the future.

The question of which temporal scale is preferable to use when predicting HEC is a challenging one to answer because natural systems are often extremely dynamic and their component interactions complex. Instead, we argue that both should be used as complementary sources of information with which to better investigate the underlying processes driving HEC at the short and long-terms. Ideally, baselines should be determined before decision-making takes place, thus our study represents an extremely useful framework to face future challenges in elephant conservation. In addition to time scale, we encourage detailed analyses of human behaviour (i.e. peoples' livelihood, migration history, etc.), elephant behaviour (habitat preferences, movement patterns, etc.), land-use (effective cultivated land, crops yielded, etc.), as well as environmental variation (annual rainfall, habitat distribution, water and vegetation availability, etc.) to be carried out so as to provide a more comprehensive understanding of additional drivers of HEC in the study area.

Nonetheless, HEC is a complex phenomenon driven not only by population and land use trends, but also historical, social, political, cultural and environmental factors that are unique to each study area. The aim of our study was not to include all of these, and we acknowledge that aspects other than population trends may be contributing towards the observed trend in conflict. For instance, a common problem in HEC is the lack of reporting of crop-raiding incidents, which could represent a potential source of bias in our measurement of HEC. Compensation schemes, which reimburse individuals who experience property damage or have been injured by wildlife in the hope of increasing tolerance towards wildlife (Nyhus et al. 2005), may inadvertently increase the likelihood of reporting. Alternatively, and most likely in the case in our study area, farmers may feel that the compensation is inadequate (DWNP 2010; Jackson et al. 2008; Songhurst 2012), and we suspect local people could be reporting less than they used to in the eastern Panhandle. The implementation of compensation schemes is challenging and in many cases difficult to monitor (Nyhus et al. 2003, 2005; Mosojane 2004; Gusset et al. 2009; Parry et al. 1992), and the compensation programme in Botswana is not an exception in terms of difficulties in the field (Nyhus et al. 2005; Mosojane 2004; Gusset et al. 2009). Nevertheless our measure of conflict is liable to misreporting, it is often the only source of information in affected areas, and therefore we used it as a conservative long-term indicator of the conflict status. Importantly, however, our study considers a single measure of HEC (i.e. crop-raiding reports), and thus, future research should ideally consider other sources of biases associated with the measurement of HEC, which may also potentially influence observed trends.

Northern Botswana holds the largest population of elephants in the world, therefore a decline in reported HEC in the Okavango Delta Panhandle can be seen as very encouraging, particularly given human and elephant populations are still increasing, and agricultural land in the long-term is still expanding. Our study suggested that the characterisation of HEC drivers was dependent on the time scale used to estimate allocated land-use over the past eight years. Specifically, it was likely to change considering the fluctuating amount of land allocated to agriculture over the past three decades, thus highlighting the spatio-temporal nature of HEC in the study area and leading us to the tentative conclusion that the decreasing trend in RRI is probably linked to the reduction of ALA in the eastern Panhandle since 2008. More generally, it is essential for conservationists to consider baselines at different temporal scales before making decisions about management and species conservation, as well as applying multidisciplinary approaches that not exclusively include population trends but also specific factors affecting the level of HEC in conflict areas. In our study area, if larger areas were used for agriculture in the future, the trend in HEC would also change. We therefore emphasize it is critical to design effective land-use planning programs in the short-term in order to minimise and prevent future conflict between people and elephants in the eastern Panhandle.

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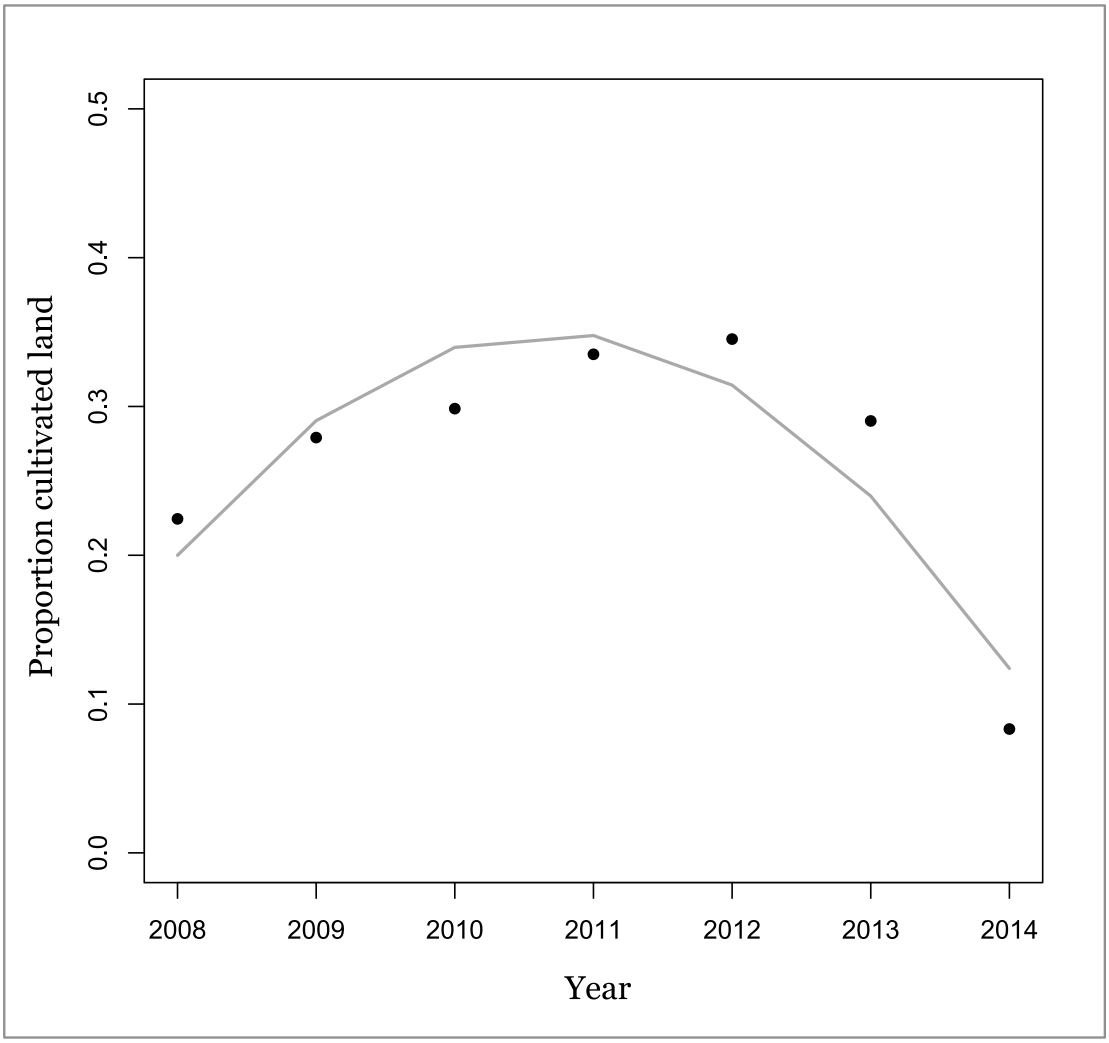
Supporting Information

Figure S1. Area of land cultivated as a proportion of agricultural land allocated in the Eastern Panhandle between the years 2008-2014. Black dots and grey line represent raw data and the best fitted model, respectively.



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Chapter 3

Elephant distribution and crop-raiding spatiotemporal overlap: using an integrative approach for future conflict management

- Running head -

Elephant movement and crop-raiding distribution interaction

- Tittle -

Elephant distribution and crop-raiding spatiotemporal overlap: using an integrative approach for future conflict management

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Abstract

Conservation conflicts are one of the most challenging issues facing conservation. Elephant crop-raiding (i.e. foraging and/or damage of crops) is a facet of conflicts that impacts people and conservation efforts in most countries where elephants occur. A unifying factor in human-wildlife impacts (HWI) is overlap in wildlife and human space use leading to competition for resources. Understanding species movement and space use patterns is key to understanding and alleviating HWI that can lead into conflict. In the eastern Okavango Panhandle (Botswana), more than 16,000 people share and compete for resources with around 18,000 elephants. Using data from 20 GPS-collared elephants, we investigated elephant space-use in relation to landscape variables during the day and night throughout the year and during the dry, wet and crop-raiding seasons. We compared elephant space use and crop-raiding occurrence during the crop-raiding seasons of 2014 to 2016. We found that movement patterns were determined primarily by the availability of water, the presence of elephant corridors, and the absence of people's fields. However, predicting elephant space use at the large scale was challenging, particularly during the crop-raiding season when the relationship between crop-raiding events and elephant distribution was found not to be linear. Based on our findings, we suggest a combination of small and large-scale mitigation strategies would be the most effective approach in the eastern Panhandle. Finally, we encourage future studies to look at the interaction of the spatial distribution of elephants and raiding events to better understand local dynamics of elephant impacts and implement appropriate conservation managements in the field.

Introduction

Human-wildlife interaction has increased in the last decades as a result of expanding human settlements and a concurrent loss of natural habitats for wildlife, as well as other factors (Liu et al. 2003; Barnosky et al. 2011). Increased interactions can result in conflict, in some cases between people affected by wildlife impacts and those who defend pro-wildlife objectives (Young et al. 2010; Redpath et al. 2015a). Currently, conservation conflicts are arguably one of the most difficult challenges in conservation (Sillero et al. 2007; Dickman 2010; Redpath et al. 2013), since they are costly for species conservation and detrimental to economic development, sustainability, and the wellbeing of local people (Thirdgood et al. 2005; Redpath et al. 2015a). Numerous biological, geographic, political, economic, social, cultural, and historical factors make each conflict in conservation unique (Madden 2004; Redpath et al. 2013). However, a common factor across conflicts due to human-wildlife impacts (Young et al. 2010; Redpath et al. 2015b) is that species frequently move across human dominated landscapes, in which both people and wildlife compete for resources. Thus, understanding species movement patterns is key to the success of conservation planning aimed at reconciling the interests of wildlife conservation and those of local stakeholders (Treves et al. 2004; Douglas-Hamilton et al. 2005; Michalski et al. 2005).

Crop-raiding (i.e. the foraging or damage of crops) by elephants is a type of human-wildlife impact that causes conflict between elephant conservation and local people’s livelihoods. Elephant crop-raiding (ECR) generally takes place during the night when people are not around their crops

(Barnes et al. 2007; Jackson et al. 2008), and occurs particularly in isolated fields rather than in populated areas (Graham et al. 2010; Songhurst and Coulson 2014). Bulls have been more frequently recorded as crop-raiders (Hoare 1999; Sitati et al. 2003; Graham et al. 2010; Chiyo et al. 2012), because of their larger home ranges in comparison to females and characteristic risk-taken behaviour to optimise nutrient intake and maximise reproductive success (Smit et al. 2017; Sukumar 1991; Hoare 1999). This increases the likelihood for males to encounter people's fields, although cow-calf groups also exhibit crop-raiding behaviours (Smith and Kasiki 1999; Sitati et al. 2003; Songhurst 2012). Either way, it is extremely dangerous for farmers to defend their fields because – unlike other crop-raiding species – elephants can cause severe harm, and even death, to people (Naughton-Treves et al. 1999; Thirgood et al. 2005). After ECR occurs farmers may kill or try to kill elephants in retaliation, completing in this way a cycle of negative impacts on both people and elephants. Thus, it is not surprising that ECR contributes towards negative, local perceptions of wildlife (Woodroffe et al. 2005; Dickman 2010; Redpath et al. 2013; Songhurst 2012) and is currently one of the most important threats to elephant conservation worldwide (Barnes 1996; Hoare 1999; Lamarque et al. 2009).

The occurrence of ECR has increased over recent decades because of the expansion of agricultural land and the occurrence of larger elephant populations living outside of protected areas (Hoare 2000). This increase is reflected in the number of studies describing the distribution and drivers of crop-raiding events (see Sitati et al. 2003, 2005; Chiyo et al. 2005; Graham et al. 2010; Songhurst and Coulson 2014). However, those studies that have focused on the spatial factors determining crop-raiding incidence have not necessarily combined these insights with observed space use by elephants. On the other hand, elephant movement studies have predominantly focused on ecological questions about home range, individual trajectories and the speed of elephants in proximity to specific landscape features such as water sources, fences or protected areas (see Loarie et al. 2009; Birkett et al. 2012; Polansky et al. 2015). Few studies have used the whereabouts of elephants to better understand their spatial preferences and the specific interactions that may lead to conflict with people (Jackson et al. 2008; Graham et al. 2010). To understand the spatial interaction between people and elephants, it is necessary to combine information on elephant space use and the distribution of crop-raiding events. Thus, the use of an integrative spatial approach combining both components of the interaction may be more informative for future conservation and management (Neumann et al. 2011).

In the eastern Okavango Panhandle in northern Botswana, one of the largest unprotected populations of African elephants (*Loxodonta africana*) has increased over the last decade (DWNP 2013; Songhurst et al. 2015a). This is not surprising considering the eastern Panhandle provides water all year round, and poaching is rare in comparison with neighbouring countries (Chase et al. 2016). Here, more than 18,000 elephants (Songhurst 2016) share resources with an increasing number of people (CSO 2011; Pozo et al. 2017) throughout the dry (May to October) and wet (November to April) seasons. In this area, subsistence agriculture is the main livelihood for local communities. Farmers traditionally plough their fields in fertile soils away from the Okavango River (Songhurst and Coulson 2014), at the beginning of the wet season, and harvest them between January and April, a period known as the crop-raiding season. In order to minimise crop-raiding, a number of mitigation strategies have been implemented in recent years, such as land-use management and the identification and protection of elephant corridors (Songhurst et al. 2015b, 2016), all of which would benefit from a clearer understanding of elephant space-use (Pozo et al. 2017).

In this study, we compare elephant space use and the distribution of crop-raiding incidents during the crop-raiding seasons of 2014-2016 in the eastern Okavango Panhandle. Our goal was first to characterise elephant distribution in the eastern Panhandle across the year and during day and night time. Secondly, we use reported crop-raiding locations to identify vulnerable agricultural land and predict a risk map of crop-raiding in the study area. Finally, we combine both datasets (i.e. distribution of elephants and crop-raiding incidents) to determine spatio-temporal overlap reflecting high levels of interaction between people and elephants.

Materials and Methods

Study area

The study area is located in the eastern Okavango Panhandle in the Ngamiland District of northern Botswana. Deep Kalahari sands cover the majority of the region, with fertile soils near the Okavango River. Vegetation cover is represented mainly by mopane (*Colophospermum mopane*) woodland (*Terminalia sericea sandveld),* mixed marginal floodplain woodland (*Acacia nigrescens* and *Hyphaene petersiana*), acacia woodland (*Acacia erioloba, Acacia tortillis*) and perennial swamp woody communities (Roodt, 1998). The Delta has a typical continental climate with annual rainfall of 360 – 500 mm, mostly concentrated during the wet season (November to

April). Daily temperatures range from 25 – 35°C during the day to an average of 8°C during the night (Ramberg et al. 2006). The hottest month of the year is October, at the end of the dry season (May to October).

Botswana holds the largest population of African elephants (*Loxodonta africana*) in the world (Blanc et al. 2007; Chase et al. 2016), and the Okavango Delta Panhandle is home to a population of more than 18,000 elephants (Songhurst 2016). The 8,732 km^2 non-protected study area in the eastern Okavango is delimited by the Namibian border to the north, the Okavango River to the southwest and the northern buffalo fence on the south-eastern edge (Songhurst 2012; Fig. 1). Due to the presence of both artificial (e.g. veterinary fencing) and natural barriers (e.g. the permanent Okavango River) to elephant movement, elephant activity is concentrated within this area. More than 16,000 people live in thirteen villages along the Okavango River from Mohembo East to Gudigwa (CSO 2011; Fig. 1). The largest village is Seronga with 3,716 inhabitants, and human livelihoods consist mainly of subsistence agriculture. Local farmers cultivate fields in fertile soils from the river edge up to 14km inland. Ploughing takes place at the beginning of the wet season (November to April) and crops are harvested every year between April and June (Jackson et al. 2008; Songhurst 2012). Most ECR events take place at the end of the wet season, between January and April.

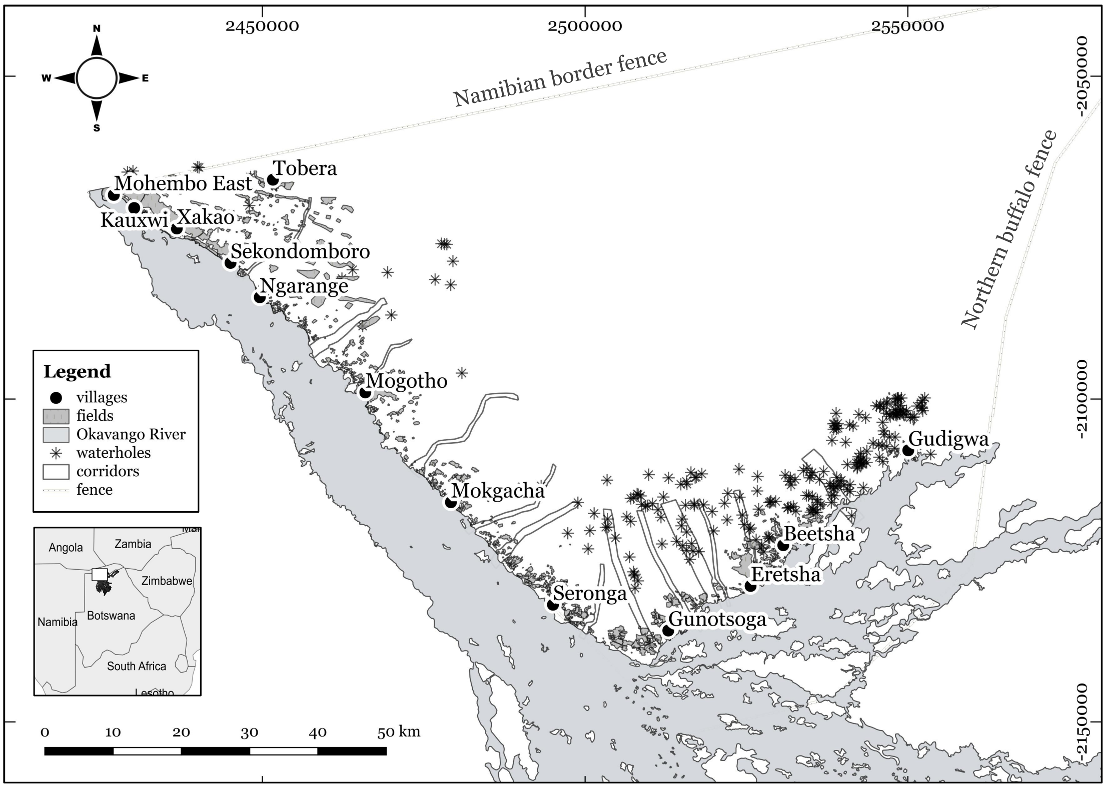


Figure 1. Study area in the eastern Okavango Delta Panhandle (Botswana). Black circles represent the thirteen villages (i.e. Mohembo East, Kauxwi, Tobera, Xakao, Sekondomboro, Ngarange, Mogotho, Mokgacha, Seronga, Gunotsoga, Eretsha, Beetsha and Gudigwa) along the Okavango River (in grey). White and grey polygons represent the thirteen elephant corridors and agricultural land respectively. Black stars show permanent waterholes. The small southern Africa inset map shows the location of the study area in northern Botswana in white.

Data collection

Elephant relocations were collected from Global Positioning Satellite (GPS) collars (Iridium Vectronic) fitted by the Ecoexist Project (www.ecoexistproject.org) on 10 females and 10 males in the eastern Okavango Panhandle in April 2014 (see Supporting Information, Table S1). Each collar was set to give hourly GPS fixes (i.e. 24 fixes per day). Individuals were selected using a spotter plane, and subsequently darted and immobilized from a helicopter. All collaring procedures were supervised by a veterinarian and performed under the research permit reference EWT 8/36/4 XVII (79) as well as affiliated immobilization permits. To reduce bias towards any specific area within the eastern Panhandle, collared individuals were selected from across the study area and from independent herds. Females were selected based on their body size (larger individuals were preferred) and on the age of their calf (older than 3 years) if any. All collared males were older than 20 years of age (Songhurst 2014). For the purpose of this study, we considered data collected between April 2014 and April 2016.

Using Quantum Geographic Information System (QGIS version 2.12.1-Lyon) and Google Earth (v 7.1.5.1557, 2016) images, we digitised layers pertaining to human land use (i.e. settlements and agricultural fields), water sources (i.e. the Okavango River and permanent waterholes) and elephant corridors. The resulting layers were ground-truthed using GPS locations taken on the ground as well as from aerial surveys and large-scale aerial photographs (1: 50,000; see Songhurst et al. 2015b). We used elephant corridors identified by the Ecoexist Project (Songhurst et al. 2015b, 2016), which were first determined from elephant footprints and spoor counts, and verified with previous maps of elephant pathways in the study area (Jackson et al. 2008; ODMP 2002).

In addition, we analysed crop-raiding data collected in the study area since 2008. Following Hoare (1999) for collection of primary data on human-elephant conflict (HEC) local enumerators were selected and trained in consultation with the village Kgosi (chief) to identify and characterise elephant crop-raiding incidents in each village (for more details see Songhurst 2012). Enumerators visited crop-raided fields following reports by farmers throughout the year. At each raided plot, enumerators took a GPS location as well as the date when the incident occurred, name of the closest village, and additional data on the scale of raiding damage. For this study, we used crop-raiding location data (i.e. presence of ECR at a particular GPS point within the study area) to match the format at which elephant collar data was collected. Equally, we used ECR data collected between April 2014 and April 2016 in order to consider the same temporal scale used for the elephant spatial data.

Data analysis

Elephant distribution

We estimated a probability utilization distribution (UD) for each of the 20 collared elephants (Jennrich and Turner 1969; Worton 1995) using a Brownian bridge movement model (BBMM, hereafter; Horne et al. 2007) applied to the corresponding trajectory. The BBMM is a continuous-time stochastic model of movement in which the probability of being in an area is conditioned on the time between consecutive locations of an individual and its estimated mobility (the motion variance, see Horne et al. 2007). It uses a sequence of time-specific location data, the estimated error associated with the location data, and a grid-cell size for the output UD (Sawyer et al. 2009) to estimate animal space use. To determine a representative grid-scale we applied BBMMs to elephant movement using grid-cells of 0.1, 0.5, 1, 2, 5, 10 and 20 km^2. Given our analyses and the fact that elephants in our study area move between 2-6 km on average per day (Loarie et al. 2009), we decided to use a grid-cell size of 5km^2 to facilitate data analysis, provide realistic large-scale movement patterns and adequate mapping resolution.

Assumptions of the BBMM are that location errors correspond to a bivariate normal distribution, and that relocations are not independent. Given that our GPS relocations are recorded every hour and that the assumption of normally distributed errors is appropriate for GPS data (Horne et al. 2007;

Sawyer et al. 2009), our dataset fulfilled both BBMM requirements. Due to satellite failure, 8.4% of all fixes were collected with more than 1-hour interval, and therefore the mean fix frequency across individuals was 1.6 hours. This was not considered a problem because, unlike fixed kernel methods, the application of BBMMs accounts for unequal time intervals between locations (Horne et al. 2007). We implemented BBMMs using functions in the R packages adehabitatHR and BBMM. Specifically, we used the function *brownian.bridge* to estimate UDs across the specified grid. The *brownian.bridge* function estimates the motion variance given an individual trajectory and a specified location error (here set to 100m). In addition, a time lag threshold can be set above which the UD between two successive relocations is not estimated. Time lags were set to 12 hours between subsequent relocations within the same year, and to 30 days between relocations within the same season across different years. In the following analyses, we consider utilisation distributions conditional on the corresponding 99% home range contours in order to avoid estimating utilisation probabilities in areas that were never used by elephants (e.g. in the western Okavango Panhandle).

We first estimated four different UDs per individual elephant, each of these representing one of four temporal periods: all study years combined, dry (May to October), wet (November to April) and crop raiding (January to April) seasons. In our study area, elephants show different movement behaviours during the day and night (Loarie et al. 2009), therefore joint UDs for all elephants (hereafter, population UD) during the day (06:00-18:00) and night (18:00-06:00) were created. The latter respectively describe the probability of finding any of the 20 collared elephants, in a given grid cell and period of time. Joint UDs were obtained by averaging relevant individual UDs and re-scaling to sum to one. We repeated the same procedure across years to obtain a single joint UD (population UD, hereafter) per season. This approach resulted in a single probability map for all individuals throughout the year, as well as during the day and night of the dry, wet and crop-raiding seasons. All UDs (i.e. 99% UD for each season) were organised on 4,270 grid-cells (i.e. excluding grid-cells not occupied by elephants), each with a specific probability of finding at least one individual from a particular category (e.g. elephants during the day on the dry season). It is important to note that our study area includes the eastern but not the western Panhandle. Thus, although we considered 4,270 grid-cells of 5km^2 each, we were consistent across analyses with the 8,732 km^2 study area because grid-cells not occupied by elephants (i.e. <1% UDs in the western Panhandle) were not represented in our results.

We performed our statistical analysis at the population and individual levels. Firstly, population UDs were used to investigate factors influencing the intensity of space use by elephants in general during a given period. To do this, we regressed the probability of cell use against the distance to five explicit landscape variables: peoples' settlements, agricultural fields, elephant corridors, permanent waterholes and the Okavango River. We used beta regressions to model elephant population UDs as a function of distances to the five landscape features. Beta regressions are an excellent tool in situations where the response variable is continuous and restricted to the unit interval (Ferrari and Cribari-Neto 2004; Cribari-Neto and Zeileis 2010), which in our case is represented by the probabilities of finding an elephant (i.e. population UD between 0 and 1) in any of the 4,270 grid-cells. Using the *betareg* function in the betareg R package, we applied a single beta regression to each population UD throughout the year and per season during the night and day, with the 99% cell utilisation probability taken as the response variable. For all seasons, Moran's I test revealed significant spatial auto-correlation (Cliff and Ord 1981; Legendre and Legendre 1998) between neighbouring UD probabilities, and as a result we included a distance-weighted autocovariate obtained using the function *autocov_dist* in the spdep R package as an additional explanatory variable in all regressions (Dorman et al. 2007; Chen et al. 2015). Secondly, we used the best possible beta regression to predict the expected distribution of the entire population of elephants (i.e. not only the 20 collared individuals) in the eastern Panhandle in each season. To do this, model selection of elephant distribution was based on the lowest Akaike's Information Criterion (AIC) (Akaike 1973), considering ΔAIC>2 as representing significantly different models (Burnham and Anderson 2002). To obtain the best possible model we used the *dredge* function in the R package MuMIn to run models with all possible combinations of explanatory variables, and the *model.avg* function to average model coefficients with ΔAIC <2. Based on the best-averaged model and using the *predict* function in R, we obtained the most likely distribution for the local elephant population in the study area.

Because of the suspected variation in space use across individual elephants, we additionally performed an analysis at the individual level. To do this, we also used beta regressions to determine the relative influence of the distance to each landscape variables on cell utilisation probability for collared females and males. To avoid bias due to spatial autocorrelation, we calculated and included a spatial autocovariate as an explanatory variable in each individual model. In both cases (population and individual analysis), we scaled continuous variables (i.e. distance to five landscape variables and autocovariates) to a mean of zero and standard deviation of one prior to model implementation so that resulting coefficient estimates could be compared.

Crop-raiding distribution

We used crop-raiding data to a) calculate a traditional fixed kernel distribution (Calenge 2015) of 50%, 20% and 10% of raiding incidents in the study area in order to identify areas more susceptible to crop-raiding; and b) to predict a risk map for the occurrence of crop-raiding incidents for the eastern Okavango Panhandle. To compare the distribution of raiding incidents with that of elephants, we organised crop-raiding data using the same 4,270 grid cells as for the elephant movement analysis. In each 5km^2 cell, we allocated a 0 (zero) when no raiding events were recorded, and a 1 (one) when elephant crop-raiding (ECR) had been reported (i.e. binomial response). We applied a traditional kernel method via the *kernelUD* function in the *adehabitatHR* package in R to produce a distribution of crop-raiding events across the study grid (Calenge 2011; Chen et al. 2015), and subset the 50%, 20% and 10% contours to identify areas that had been more affected by ECR. Subsequently, to identify areas more susceptible to raiding we used generalised linear models (GLM) with quasibinomial errors and a logit link function to regress raiding response. With the binomial crop-raiding response, Moran's I test revealed spatial auto-correlation between ECR locations, and so we added an autocovariate as explanatory variable to each model. We built our GLM with grid cells raided (1) or not (0) as a function of the same landscape features used for the elephant distribution analysis (i.e. distance to peoples' settlements, agricultural fields, elephant corridors, waterholes and the Okavango River), and corresponding autocovariate. Lastly, we used model-averaged parameters (based on models with delta AIC < 2) to predict the likelihood of crop-raids occurring throughout the eastern Okavango Panhandle.

To better understand the spatial relation between ECR events and elephant distribution, we used linear models to regress predicted ECR values against the predicted distribution of the elephant population during the crop-raiding season.

In all cases, model selection of individual elephant distributions and crop-raiding occurrence were based on the lowest AIC. We used the *dredge* and *model.avg* functions to obtain the best possible averaged models. We used R (ver. 0.13.17) for all analyses.

Results

Elephant distribution

The data collected from the 20 collared individuals in our study showed that, overall, elephant space use is primarily determined by distance to water sources and to people's fields (Fig. 2, Table 1 and 2). Moreover, there was considerable variation between individual movement patterns (Fig. 3). Our most general model (i.e. included all seasons at all times) showed that longer distances to elephant corridors, waterholes and to the Okavango River had a negative effect on the distribution of elephants (Table 1 and 2), and that elephants in general stayed away from people's fields throughout the year.

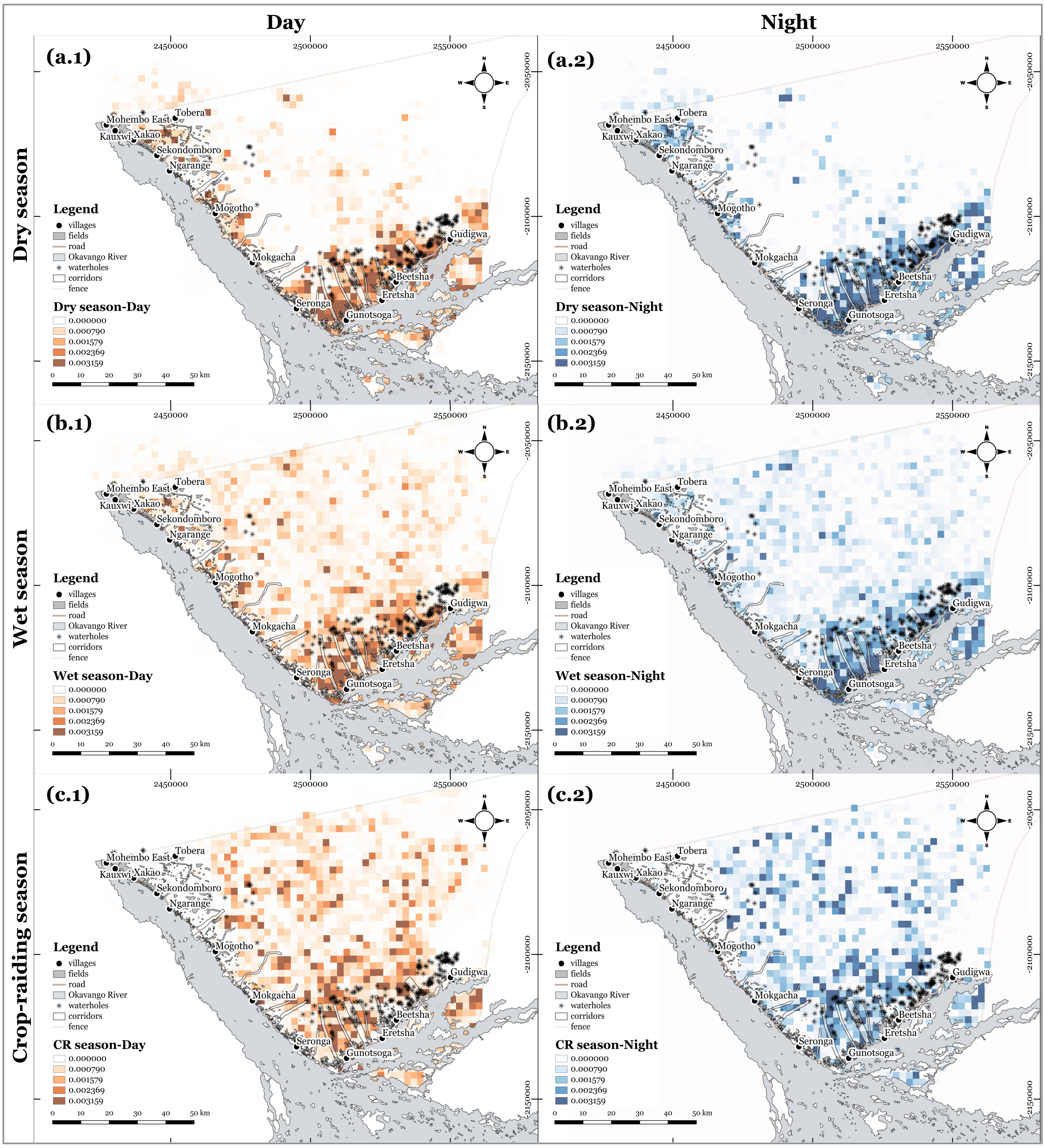


Figure 2. Utilisation distribution (UD) maps of the elephant population in the eastern Okavango Delta Panhandle. First, second and third rows represent population UDs during the dry (May-October), wet (November-April) and crop-raiding (January-April) seasons at day (06:00-18:00; orange) and night (18:00-06:00; blue) times, respectively.

Table 1. Summary of elephant distribution regression selection with Akaike's Information Criterion (AIC). AIC values used to evaluate relationships between elephant population utilisation distribution and distance to five landscape variables: the Okavango River (Rv), permanent waterholes (Wh), elephant corridors (Cr), agricultural fields (Fl) and people settlements (i.e. villages; Vill); as well as each regression distance-weighted autocovariate (autocov). The model, time period and explanatory variables columns indicate specific combination of variables included in each function throughout the year (all seasons) and during the dry, wet and crop-raiding seasons. In addition, each season (i.e. dry, wet and crop-raiding) contains specific models for GPS fixes collected during the day (6:00-18:00) and night (18:00-6:00) times. AIC and delta AIC (Δ AIC) columns show the specific AIC rank per model and the difference between each model and the best model selected for our analysis. The weight column represents the relative likelihood of each model.

Model	Period	Explanatory variables						AIC	Δ AIC	Weight
		Rv	Wh	Cr	Fl	Vill	autocov			
all seasons	all times	-0.1244	-0.1732	-0.0939	0.2930		0.4309	-19660.0	0.00	0.553
		-0.1230	-0.1733	-0.0942	0.2433	-0.0050	0.4308	-19658.0	2.00	0.204
dry season	day	-0.1388					0.2490	-5748.4	0.00	0.190
		-0.1333	-0.0397				0.2401	-5747.5	0.90	0.121
		-0.1299		-0.0295			0.2418	-5747.0	1.46	0.091
		-0.1911	-0.0905			0.0944	0.2401	-5746.9	1.53	0.088
		-0.1328			-0.0116		0.2472	-5746.5	1.93	0.072
		-0.1646	-0.0890		0.0727		0.2398	-5746.5	1.96	0.071
	night	-0.0562					0.3406	-6184.3	0.00	0.092
		-0.0532	-0.0426				0.3314	-6183.9	0.45	0.074
						-0.0485	0.3414	-6183.7	0.67	0.066
							0.3533	-6183.6	0.72	0.065
			-0.0480				0.3420	-6183.6	0.74	0.064
				-0.0432			0.3417	-6183.2	1.11	0.053
					-0.0419		0.3438	-6183.2	1.17	0.051
		-0.0480		-0.0284			0.3350	-6183.0	1.37	0.047
		-0.0774	-0.0812		0.0557		0.3293	-6182.6	1.72	0.039
		-0.0472			-0.0189		0.3385	-6182.6	1.76	0.038
		-0.0429				-0.0208	0.3386	-6182.6	1.78	0.038
		-0.0826	-0.0694			0.0482	0.3303	-6182.4	1.95	0.035
wet season	day	-0.1680	-0.1361		0.1734		0.2833	-12956.7	0.00	0.252
		-0.2017	-0.1084			0.1791	0.2858	-12955.5	1.11	0.145
		-0.1656	-0.1279	-0.0157	0.1774		0.2825	-12954.7	1.93	0.096
		-0.1485	-0.1353		0.1485	0.0334	0.2837	-12954.7	1.96	0.950
	night	-0.0839		-0.1618	0.1525		0.3139	-13156.6	0.00	0.171
		-0.1001	-0.0713	-0.1303	0.1983		0.3094	-13156.2	0.36	0.143
				-0.1714	0.2660	-0.1819	0.3136	-13156.0	0.59	0.128
			-0.0602	-0.1462	0.3180	-0.2067	0.3099	-13155.2	1.37	0.086
				-0.1645	0.0849		0.3206	-13155.0	1.63	0.076
		-0.0588		-0.1659	0.2183	-0.0866	0.3126	-13155.0	1.63	0.076
		-0.0738	-0.0724	-0.1344	0.2692	-0.0923	0.3079	-13154.7	1.94	0.065
crop-raiding season	day		-0.2335		0.3980	-0.2451	0.1717	-9513.2	0.00	0.217
			-0.2181		0.1443		0.1755	-9512.7	0.56	0.163
		-0.0668	-0.2277		0.2141		0.1747	-9511.7	1.57	0.099
		0.0453	-0.2321		0.4353	-0.3268	0.1709	-9511.4	1.82	0.087
	night		-0.1819		0.4033	-0.2848	0.1479	-9369.4	0.00	0.204
			-0.1595		0.1052		0.1534	-9367.9	1.52	0.095
		0.0553	-0.1809		0.4434	-0.3788	0.1469	-9367.7	1.76	0.085
			-0.1912	0.0181	0.4007	-0.2902	0.1484	-9367.5	1.95	0.077

Table 2. Summary of model-averaged elephant population distribution regressions. Best regressions and coefficients estimated from models for all seasons, and during the dry, wet and crop-raiding seasons. The period column shows models including data collected 24 hours a day, during the day (6:00-18:00) and night (18:00-6:00) only. Each of the regressions shows the relationship between elephant population utilisation distribution as a function of the effect of distance to five landscape variables: the Okavango Rover (Rv), permanent waterholes (Wh), elephant corridors (Cr), agricultural fields (Fl) and people settlements (i.e. villages; Vill); as well as its respective distance-weighted autocovariate (autocov).

Model	Period	Estimates effect					
		Rv	Wh	Cr	Fl	Vill	autocov
all seasons	all times	(-)**	(-)***	(-)*	(+)***	(-)	(+)***
dry season	day	(-)**	(-)	(-)	(+)	(+)	(+)***
	night	(-)	(-)	(-)	(-)	(-)	(+)***
wet season	day	(-)**	(-)*	(-)	(+)	(+)	(+)***
	night	(-)	(-)	(-)**	(+)	(-)	(+)***
crop-raiding season	day	(-)	(-)**	(+)	(+)	(-)	(+)***
	night	(+)	(-)**	(+)	(+)	(-)	(+)***

( ) *p-value > 0.05;* (*) *p-value* < 0.01; (**) *p-value* < 0.001; (***) *p-value* < 0.0001

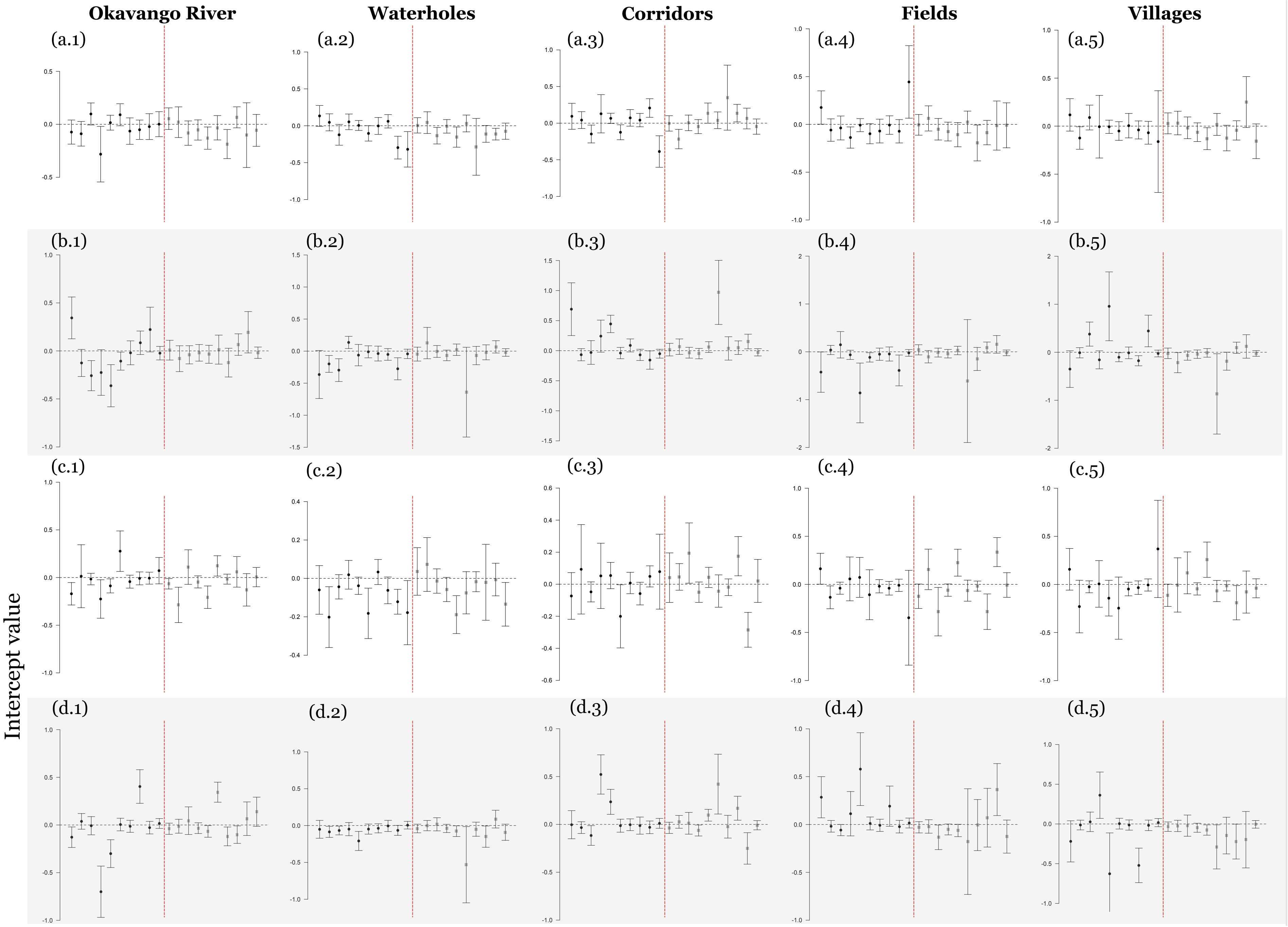
However, these results represent an overview of the population movement in our study area and they do not give specific information about the whereabouts of elephants at a given point in time. In addition, our general model explained little of the variance associated with elephant distribution and therefore we also investigated each season separately.

With the exception of the crop-raiding season at night-time, all models showed a negative effect of distance to the river on elephant space use, a tendency that was also found for distance to waterholes and corridors (Table 2). In other words, elephants were more likely to be found closer to these three landscape features. For most season models, the distance to agricultural fields had a positive effect on the occurrence of the species. Thus, elephants throughout the year generally stayed away from people's fields (Fig. 2, Tables 1 and 2). The dry season analysis showed that elephants spent time in areas close to the river mainly during the day, (Fig. 2, Table 2). During the driest months of the year (May to October) elephants also spent more time along corridors at night-time and close to waterholes during the day (Fig. 2, Table 2). During the dry season our BBMM distributions showed elephant movement between highly used sites was more likely to be 'inter-connected' via pathways than during any other time throughout the year (Fig. 2).

During the wet season (November to April), the BBMM analysis showed that collared elephants dispersed more across the Eastern Panhandle than during the dry season (Fig. 2). Our beta regression analysis revealed elephants significantly prioritised areas close to the Okavango River and waterholes during the day and to corridors during the night (Fig. 2, Table 2). Lastly, during the crop-raiding season (January-April), elephants spent most of their time around waterholes (Fig. 2, Table 2). In addition, during crop-raiding months our spatial analysis suggested collared individuals stayed away from fields (Fig. 2, Table 1). However, we did not find significant differences for this in our best averaged-models (Table 2).

The individual analysis revealed significant variation between the space use patterns of elephants, and non-significant differences between, females and males movement patterns (Fig. 3). Across the dry season, elephant movement was clearer at night-time than during the day (Fig. 3, a and b). During the night, both males and females showed similar movement patterns in relation to water sources and corridors, although females seemed to stay closer to the river (Fig. 3, b.1). In general, elephants stayed near the river, waterholes and corridors during the dry months, however at night-time their behaviour appeared to change and some individuals were more likely to move away from corridors (Fig. 3, b.3). Similarly, individual movement behaviour seemed to differ more at night than during the day in relation to fields and villages. In particular, some individuals (e.g. male E11) showed a completely different space distribution than the rest of the sampled population during the night (Fig 3, b.4 and 5).

Individual movement patterns during the wet months were more scattered throughout the day than at night (Fig. 3, c and d). During the day, we did not find any specific trend across individuals in any of the landscape variables we assessed, with the exception of distance to the Okavango River and waterholes that females and males preferred to stay close to (Fig. 3, c.1 and 2). On the other hand, during the night, elephants showed much clearer patterns in their individual movement behaviour. For instance, female E10 stayed away from fields and closer to villages during the night (Fig. 3, d.4 and 5); and males E11, 13, 14 and 18 showed a wider variance within their movement estimates for the same landscape variables (i.e. fields and villages) in comparison to the rest of the population (Fig. 3, d.4 and 5). Considering that the crop-raiding season (January-April) is a sub-sample of the wet season (November-April), it is not surprising that this period also showed the distribution of individual estimates to vary greatly (Fig. 3, e and f). We also found clearer patterns during the night-time, at which elephant movement showed preferences for areas near waterholes and outside of fields (Fig. 3, f.2 and 4). It is important to highlight that we did not find any significant trends for closeness to agricultural fields during the crop-raiding season. Yet, a few elephants - most of them males - increased the variance around their movement estimates mainly during the night (Fig. 3, f.4).


Okavango River
Waterholes
Corridors
Fields
Villages
Intercept value
(a.1)
0.5
0.0
-0.5
(a.2)
1.0
0.5
0.0
-0.5
-1.0
(a.3)
1.0
0.5
0.0
-0.5
-1.0
(a.4)
1.0
0.5
0.0
-0.5
-1.0
(a.5)
1.0
0.5
0.0
-0.5
-1.0
(b.1)
1.0
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-1.5
(b.4)
2
1
0
-1
-2
(b.5)
2
1
0
-1
-2
(c.1)
1.0
0.5
0.0
-0.5
-1.0
(c.2)
0.4
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0.0
-0.2
-0.4
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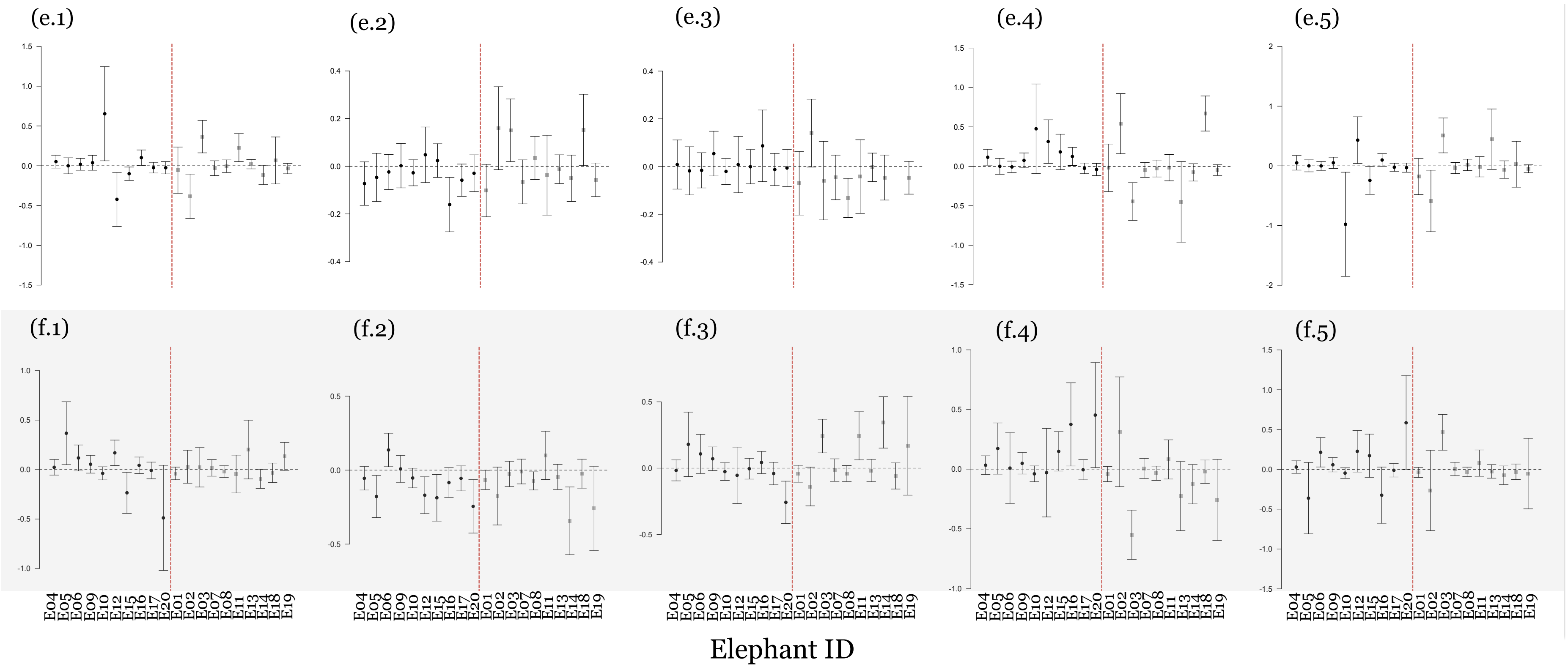

Figure 3. Individual elephant movement intercepts and standard deviations during the dry (a & b), wet (c & d) and crop-raiding (e & f) seasons at day (06:00-18:00; in white) and night (18:00-06:00; in grey) times. Each graph represents one of the five landscape variables included in our analysis (i.e. the Okavango River, permanent waterholes [Waterholes], elephant corridors [Corridors], agricultural fields [Fields] and people settlements [Villages]). Black circles and grey squares represent female and male intercepts, respectively.

Crop-raiding distribution

The susceptibility analysis to identify areas more vulnerable to crop-raiding showed that more than 50% of crop-raiding events are likely to take place in the north-west and southern part of our study area (Fig. 4a). Our risk-map predicted that agricultural land near to Tobera and Mohembo East, as well as fields between Gunotsoga and Beetsha represented areas of high risk of ECR (Fig.4a). The averaged GLM showed that areas close to fields were more likely to be crop-raided (-19.467 ± 3.97, $p < 0.0001$; Fig. 4a). However, we know that in our study area, raiding incidents take place in agricultural land, and therefore we removed 'distance to fields' as a variable from our GLM to better understand the relative contribution of the other explanatory variables. This new binomial GLM showed crop-raiding incidents were expected in agricultural land located close to villages (-3.949 ± 0.91, $p < 0.0001$), waterholes (-1.417 ± 0.66, $p < 0.01$) and corridors (-0.923 ± 0.47, $p < 0.01$).

Finally, our spatial regression showed a positive correlation between predicted crop-raiding events and predicted elephant distribution during the day (4.15 ± 5.2; $p < 0.1$; Fig.4b) and night (12.16 ± 5.6; $p < 0.01$; Fig.4c). Nevertheless, the model fit was very poor ($R^2 = 0.0048$; $DF = 4267$; $p < 0.0001$), and so we fitted a local polynomial regression using the *loess* function in R, which revealed that the predicted probability of ECR was highest at an intermediate level of predicted elephant distribution, i.e. 0.001-0.002 at night time (Fig. 5). This suggests that elephant distribution is associated with crop-raiding incidence in a non-linear way. More specifically, we highlight an intermediate to low levels of space use by elephants at which most crop-raiding incidents occur.

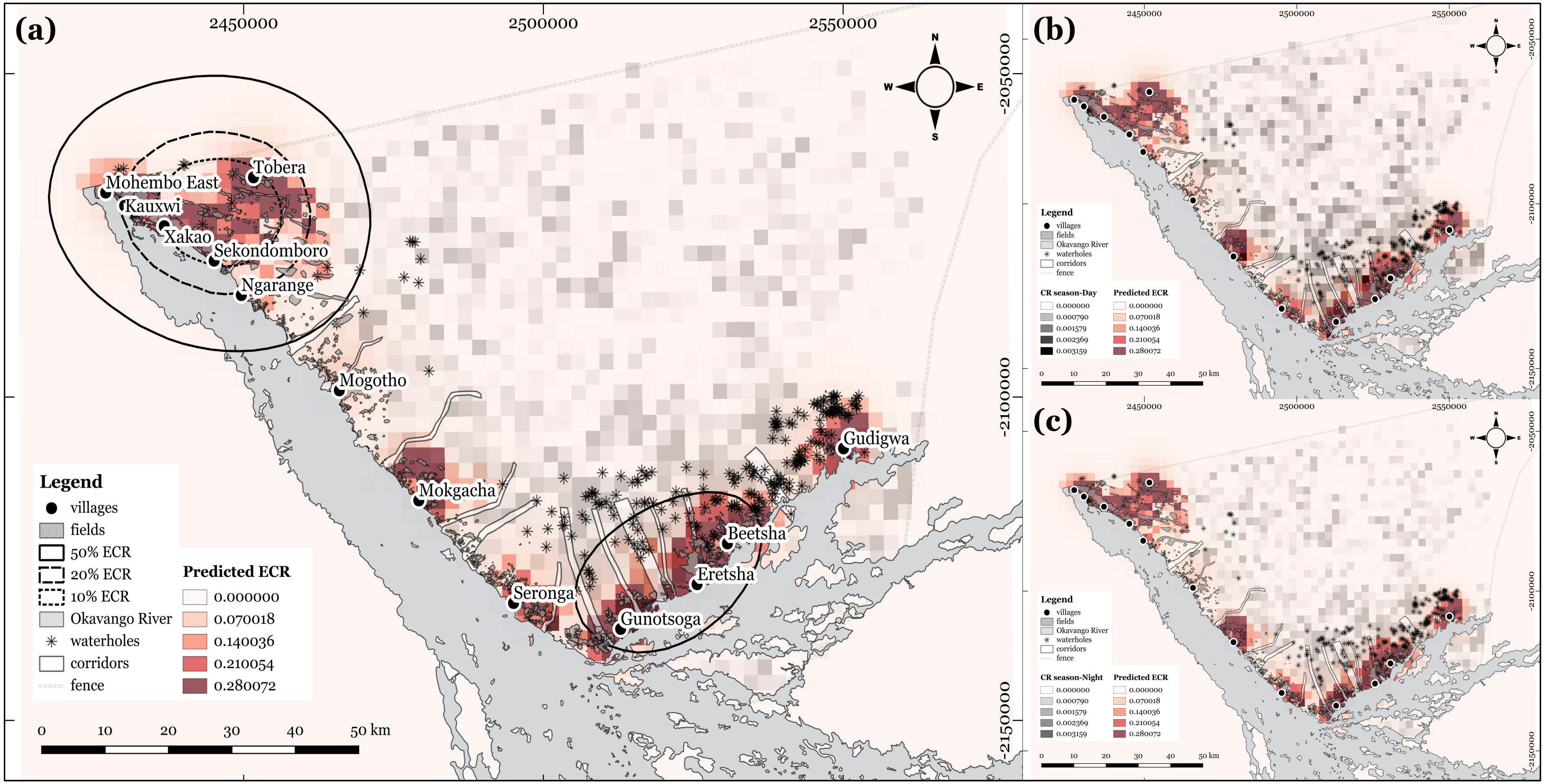

Figure 4. Crop-raiding risk map for the eastern Okavango Delta Panhandle. a) circled areas show 50% (continuous black line), 20% (dashed black line) and 10% (dotted black line) likelihood of crop-raiding events in the study area based on traditional fixed kernel analysis. Risk-map (heat map in red; a) shows predicted elephant raiding event distribution during the crop-raiding season (January-April), and it spatial overlap with the five landscape variables (i.e. the Okavango River, permanent waterholes, elephant corridors, agricultural fields and villages). Small maps (b & c) represent the overlap between predicted crop-raiding events and predicted elephant distribution during the day (06:00-18:00; b) and night (18:00-06:00; c) times.

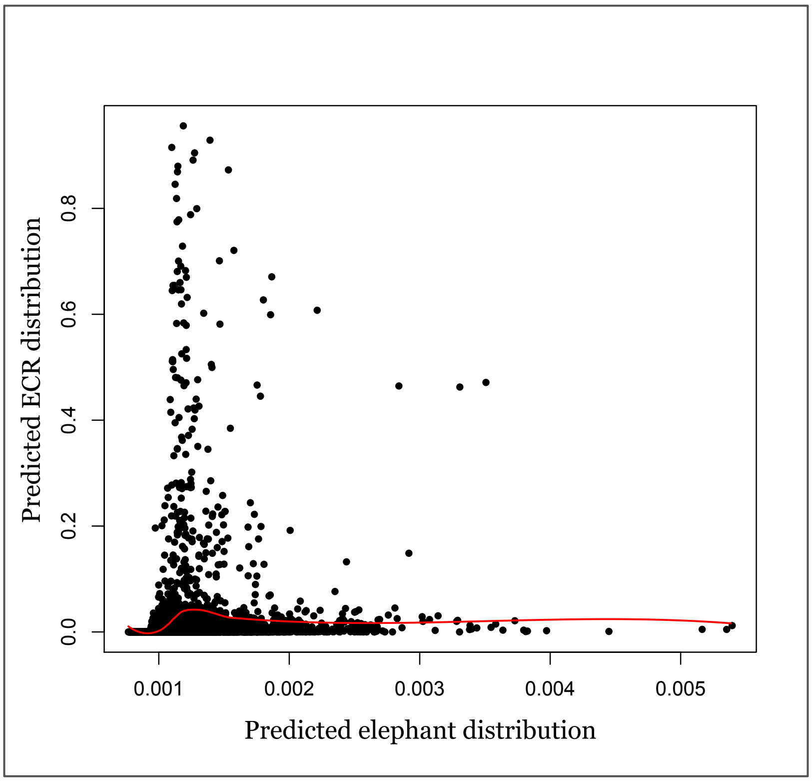

Figure 5. Polynomial regression of predicted crop-raiding events as a function of predicted elephant distribution. Red line represents the best-fitted model.

Discussion

Our study shows that elephant distribution in the Okavango Panhandle is challenging to predict at the population level because of the high variation of individual movement patterns. Although the variance explained in movement patterns was primarily related to the availability of water sources, the presence of elephant corridors, and the absence of people's fields, our analysis explained comparatively little variance in elephant space use. Nonetheless, our findings are in agreement with previous research showing that elephant movement is influenced by water availability (Jackson et al. 2008; Loarie et al. 2009; Polansky et al. 2015) and corridor usage as a risk avoidance strategy in proximity to people's settlements (Hoare and du Toit 1999; Douglas-

Hamilton 2005; Graham et al. 2009; Songhurst et al. 2015b). During the crop-raiding season, collared individuals in the eastern Panhandle stayed away from people's fields. To this end, we developed a crop-raiding risk map to better understand the relative likelihood of raiding incidents and its relation to landscape variables in the study area, and we compared this with elephant space use measured over the same time period. We found elephant space use to be correlated with the likelihood of crop-raiding events through the harvesting season, but in a non-linear way.

Although our models explained a small amount of variation, they suggest that throughout the year elephant distribution is primarily determined by areas close to sources of water (i.e. the Okavango River and waterholes). We expected elephants to be close to the river during the dry season when there is little or no water available in waterholes, but not during the wet season when there is more vegetation and water sources available away from the Okavango River, and therefore also away from people's settlements (i.e. fields and villages along the river). Nevertheless, our study agrees with previous works suggesting elephants rely on the Okavango River and waterholes throughout the year (Douglas-Hamilton et al. 2005; Songhurst et al. 2015b). Our study highlights that elephants are equally expected to use areas nearby waterholes during both the dry and wet seasons. This is likely the combination of two potential explanations; first, waterholes are certainly more frequent and abundant during the wet season, and therefore we expected elephants to stay for longer periods of time nearby waterholes during the wet season in comparison with the dry season when waterholes, if present, are scarce. Additionally, the wet season also includes the crop-raiding period, time during which waterholes were preferred in relation to the Okavango River. Consequently, we foresee elephants will stay for longer periods in areas around waterholes and they will use corridors to travel between these and the Okavango River (Douglas-Hamilton et al. 2005; Songhurst et al. 2015b), probably aided by their highly developed spatial memory (Polansky et al. 2015; Loarie et al. 2009). However, because of the high variation across collared individuals it is certainly difficult to predict areas use by elephants with precision. Consequently, future conservation actions, including land use planning, should ideally aim to secure as much of the elephant home range as possible in areas that maintain connectivity between waterholes and the Okavango River (Goswami and Vasudev 2017).

Another important difference between both seasons was the movement patterns between intensively used sites. The elephant spatial distribution during the dry season appeared to show clearer "routes" connecting areas most occupied by elephants than during the wet season. This may arise from pre-existing knowledge of reliable water and foraging sources during the driest months of the year (Polansky et al. 2015). Moreover, owing to a drop in temperature after the dry season, elephants may be able to cover greater distances during the day and not only move during the coolest hours of the night as they usually do during the driest months (Wittemyer et al. 2008; Loarie et al. 2009). These contrasting patterns of elephant space use between the dry and wet seasons respectively are consistent with previous data collected in the eastern Panhandle and elsewhere across Africa (Jackson et al. 2008; Loarie et al. 2009; Birkett et al. 2012).

We found marginally different patterns of elephant space use during the night than during daylight hours, which could be a consequence of elephants moving at times of lower temperatures in the dry season. However, because this pattern was present throughout the year, we argue this behaviour may also be the result of elephants prioritising use of areas at times of low human activity (Douglas-Hamilton et al. 2005; Hoare and Du Toit 1999; Graham et al. 2009; Songhurst et al. 2015b). Such a risk-avoidance strategy, whereby elephants use the cover of darkness, has been demonstrated previously. For instance, Graham et al. (2009) showed elephants in Tanzania and Kenya were more active at night outside of protected areas (Galanti et al. 2006; Wittemyer et al. 2008). However, unlike Graham et al. (2009), our study area is not protected, and therefore, it is interesting to find free-range elephants potentially using similar strategies to avoid people as elephants residing in protected areas. Yet, differences between day and night patterns should be taken with caution because of the marginal difference between the two.

During the crop-raiding season elephants tended to stay away from people's fields and not use corridors as much by focusing their activity around waterholes rather than the Okavango River. In our study area, elephants usually have to cross peoples' fields - or areas near fields - in order to gain access to the river. Thus, this finding is surprising since during the crop-raiding season we expected elephants to stay closer to people's crops. A possible explanation for this finding might be that none of the 20 collared elephants are crop-raiding individuals (although see male E03 closeness to fields during the crop-raiding season in Fig. 3), and therefore they stayed in remote areas near waterholes in order to avoid people guarding their crops inland. Alternatively, natural resources available during the crop-raiding season – which overlaps with the wet season – can be nutritionally as attractive as crops for elephants, but less risky and so they are more likely to forage in areas away from people's fields. For all seasons, considering elephants in the eastern Panhandle move more randomly than we expected (i.e. there is great variation across individual distributions), that we did not account for additional environmental variables such as vegetation types and rainfall, and that our study included the movement behaviour of 20 individuals out of more than 18,000 in the region, our findings should be taken as a starting point for longer-term studies of elephant movement and interaction with local people at the large-scale in our study site.

In addition, the relationship between the distribution of crop-raiding events and elephant space use suggested a more complex process. Indeed, crop-raiding was more likely to occur within an intermediate range of elephant space use intensity. This may mean that ECR usually occurs in areas that large elephant herds use for shorter periods of time, or either areas that are visited by relatively small groups of elephants in the eastern Panhandle. Crop-raiding and the relationship between the relative interaction of elephant and human populations coexisting in Africa is known to be spatial rather than numeric (Hoare 1999; Hoare and du Toit 1999), and in our case study this spatial relation proved not to be linear. This non-linear relationship could represent a possible explanation to the general 'failure in predicting elephant crop-raiding patterns' found by previous studies (Hoare 1999; Sitati et al. 2003). Our findings suggest that concentrations of elephants are not associated with a higher likelihood of ECR (Hoare and du Toit 1999), and that raiding incidents are more likely to happen in areas that elephants use for shorter periods of time. Nevertheless, because of the large scale of our study, we suggest that - when data and resources are available - more individuals should be included in future analyses in order to have a more representative sample of the elephant population and its movement patterns in the eastern Panhandle. Similarly, the non-linearity between both spatial components (ECR and elephant distribution) should be considered to better incorporate unpredictable elephant behaviour and/or space use uncertainty in management plans at such large-scale. For instance, this could be done by focusing on vulnerable agricultural areas where relatively small elephant group transit.

Despite finding that certain landscape covariates determined elephant movement patterns better than others, predicting elephant space use remained challenging, particularly during the crop-raiding season (Pittiglio et al. 2013; Sitati et al. 2003) when multi-dimensional variables influence species distribution at the population and individual levels. In general, there is considerable variation in individual elephant behaviour, especially in terms of crop-raiding patterns (Hoare 1999; Sitati et al. 2003; Graham et al. 2010; Chiyo et al. 2012). To effectively manage elephant crop-raiding and inform appropriate land use planning interventions, it is therefore important to focus on deterring elephants from people's crops at the local scale alongside understanding elephant movements at a landscape level. Throughout the two year period of this study, 50% of crop-raiding incidents were reported in two sites within the study area. One was in the northern distribution of the eastern Panhandle within Mohembo East, Sekondomboro and Tobera; and the other was clustered in the south in fields between Gunotsoga and Beetsha. Unsurprisingly, agricultural land in these two hotspots was close to low populated villages, to large elephant corridors, and/or away from the Okavango River. Previous studies have found similar indications for vulnerable cropland to elephant crop-raiding (Newmark et al. 1994; Pittiglio et al. 2014; Songhurst and Coulson 2014; Songhurst et al. 2015b). Elephants often utilise traditional routes to return to areas where they remember having successfully raided in the past (Sitati et al. 2005). While we suggest both ECR hotspots should be a priority in long-term land management plans, they face different challenges and should be treated differently in future conflict management. The two sites have a similar human population size; nevertheless our elephant distribution and crop-raiding heat maps suggest the northern hotspot of Mohembo East, Sekondomboro and Tobera has reached a point at which elephants are partially excluded from cropland at the end of the crop-raiding season (Hoare and du Toit 1999; Smith and Kasiki 1999; Graham et al. 2010). On the other hand, the southern hotspot of Gunotsoga and Beetsha is located in an area of very high use by elephants throughout the year and thus herds will probably try harder to move from waterholes across fields to the river looking for vegetation or moving to more remote and safer areas connected with the Okavango River such as Moremi Game Reserve or Chobe National Park. The higher pressure of elephant movement in the southern hotspot could potentially increase the risk of elephant crop-damage at the local level (Webber et al. 2011; Chen et al. 2015). In these areas in particular, the use of local mitigation strategies such as unpalatable crops and elephant deterrents represent important measures to alleviate crop-damage by elephants.

Our findings suggest that an integrative approach looking not only at elephant movement patterns, but also its interaction with the spatial distribution of crop-raiding events is key to better prevent and tackle ECR impacts in areas of conflict. In the specific case of our study area, we suggest that a combination of regional and local mitigation strategies is the most long-lasting approach to sustainable conservation management. More specifically, we believe focusing in areas of intermediate to low elephant distribution near to agricultural land, as well as the protection and enlargement of elephant corridors (Songhurst et al. 2015b) that connect waterholes with the Okavango River are as important as local mitigation methods to maintain natural resource connectivity for elephants and to keep people's fields safer from raids.

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Supporting Information

Table S1. Summary of the 20 collared elephants in the Easter Okavango Delta Panhandle. Each column gives specific information about individuals ID, sex, number of relocations received between April 2014 and April 2016, and the mean number of relocations per elephant per hour, respectively.

ID	Sex	No. relocations	Mean time between relocations (hours)
E01	male	16839	1.05
E02	male	11814	1.5
E03	male	16193	1.09
E04	female	17133	1.04
E05	female	9848	1.8
E06	female	14239	1.24
E07	male	16951	1.05
E08	male	11783	1.51
E09	female	16831	1.05
E10	female	8668	2.05
E11	male	5150	3.43
E12	female	8484	2.09
E13	male	11444	1.55
E14	male	11135	1.59
E15	female	16606	1.07
E16	female	16210	1.09
E17	female	5924	2.99
E18	male	16724	1.06
E19	male	11426	1.55
E20	female	5878	3.01

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Chapter 4

Chilli-briquettes modify elephant temporal behaviour but not numbers

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- Running head -

Effectiveness of chilli-briquettes

- Tittle -

Chilli-briquettes modify elephant temporal behaviour but not numbers

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Abstract

Crop loss due to foraging elephants represents one of the most important human-elephant impacts (HEI) in areas where wild elephants interact with people. Effective solutions to reducing HEI on local livelihoods are thus essential to fostering co-existence between elephants and people. In this study, we assess the effectiveness of chilli-briquettes in altering elephant space-use in the eastern Okavango Panhandle, Botswana. We burned >600 briquettes during the night over a two month period to test five treatments: frequent burning of (1) chilli and (2) chilli-free briquettes, occasional burning of (3) chilli and (4) chilli-free briquettes and (5) control. Using camera-traps and footprints surveys, we assessed the number and times at which elephants used experimental sites. We found elephants changed their movement behaviour from pronominally nocturnal towards the daytime in areas where chilli-briquettes were burned throughout the night, however there was no difference in the mean numbers of individuals between treatments with and without chillies. In other words, chilli-briquettes had a repellent but no deterrent effect on elephants, keeping them away exclusively at times when chilli-briquettes were smouldering. Based on these findings, we recommend the use of chilli-briquettes as a method to deter elephants in the short-term. In the long-term, chilli-briquettes should be applied in combination with other larger-scale mitigation approaches such as land management and cooperative community-based tools.

Introduction

Elephant crop-foraging (i.e. damage/destruction of crops) is one of the most widespread form of human-elephant impacts (HEI; see Young et al. 2010) across Africa (O'Connell-Rodwell et al. 2000; Lamarque et al. 2009), and is often perceived as a threat to the livelihoods and wellbeing of local people. The physical (e.g. destruction of people's crops and properties), social (e.g. children missing school because guarding fields during the night), economic (e.g. food insecurity) and health (e.g. increased risk of contracting malaria) implications for people living with elephants (Thirgood et al. 2005; Barua et al. 2013) endangers both human and elephant lives (Hoare and du Toit 1999) generating negative attitudes towards elephants often undermining efforts to conserve the species (Nyhus and Tilson 2000; Osborn and Parker 2003). A key strategy to decrease HEI involves developing and testing mitigation strategies to prevent elephant crop-foraging (Naughton and Treves 1999; Hoare 2000). However, few published studies assess the performance of elephant deterrents (but see Davies et al. 2011; Graham and Ochieng 2008; Sitati and Walpole 2006). Here, we test the effectiveness of one of the most popular forms of elephant deterrent in Southern Africa and in our study area: the burning of chilli-briquettes.

Elephant deterrents include the use of traditional methods (noise, fire), spotlights, electric and beehive fences, and chilli-pepper based methods (fences, bombs and briquettes). Since the 1990s the use of chilli-peppers (*Capsicum spp.*) has expanded across Africa and Asia (Hedges and Gunaryadi 2009; Osborn and Rasmussen 1995), representing a promising elephant crop-foraging mitigation option. Chillies have low palatability for wildlife (Parker and Osborn 2006), can be applied at low cost, and have the added advantage of producing extra income from the sale of chillies that ultimately contributes towards improving local peoples' livelihood (Kadizoro and Osborn 2015). The most common forms of chilli-based deterrents are fences (i.e. poles connected with ropes and pieces of cloth greased with chillies) and briquettes (i.e. bricks made of dry chilli, elephant dung and water) (Hoare 2012). Although farmers report a preference for chilli fences (Davies et al. 2011; Noga et al. 2015), this method often fails because people are unwilling or financially unable to maintain the fences (Graham and Ochieng 2008). In contrast, chilli-briquettes represent an affordable option for many subsistence farmers.

Chilli-methods reported success varies from one study to the next, with some reporting 100% success (Karidozo and Osborn 2015; Sitati and Walpole 2006) and others observing an absence of deterrent effect despite added expenses and labour (Hedges and Gunaryadi 2009). This inconsistency may be due to methodological and analytical factors. Firstly, chilli-methods are often tested in combination with other elephant deterrents (Davis et al. 2011; Graham and Ochieng 2008; Osborn and Parker 2002), thus rendering the effect of each unclear. Secondly, criteria used to evaluate the effectiveness of deterrents vary considerably across studies, with some basing success on the number of crop-foraging events (Graham and Ochieng 2008; Sitati and Walpole 2006), the area of crops destroyed (Graham and Ochieng 2008; Karidozo and Osborn 2015), the time lag of elephant reaction to the effect of chillies (Osborn and Parker 2002), and local farmer's perception of effectiveness (Graham and Ochieng 2008; Noga et al. 2015).

Botswana has the largest population of African elephants (*Loxodonta africana*) on the planet (Chase et al. 2016), with northern Botswana holding the highest proportion of it in the country (DWNP 2013). Elephant numbers have increased in the last decades (Songurst et al. 2015a), specifically in areas with permanent sources of water, such as the eastern Okavango. In this region, levels of poverty are high (CSO 2011; Noga et al. 2015) and subsistence agriculture is the main people's livelihood (Songhurst and Coulson 2014). As in other African countries, NGOs in collaboration with the government of Botswana have included the use of chilli-methods in their management plans. In particular, in the eastern Panhandle, chillies have been the only elephant deterrent recommended in the region. Although, local people in northern Botswana tend to have a favourable perception of chillies as elephant deterrent (Noga et al. 2015), the effectiveness of this method has not been tested, despite it being recommended. Evaluation of crop-foraging deterrents is important to avoid irreversible consequences of poorly planned conservation management (Webber et al. 2007).

In this study, we implement the first controlled and replicated experimental trial in the region to test the use of chilli-briquettes as an elephant deterrent. To do this, we applied five treatments with and without chillies in the eastern Panhandle, during the dry season of 2015. Our experiment has the potential to be widely applied in areas where elephants forage on crops. Such an assessment will enable the development of novel ways of altering elephant pressure on crops, and provides a replicable model for testing effectiveness elsewhere.

Materials and Methods

Study area

Our study was conducted between the villages of Seronga (E22.4132129; S18.803812) and Beetsha (E22.7337546; S18.725417) in the eastern Panhandle, northern Botswana (Fig. 1).

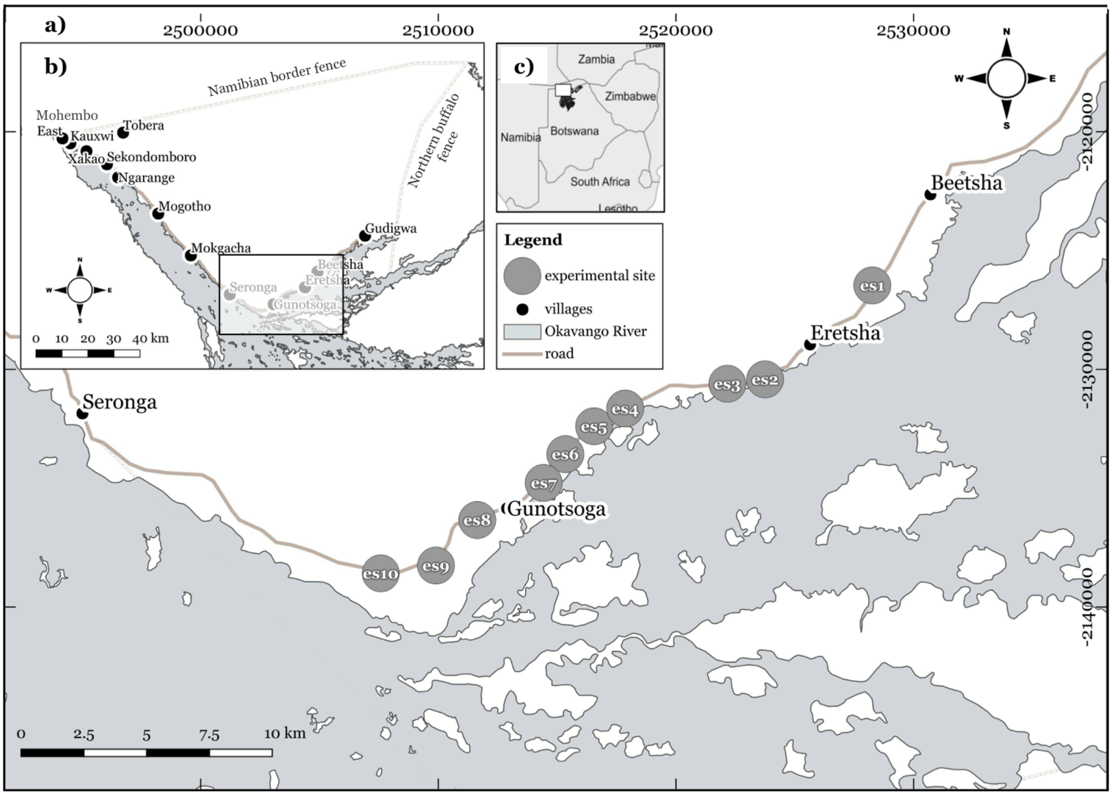

Figure 1. Study area in the eastern Panhandle (Botswana). a) experimental sites' map. Grey circles represent experimental sites (es) between the villages of Seronga and Beetsha. b) eastern Panhandle map. Black circles represent the thirteen villages along the Okavango River. White rectangle represents experimental sites' location. c) Southern Africa map. White rectangle shows the location of the eastern Panhandle.

The area is delimited by the Botswana-Namibian border fence to the north, the Okavango River to the southwest and the northern buffalo fence to the south and east (Fig. 1). The Okavango Delta is formed from the Okavango River that flows from Angola, along the Caprivi Strip in Namibia, and reaches a tectonic trough in the centre of the Kalahari in Botswana. The Delta has a continental climate with a wet (November to April), and dry (May to October) seasons. Daily temperatures range from 25-35°C during the day to an average of 8°C during the night (Ramberg et al. 2006). The hottest month of the year is October with temperatures over 48°C; annual rainfall ranges between 360 – 500mm during the wet season.

The eastern Panhandle has one of the highest populations of elephants in the country, with more than 18,000 individuals (Songhurst 2016) that remain closer to the river during the driest months (Jackson et al. 2008). Approximately 16,000 people live in the eastern Panhandle (CSO 2011), concentrated in thirteen villages along the Okavango River from Mohembo East to Gudigwa (Fig. 1). The primary livelihood is subsistence agriculture and farmers harvest their crops between April and June (Songhurst and Coulson 2014). During this time they use traditional (drums, fire) and non-traditional crop-foraging mitigation methods (chilli fences) to deter elephants from their fields (Noga et al. 2015; Songhurst 2012).

Briquettes

We used 1,176kg of elephant dung and 235.2kg of chilli powder to make 672 briquettes of two different types: chilli-briquettes and non-chilli briquettes. For the chilli-briquettes, we mixed chilli powder from dry chilli-pepper fruits with crushed elephant dung at a ratio of 1/2, respectively (Karidozo and Osborn 2015). To create a thick paste we added water to the mix, which was then pressed into moulds of 40 x 20 x 15cm. Once the mixture was set, we removed the moulds and left the briquettes in the sun for a minimum of two weeks. We turned over each briquette every second day to make sure they dried evenly. For non-chilli briquettes, we repeated the same protocol replacing the amount of chillies with elephant dung. We used separate moulds for each type of briquette to avoid cross-contamination of non-chilli briquettes with chillies.

Experimental design and data collection

Our experiment took place during the dry season of 2015, from late September to the beginning of November. We chose this time of the year because elephant density in the study site peaks (Songhurst 2012). We used previous years satellite tracking data to identify ten experimental sites in areas that were frequently used by elephants (Fig. 2). We fitted 20 satellite-collars on 10 females and 10 males elephants in 2014, since when relocation data was collected. Each collar was set to give an hourly Global Positioning Satellite fix for every individual, and the data collected was used to estimate the probability utilization distribution for all individuals. We combined all data collected during the dry seasons of 2014 and 2015 to develop a heat distribution map, which represents the probability of finding any elephant within the study area (Fig. 2).

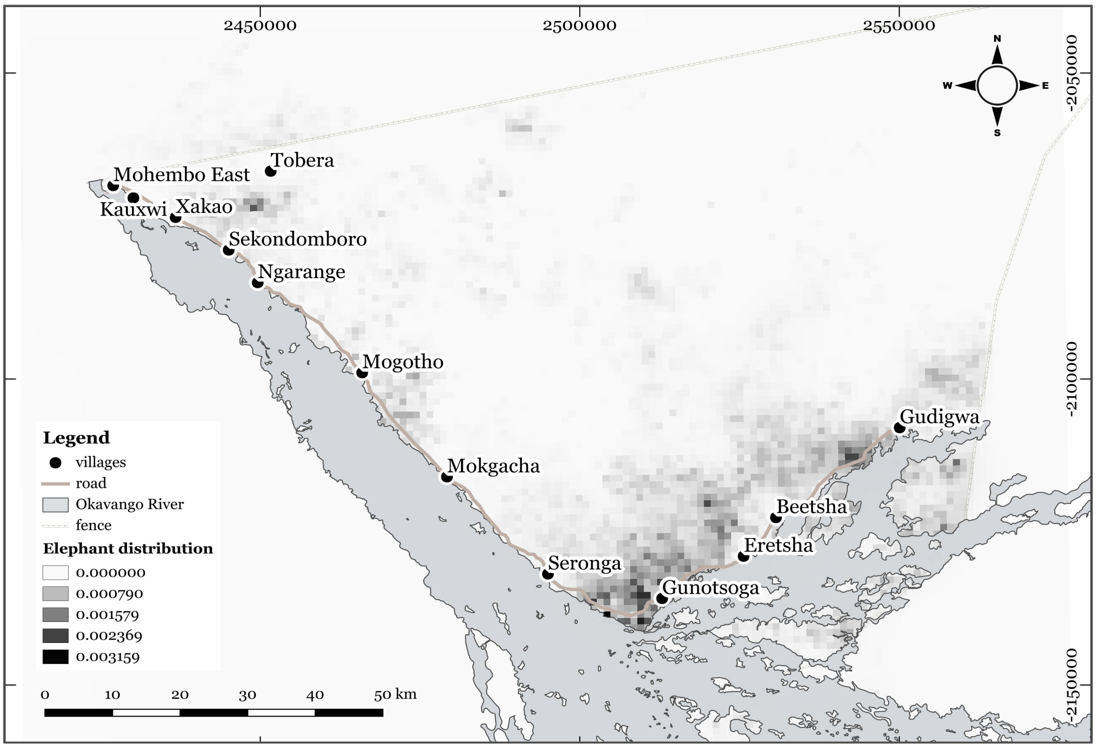

Fig. 2. Dry season utilization distribution map of elephant distribution in the eastern Panhandle. Grey shades represent the population probability distribution combined for the dry seasons (May-October) of 2014 and 2015. Each grid square represents 1km².

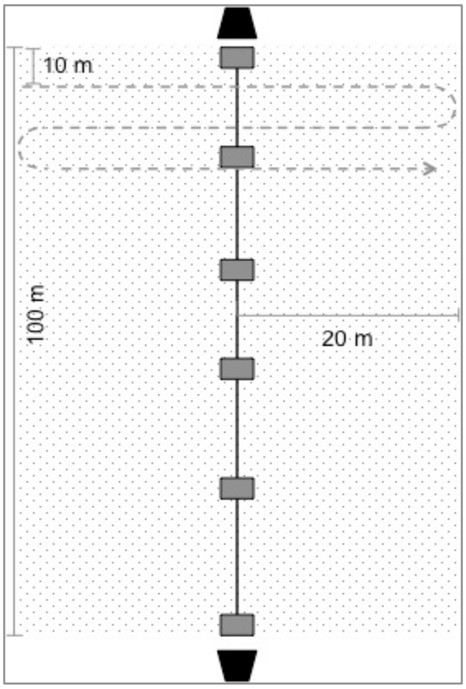

Figure 3. Experimental sites design. Vertical black line represents 100m transect and black trapezoids correspond to camera traps. Grey rectangles represent briquettes at 20m intervals. Dotted area denotes the 4,000m² survey area for elephant footprints. The dashed grey arrow crossing the survey area represents 40m transects separated by 10m used for the survey.

Each experimental site consisted of a 100m transect with a camera trap at either end ('experimental transect', hereafter), plus a surrounded area of 4,000m² ('survey area', hereafter; Fig. 3). In our study area, elephants move towards the Okavango River mainly during the night, time at which they adopt safety in numbers behaviour and gather in larger groups (i.e. several herds get together) before crossing road to access water (Songhurst 2012). Thus, experimental sites were placed at a maximum of 200m from the main road and parallel to it to detect as many elephants as possible. In addition, experimental sites were situated outside villages, away from corridors (see Songhurst et al. 2015b), and at least 1km apart from each other in order to control for variation due to cross treatment effects and maintain spatial independence.

To test the effect of chillies independently from the effect of smoke on elephant trajectories, we applied two treatments every day: 'chilli' i.e. experimental sites with chilli briquettes (C, hereafter), and 'no-chilli' i.e. sites with briquettes without chilli (NC, hereafter). Two additional treatments were used to investigate whether the effect of chillies varied depending on exposure rates: 'chilli once' i.e. sites with chilli briquettes lit once a week (C1, hereafter); and 'no-chilli once' i.e. sites with non-chilli briquettes lit once a week (NC1, hereafter). In parallel to the above treatments we ran a control group (i.e. sites without briquettes), totalling five treatments. Each treatment had two replicates, and so ten experimental sites were established in the field. Briquettes were placed at 20m intervals along relevant experimental transects following Karidozo and Osborn (2015), which resulted in six briquettes per transect per night (Fig. 3).

We divided our experimental period into four 2-week blocks (i.e. survey 1, experiment section 1 and 2, and survey 2). During surveys 1 and 2 no treatments were implemented. In experiment section 1, all treatments were randomly allocated across sites. Treatments were re-randomised at the start of experimental section 2. Briquettes were lit every day before sunset (17:00-19:00), when elephants move from bush covered areas to the river. Our camera traps detected that briquettes smouldered between 6 - 7 hours every night. All experimental sites were surveyed the morning after for footprint counts.

We used two methods to obtain an estimate of the frequency with which elephants visited experimental sites: the estimated number of elephants from footprint counts, and the number of elephant pictures taken by camera traps (20 camera traps set up in total). Footprint surveys took place on a daily basis within the 4,000m^2 survey area at each site from week 2 (survey 1) to week 7 (survey 2). We did not perform footprint surveys in weeks 1 and 8, but camera traps collected data throughout this period in order to consider the effect of the principal researcher (Pozo, R.A.) disturbance on elephant occurrence. Experimental sites were checked every morning (07:30-09:30) when the risk of encountering elephants in the field was lower. The substrata in the eastern Panhandle are deep Kalahari sands, which enable clear identification of footprints. We followed a standardised footprint protocol (Lee and Moss 1995) in which the principal researcher and one field assistant visited each site and estimated the number of elephants crossing each 4,000m^2 survey area over the last 24-hours. To do this, we used 40m long transects separated by 10m each and perpendicular to the 100m experimental transect (Fig.3). After every survey, the survey area was cleared using a rake to remove elephant tracks. In addition to the footprints survey, camera-traps photographed elephant crossing transects continuously. Two camera-traps were located at each end of every experimental transect, both facing each other, i.e. surveying the middle section of that particular transect (Fig. 3). All cameras were set up on trees at least 1m above the ground, and they were programmed to take 3 photos per trigger throughout the day and night. We used a combination of Bushnell (Night Vision Infrared Trophy Cam HD, California, USA) and Reconyx (HC500, Reconyx, Inc., Holmen, Wisconsin, USA) cameras. Both models use infrared flashes that cause minimal disturbance to elephants during the night. The time stamp on camera trap images enabled us to get more detailed information about the exact time elephants visited experimental sites.

Statistical analysis

We recorded the number of elephants at experimental sites using both footprint surveys and camera-trap images. The type of information collected through both methods differed in their formats (i.e. estimated number of elephants and number of elephants' photos), making it difficult to combine them. Consequently, we used the different datasets for different purposes. To investigate the occurrence of elephants we used footprint surveys, and to assess elephant temporal use we used camera-trap data.

We analysed the occurrence of elephants across experimental sites as the average number of elephants crossing per day per transect per treatment. Each average provided an estimate of elephant space-use per day at each treatment, and it represented an efficient way of dealing with spatial pseudoreplication (see Crawley 2007) at experimental sites. We modelled mean number of elephants as a function of treatment type and transect identity using linear models. We included the effect of 'transect' to measure the response of elephants to the specific site location. In this way we accounted for environmental variation between sites, which may otherwise affect the outcome of our treatments. In addition, in our study area elephants usually prefer habitats with proximity to water (Loarie et al. 2009), and they avoid areas occupied by people (Songhurst et al. 2015b). Therefore, we also included in our analysis the effect of the distance between experimental sites and the nearest independent settlement (including houses outside villages) and permanent water sources (i.e. waterholes and/or the Okavango River). Our final linear model included the mean number of elephants as a function of treatment, transect identity, distance to water and to the nearest settlement. Model selection was based on the lowest Akaike's Information Criterion (AIC) (Akaike 1973), considering ΔAIC>2 as representing significantly different models (Burnham and Anderson 2002). We used the *dredge* function in the MuMIn package in R (ver. 0.13.17) to run models with all possible combinations of factors.

We investigated elephant temporal-use using the camera-trap data in order to detect if the use of chilli-briquettes changed the timing of elephant activity at experimental sites. To identify if the proportion of elephant photos changed within 24-hours across different treatments we split each day into "day" (06:00-18:00) and "night" (18:00-06:00) periods. We used thresholds at 6pm and 6am based on Loarie et al. (2009). In the eastern Panhandle elephants are more active during the night, when they move towards the river (Jackson et al. 2008). Thus, we analysed the proportion of elephant photos taken during the night (y = two column object containing the counts of night and day images), per transect, per treatment using generalised linear models (GLM) with quasibinomial errors and a logit link function because of data overdispersion. We built our GLM with the proportion of elephant photos taken during the night as a function of treatment and transect identity. For all statistical analysis, we used R v3.0.1 (R Core Team, 2014).

Results

The mean number of elephants did not vary across chilli treatments (i.e. C and C1) in relation to non-chilli treatments (i.e. NC, NC1 and control) in our experiment. The best model to explain mean number of individuals observed per day in our footprint survey included the additive effects of treatment and transect location (Table 1; AIC=136.4). Although there was a negative effect of chillies on the number of elephants, the mean number of individuals in experimental sites was not statistically different for chilli (-7.15 ± 5.29, $p > 0.1$; -4.49 ± 6.02, $p > 0.1$ for C and C1, respectively) and non-chilli treatments (1.42 ± 6.47, $p > 0.1$; -7.79 ± 7.09, $p > 0.1$ for NC and NC1, respectively). Therefore, the difference between the number of elephants crossing experimental sites was equally due to variation across treatment type and transect identity (Table 1; Fig. 4). To identify the effects of transect identity on treatments, we also assessed the relation between transect location and distance to people settlement and water sources in our analysis. However, we found that the effect of treatments and transects were greater than distance to both people's settlements and water (Table 1).

Table 1. Summary of footprint and camera-trap model selection with Akaike's Information Criterion (AIC). AIC used to evaluate relationships of the mean number of elephants (footprint survey) and proportion of elephants photos (camera-trap survey) with 5 explanatory variables: experimental treatment (treatment), transect identity (transect), distance to people's settlements (people), villages (village) and water sources (water). Model and explanatory variables columns indicate specific combination of variables included in each function. Delta AIC (ΔAIC) shows the difference between each model and the best model selected. The weight column represents the relative likelihood of each model.

Model	**Explanatory variables**						**AIC**	**Δ AIC**	**Weight**
Footprint survey	intercept	transect	people	treatment	village	water			
model 1	4.70	+		+			136.4	0.0	0.113
model 2	1.83	+					140.9	4.6	0.012
model 3	-6.11		47.87				151.0	14.7	0
model 4	0.58		44.04		-1.50		151.8	15.5	0
model 5	-10.88		53.29			2.48	152.6	16.3	0
model 6	-1.58		46.16		-1.37	0.82	153.8	17.4	0
model 7	8.80		45.25	+	-2.81		155.5	19.1	0
model 8	-3.60		50.92	+			156.5	20.1	0
model 9	15.26		39.31	+	-3.28	-2.33	157.2	20.8	0
model 10	28.12				-3.06	-5.62	157.5	21.2	0
model 11	19.72				-2.50		157.6	21.2	0
null	10.83						157.9	21.5	0
model 12	-5.90		53.55	+		1.23	158.4	22.0	0
model 13	15.18					-3.79	159.0	22.7	0
model 14	42.59			+	-5.19	-8.38	160.1	23.7	0
model 15	28.89			+	-4.12		162.9	26.5	0
model 16	13.46			+			165.0	28.7	0
model 17	19.95			+		-5.62	165.3	28.9	0
Camera-trap survey	intercept	transect	people	treatment	village	water			
model 1	0.93	+		+			208.1	0	1
model 2	-2.02	+					546	337.9	0
model 3	3.21			+			674.1	446.9	0
model 4	0.41						1166.7	958.6	0

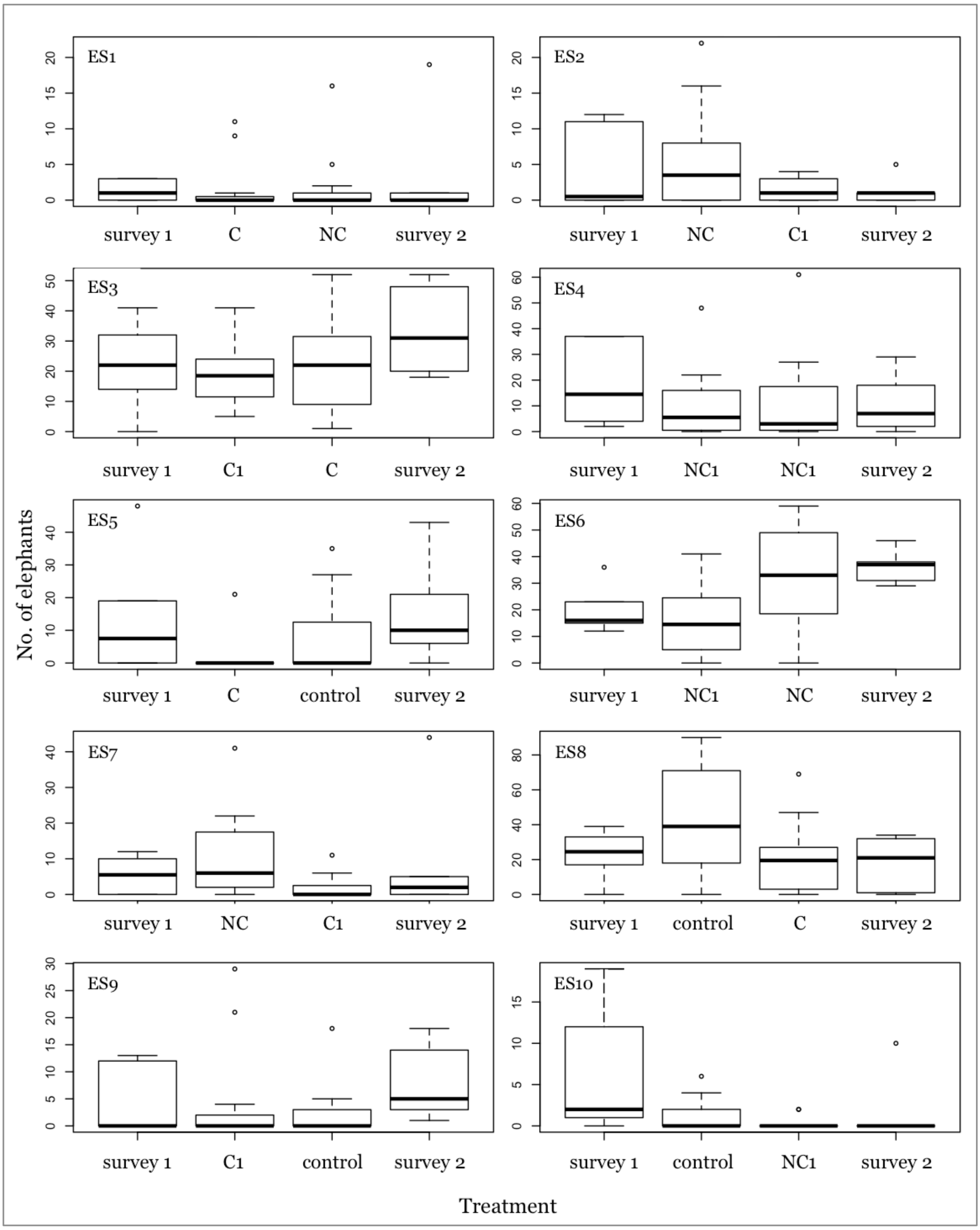

Figure 4. Elephants per transect per treatment. Graphs represent experimental sites (ES, denoted on high-left corner), each divided in four slots of two-weeks. In surveys 1 & 2 no treatments were implemented. Five treatments were randomly located across sites during experimental sections 2 & 3: chilli briquettes lit every day (C), and once a week (C1); non-chilli briquettes lit every day (NC), and once a week (NC1); and control group.

The camera-trap data supported our survey results, showing the proportion of elephant photos captured during the night was influenced by treatment and transect location (Table 1; AIC=208.1). We found the number of elephants captured during the night at chilli and non-chilli sites to be smaller than for the control group (Fig. 5). Moreover, the proportion of photos taken at night was smaller for chilli (-3.58 ± 1.63, $p < 0.1$; -3.66 ± 0.74, $p > 0.1$ for C and C1, respectively) than for non-chilli treatments (-2.3 ± 2.75, $p > 0.1$; -3.32 ± 2.85, $p > 0.1$ for NC and NC1, respectively) (Fig. 5).

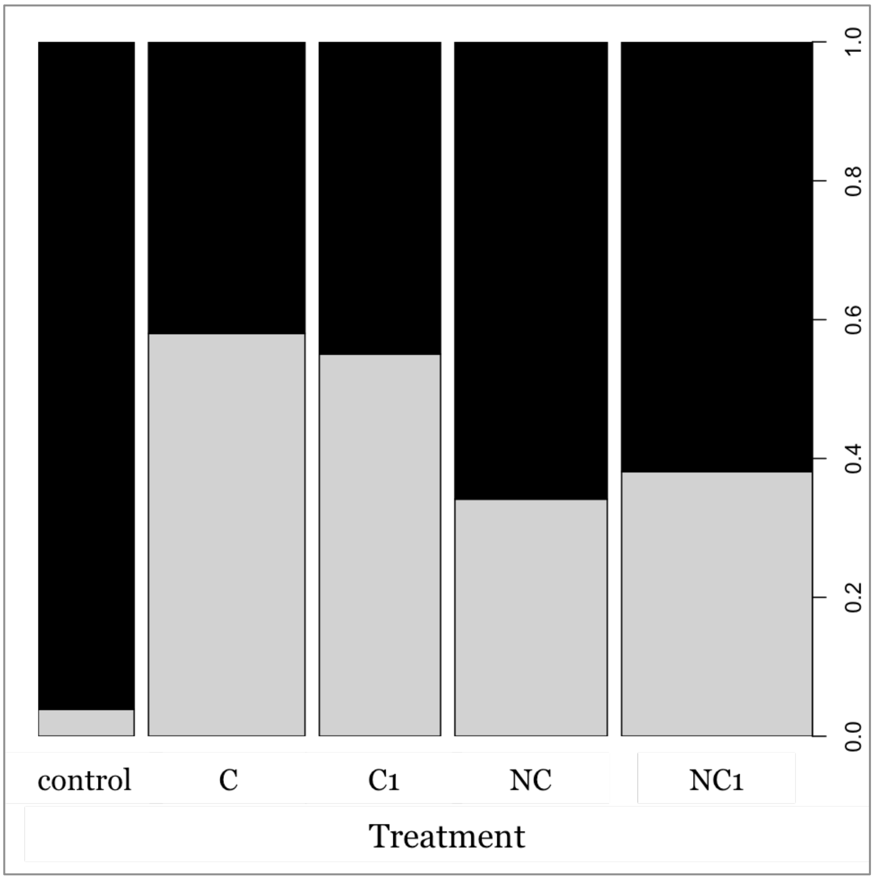

Figure 5. Temporal distribution of elephant photos per treatment. Black and grey sections represent the proportion of elephants detected on camera-traps during the night (18:00h-06:00) and day (06:00h-18:00), respectively. Treatments correspond to: chilli briquettes lit every day (C), and once a week (C1); non-chilli briquettes lit every day (NC), and once a week (NC1); and control group. The width of each bar represents the number of elephant photos taken within each period.

Overall, chilli-briquettes altered elephant temporal behaviour during our experiment (although not significantly), keeping elephants away from sites with chilli treatments at night. However, chilli-briquettes did not affect the mean number of elephants crossing sites throughout a 24-hour period. In other words, herds only stayed away from chilli-briquettes during times they were smouldering, and therefore a similar number of elephants crossed chilli sites everyday but at times when briquettes were off.

Discussion

In the short term, burning chilli-briquettes changes the timing of elephant visits to a given area to hours when briquettes are not smouldering. However, they do not significantly alter the number of elephants occurring in a specific area over a 24-hour period (Graham and Ochieng 2008; Graham et al. 2009; Hoare 2012). Thus, chillies have a repellent, but not necessarily a deterrent, effect on elephants (Osborn and Rasmussen 1995). However, our unique controlled and replicated experimental design is the first to show that chilli-briquettes change elephant temporal behaviour by keeping the species away during hours when the pungent effect of chillies is present (i.e. night). Therefore, we suggest the use of chilli-briquettes by farmers at night-time when people and property risk due to elephant damage is higher (Chiyo and Cochrane 2005).), in order to obtain rapid results that will alleviate immediate elephants impacts on crops by deterring the species in the short-term.

Crop-foraging by elephants is a significant challenge for subsistence farmers. Finding effective ways to deter elephants from fields can help strengthen food security, reduce conflicts with elephant conservation, and improve local perceptions of the species (Davies et al. 2011). Testing mitigation methods advised in the field is key to ensuring their effectiveness and feasibility. Despite this, our understanding of the effectiveness of elephant crop-foraging deterrents is limited due to the absence of controlled trials and published studies on their exclusive use (Graham et al. 2009). In this context, we implemented a controlled and replicated experimental design to test the most popular form of chilli deterrent recommended in our study area. We controlled for environmental variation between experimental sites assigning them to areas away from villages and outside from protected corridors, as well as controlling for the distances between experimental sites and from the main road to each experimental location. In addition, and in contrast to other studies, we did not enlist the help of farmers to implement our experiment. We did this in order to ensure our experimental protocol was efficient before being recommended to the local communities, not because we did not trust farmers. Equally, we did not perform our experiment during the harvesting season. In this way, we aimed to decrease bias associated with the palatability of crops in experimental trials, as well as inconsistent experimental protocols. Therefore, the main researcher (Pozo, R.A.), in collaboration with two local fieldwork assistants, built and smouldered briquettes during the whole experiment, thus ensuring continuity and consistency throughout the experiment. Each site followed the same protocol and level of effort, which also allowed selection of random experimental sites in the study area.

Despite the above efforts to implement a controlled experiment, the spatial distribution of elephants as well as their temporal movement had a great influence on the performance of treatments relative to experimental sites. Previous studies of chilli-based approaches have faced similar challenges when working under field conditions. For instance, two experiments of chilli-methods concluded that the overall decline in crop-foraging recorded may have been due to increased rainfall (Sitati and Walpole 2006), or other unmeasured environmental factors causing a high level of variation in elephant space-use (Osborn and Parker 2002). Therefore, it would be useful for future studies to clarify to what extent environmental variation, and its effect on elephant movement, affect the performance of chilli deterrents.

Yet, the behavioural change in elephant temporal-use and the decrease in the number of elephants crossing chilli sites (although not significant) are indicators that chilli-briquettes represent an effective method to modulate elephant trajectories during harvesting seasons. Finding effective crop-foraging deterrents for intelligent and social animals such as elephants is particularly challenging. Elephant communication and cognitive skills, in combination with their large body size, dietary and behavioural flexibility (Barnes 1996; O'Connell-Rodwell et al. 2000) make them extremely adaptable and successful at foraging crops (Chiyo and Cochrane 2005). Previous studies have shown elephants are able to find alternative ways to forage people's fields, either by avoiding deterrents or learning from other members of the group (Chiyo and Cochrane 2005). Despite this, their sophisticated learning skills can also be part of the solution. Our study suggests that in a short period of time (i.e. two weeks), elephants identified not only the location but also the time at which chilli-briquettes were smouldering, and as a response modified their movement patterns to cross chilli sites either before or after the presence of chilli smoke. This indicates that in the short-term chilli-briquettes may trigger a rapid and effective behavioural response by elephants, which will ultimately also increase the likelihood of safer areas for people.

Chilli-briquettes were tested for a relatively short period of time. Which could represent a weakness of our experiment in comparison with previous studies (see Graham et al. 2009). However, it has to be considered that we conducted our experiment during the dry season, when elephant densities - spatially and temporally- are at its highest in the study area. Despite any effects of elephants grouping (e.g. elephants closeness to the Okavango River; elephant risk-avoidance aggregations near the main road), we demonstrated that the chilli-briquettes had a repellent effect.

Nevertheless because of the short-term effect of chilli-briquettes, the latter alone are unlikely to be effective in the long-term. Integrated or rotated interventions have a greater chance of success than a single approach on its own (Hedges and Gunaryadi 2010; Noga et al. 2015; Osborn and Parker 2003; Sitati and Walpole 2006). Land-use planning, protection of elephant corridors, use of chilli plantations as buffer zones and cooperative community-based tools, are some examples that have been suggested to improve coexistence between people and elephants (Jackson et al. 2008; Parker and Osborn 2006; Songhurst et al. 2015b). The appropriate combination of methods will depend on the specific dynamics of elephant crop-foraging in the field. For the particular case of the eastern Okavango Panhandle, we recommend the use of chilli-briquettes as an addition to mitigation strategies already in place because of the rapid repellent effect on elephant space-use observed in our study. In addition, people in the region have positive perceptions of chillies and the plants have potential as an alternative source of livelihood for local farmers (Noga et al. 2015; Songhurst 2012).

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Chapter 5

Modelling the impact of selective harvesting on red deer antlers

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- Running head -

Effects of hunting in red deer

- Tittle -

Modelling the impact of selective harvesting on red deer antlers

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Abstract

Hunting is a common component in the management of ungulate species. Despite its widespread use, the influence of selective harvesting on phenotypic trait change is still ambiguous, and represents a critical gap in our understanding of the responses of wild populations under harvest. Using the long-term red deer (*Cervus elaphus*) dataset (1972-2012) from the Isle of Rum National Nature Reserve, Scotland, we assessed the relationship between antler length and key demographic processes (i.e., survival, recruitment, antler growth, parent-offspring trait correlation) for the male component of the population. We then constructed the first integral projection model for this species to examine the effects of simulated trophy hunting on 2 population-level parameters: the stable antler size distribution and the relative reproductive value of males. When male mortality rates due to hunting were <20% the effect on antler size distribution and the reproductive value function were relatively small. However, as mortality due to hunting increased to 50% in large individuals, the direct effects of hunting on mean antler size and reproductive value became evident. Our model acts as a useful starting point to investigate the ecological and evolutionary consequences of hunting in red deer.

Introduction

Wild ungulates have been hunted for centuries, however the consequences of their exploitation remain unclear. In particular, the influence of selective harvesting on phenotypic change is not well understood, and represents a critical gap in our knowledge of the responses of wild populations to harvest. Trophy hunting represents one form of selective harvesting that has been traditionally implemented in wild cervids. This harvesting regime is a non-random process whereby humans select individuals to be removed from a population based on 1 or several phenotypic traits (Festa-Bianchet 2003; Mysterud 2011). Typically, males with the largest trophies (e.g. antlers or horns) are sought and removed from the population, imposing an unnatural mortality rate on prime-age males (i.e. those that have attained asymptotic body mass prior to senescence) or young adults (Gaillard et al. 1998; Monteith et al. 2013). This harvesting regime can result in negative demographic consequences including changes in population structure (Traill et al. 2014), skewed sex-ratios (Ginsberg and Milner-Gulland 1994; Milner-Gulland et al. 2003), and decreased antler or horn size (Milner et al. 2007; Monteith et al. 2013). Such deleterious effects have been observed in bovidae (Pérez et al. 2011; Festa-Bianchet et al. 2014) and cervidae (Monteith et al. 2013).

Antler size is often under natural and sexual selection. In wild populations of deer, males differ markedly in their fertility rates (Malo et al. 2005*a*) and antler size (Kruuk et al. 2002), with adult males with larger antlers attaining the highest breeding success (Clutton-Brock 1981; Andersson 1994; Kruuk et al. 2002; Malo et al. 2005*b*). In addition, the key role of antlers in male-male combat (Clutton-Brock 1982; Andersson 1994) suggests that individuals with larger antlers may live longer (Lemaître et al. 2014). Because sexually selected characteristics are by definition under selection, any unnatural intervention that changes mortality or reproductive schedules of individuals with specific trait values has the potential to generate evolutionary change. Harvest by humans has been reported to cause changes in phenotypic traits (Darimont et al. 2009), and to generate evolutionary responses (Palumbi 2001). Trophy hunting may impose selective impacts on wild populations. One way to investigate this is to evaluate how hunting is likely to influence fitness. We examined how hunting might affect the distribution of trophy sizes within the population and reproductive value (i.e., a quantity describing the expected representation in terms of descendants across all trait values of an individual with a specific character value in the future population; Fisher 1930).

Artificial removal of males with large trophies will likely lower the reproductive value of large individuals and mean trophy size within the population. However, trait size response to trophy hunting has not been consistent across species, and in many cases environmental factors play a much stronger role on mean values than selective removal (Schmidt et al. 2007; Mysterud 2011). However, other studies have reported that phenotypic change in hunted populations can also be due to an evolutionary response (Coltman et al. 2003), although it should be noted that this conclusion is controversial (Traill et al. 2014).

In long-term studies of individual life histories, experimental culling of individuals often conflicts with other research interests and cannot therefore be used to test harvesting hypotheses. As a result of this, the use of structured models to represent population structure has become popular (Caswell 2001;

Ellner and Rees 2006; Coulson 2012). In particular, integral projection models (IPMs), a generalization of matrix models, have been developed to study and track the dynamics of continuous characters (Easterling et al. 2000; Coulson 2012). Integral projection models can be parameterized directly with observational data (Ellner and Rees 2006), and enable key population-level parameters, such as a stable phenotypic trait distribution and reproductive values, to be predicted from individual-level data (Caswell 2001). Importantly, IPMs can be perturbed to simulate harvesting regimes in wild populations and have provided reliable information on how demographic parameters change within and between age groups (Traill et al. 2014).

We used individual based data on red deer (*Cervus elaphus*) from the Isle of Rum National Nature Reserve, Scotland (Clutton-Brock et al. 1982; Pemberton et al. 1996) to assess the effects of trophy hunting on 2 population-level parameters: stable antler size distribution (i.e. the expected distribution of antler length/age-group within the population) and reproductive value (i.e. the relative contribution of an individual with a specific antler size to the future population). We investigated the relationship between antler size and key demographic processes relating to the male component of the population because we expected selective hunting to change the relative reproductive value between males with different antler sizes, and because the relative contribution of individuals with different character values to future populations elucidates the likely consequences of selective harvesting. We then constructed the first IPM for the species (exclusively for males), from which we extracted estimates of stable antler size distribution and reproductive value. Finally, we perturbed the resulting IPM to simulate the effects of different harvesting regimes at the population and age-group levels.

Materials and Methods

Study Area

The data used in this study come from the unmanaged red deer population in the North Block of the Isle of Rum National Nature Reserve (578019 N, 068179 W; NM-402996), Scotland. A detailed description of the Isle is presented by Clutton-Brock et al. (1982). The 10,600-ha island has a mild, wet and windy oceanic climate. Rainfall varies widely across the island, with April generally the driest month and November and January the wettest (Clutton-Brock et al. 1982). Rum is a mountainous island characterized by productive valleys, including extensive grassland cover closer to seashores, and fen vegetation on higher elevations (Virtanen et al. 2002; Ball 1987).

In 1972, the routine 14% red deer cull of the North Block stopped and a long-term, individual-based investigation into behavior, evolution, life history, and population dynamics was initiated (Clutton-Brock 1981; Pemberton et al. 1996). Females give birth in May and June each year, and since culling stopped, approximately 90% of calves born in the North Block have been caught, individually marked (i.e. collar, ear tags or ear punches attached as calves) and followed throughout their lives. Censuses in the study area are carried out at least 5 times a month between January and May (Coulson et al. 1997), during which all individuals are recorded as present or absent. Although all breeding attempts and deaths are recorded within the study area, animals that emigrate to other parts of the island cease to be monitored and their whereabouts are thereafter often unknown (Clutton-Brock et al. 1982).

Male red deer grow antlers annually from the age of 1 or 2 years old (Kruuk et al. 2002). Antlers are used in male-male encounters once the individual is sexually mature (at 3–4 years of age), even though they are unlikely to sire any offspring until they are ≥4 years old (Nussey et al. 2009; Kruuk et al. 2014). Males cast their antlers annually between March and May (casting season), following which they grow a new set of antlers until August. These lose their velvet (i.e. cleaned) around September prior to the start of the rutting season. To fit in with antler growth, the deer year in our study ran from 1 August to 31 July of the next year. This ensured that only pairs of antlers used during the latest rutting season were assessed in relation to male calves recruited the following year.

Antler Measurements

The Isle of Rum Red Deer Project recovered antlers in the field during the casting season (March-May) every year since the 1970s. In our study we used data collected by the project between 1972 and 2012. Members of the survey team followed each male within the study area and collected antlers immediately after they were shed. Thus, each antler was associated with a specific individual identified by observation of unique ear tags or punches. Previous genetic analysis has suggested this method is 93% accurate (J. P. Petley and J. M. Pemberton, Institute of Evolutionary Biology, University of Edinburgh unpublished data). The project collected antler length, mass, the number of tines, genetic samples, and other measurements in the field (Kruuk et al. 2002; Walling et al. 2010). They used genetic samples to construct a multigenerational pedigree, in which they estimated paternity using genetic (genotypes at ≤15 microsatellite loci), phenotypic, and behavioural data (Kruuk et al. 2014). We focused on the length of antlers, which we used as an indicator of antler size, because antler length is one of the main characteristics targeted during trophy hunting activities.

The Red Deer Project team measured antler length as the distance from the coronet to the furthest tip of the main beam, around the curves (Fig. 1).

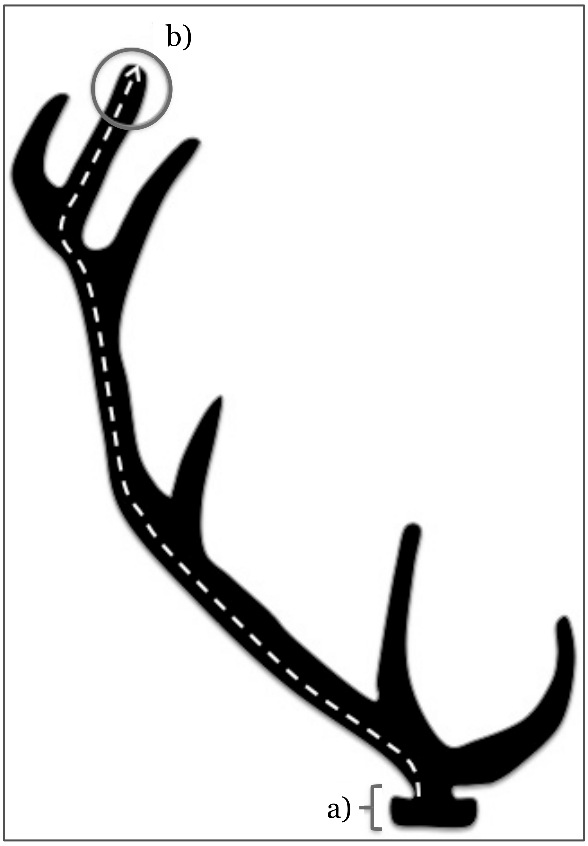

Figure 1. Antler length measurements taken for red deer on the Isle of Rum, Scotland, during casting seasons 1972-2012. The white dashed line shows the distance between a) the antler coronet and b) the highest point of the mean beam around the curves.

Where measures from both antlers (i.e. left and right) were available for the same individual for a given casting season, we used the average. For juveniles (1–3 years old), antlers are often simple spikes. Members of the project estimated spike length of living male calves by eye in the field. For any 1 male calf, multiple observers (2–4) estimated spike size using the ear length of the same individual as a reference. The project recorded observed spike length as the consensus between observer measurements.

We organized individual information in a file with equivalent structure to that used in Coulson (2012; Table S1, Supporting Information). All animal measurements in this study were collected noninvasively. The data used in this study was gathered in the field under the approval of the University of Edinburgh's Animal Welfare and Ethical Review Body.

Construction of IPM and Statistical Analysis

Because only individuals that have reached reproductive maturity are able to defend harems and reproduce, both antler size and reproductive status can be expected to vary between male life stages. Consequently, we included age class as a factor in our analyses. Considering that environmental variation imposes different selective forces on individual survival and reproduction, we grouped males into 4 reproductive and 4 survival age classes. Reproductive age classes consisted of juveniles (1–3 years old), young adults (4–6 years old), adults (7–11 years old), and seniors (≥12 years). Survival age classes consisted of calves (0–1 years old), juveniles (2–3 years old), adults (4–8 years old), and seniors (≥9 years). In both cases, age classes were based on Kruuk et al. (2002), with the exception of the adult age class, which in our case was extended to include individuals of 4 years old because these were observed to reproduce in our study population.

Integral projection models are composed of 4 fundamental functions describing the processes of survival (S), recruitment (R), growth (G), and parent-offspring trait correlation (D; inheritance), which together predict, in this case, the distribution of antler length (l) per age-class (a) at time $t + 1$, as a function of antler length at time t (Ozgul et al. 2010; Traill et al. 2014). Together, these predict the distribution of the number of individuals (n) with antler length (l) per age-class (a) at time $t + 1$, as described by the following equations:

$n(1, t+1, l') = \sum_a \int dl\, D(l' \mid l)\, R(a, l) n(a, t, l)$ Equation 1

$n(a+1, t+1, l') = \int dl\, G(a, l' \mid l)\, S(a, l)\, n(a, t, l)\, , a \geq 1$ Equation 2

Equation 1 describes the distribution of offspring antler length at time $t+1$, which is calculated from the number of offspring produced by a male with antler length l per age class (i.e. $R(a, l)$) and the offspring distribution of a parent of age a and antler length l (i.e. $D(l' \mid l)$. Together these describe the probability that an individual with antler length l at time t of age a will produce a son with antler length l' at time $t+1$. In both cases dl belongs to the integral sign and means that the integral is taken over the whole range of l. Additionally, $R(a, l)$ includes the product of fertility (R_F), which describes the probability that a male will reproduce or not, and the number of offspring produced from those individuals that do reproduce (R_N). In our model, we considered only individuals ≥4 years (i.e. males producing offspring) in the reproduction analysis.

Equation 2 describes the probability that an individual of age a and antler length l will survive from time step t to time step $t+1$ (i.e. $S(a, l)$). The growth function (i.e. $G(a, l' \mid l)$) describes the growth of antler from l at time t to l' at time $t+1$ of individuals from an age class a. Both functions in equation 2 describe the distribution of antler lengths from individuals that survive from one time step to the next one. Below, we describe how we parameterized and statistically analysed each of the 4 fundamental functions.

Effects of antler length on survival.— We performed a mark-recapture (MR) analysis to test for the effect of age and antler length on male survival, while accounting for imperfect detection of individuals (Lebreton et al. 1992). We considered a Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992) with 2 states to describe the fate of an individual (1 = alive; 0 = dead), and 2 events to describe the observation process (0 = antler not found, 1 = antler detected). At each time step t (i.e., 1 year), an individual can be alive with probability S_t, and its antler can be found with probability P_t.

We first performed goodness-of-fit tests starting from a general CJS model allowing survival and detection probabilities to vary with time (Lebreton et al. 1992) using program U-CARE (Choquet et al. 2009). We detected a lack of fit due to transient (i.e. individuals in transit across the study area) and trap-happiness (i.e. individuals whose antlers are found once are usually more likely to be found again in the field) effects (Pradel et al. 1997). Once we had accounted for the presence of transient individuals, the over-dispersion coefficient relating to the trap-happiness effect was acceptable ($\hat{c} = 2.48 < 5$; Burnham and Anderson 2002). To account for the transient effect, we considered a 2 age-class structure for survival (Pradel et al. 1997), whereby we defined individuals as being either juveniles (i.e. calves and juveniles from the IPM age classes) or adults (i.e. adults and seniors from the IPM age classes). This choice is sensible because younger individuals tend to stay with their mothers (and therefore within the study area) in their first 2 years whilst older males disperse across the island. Thus, using a CJS model that included a time-varying individual covariate (Choquet and Nogue 2011), we tested for additive effects and an interaction between age class and antler length on survival. Collinearity was not an issue, even when the range of antler length varied within age classes and its relationship with survival because we used age as a group (Fig. 2).

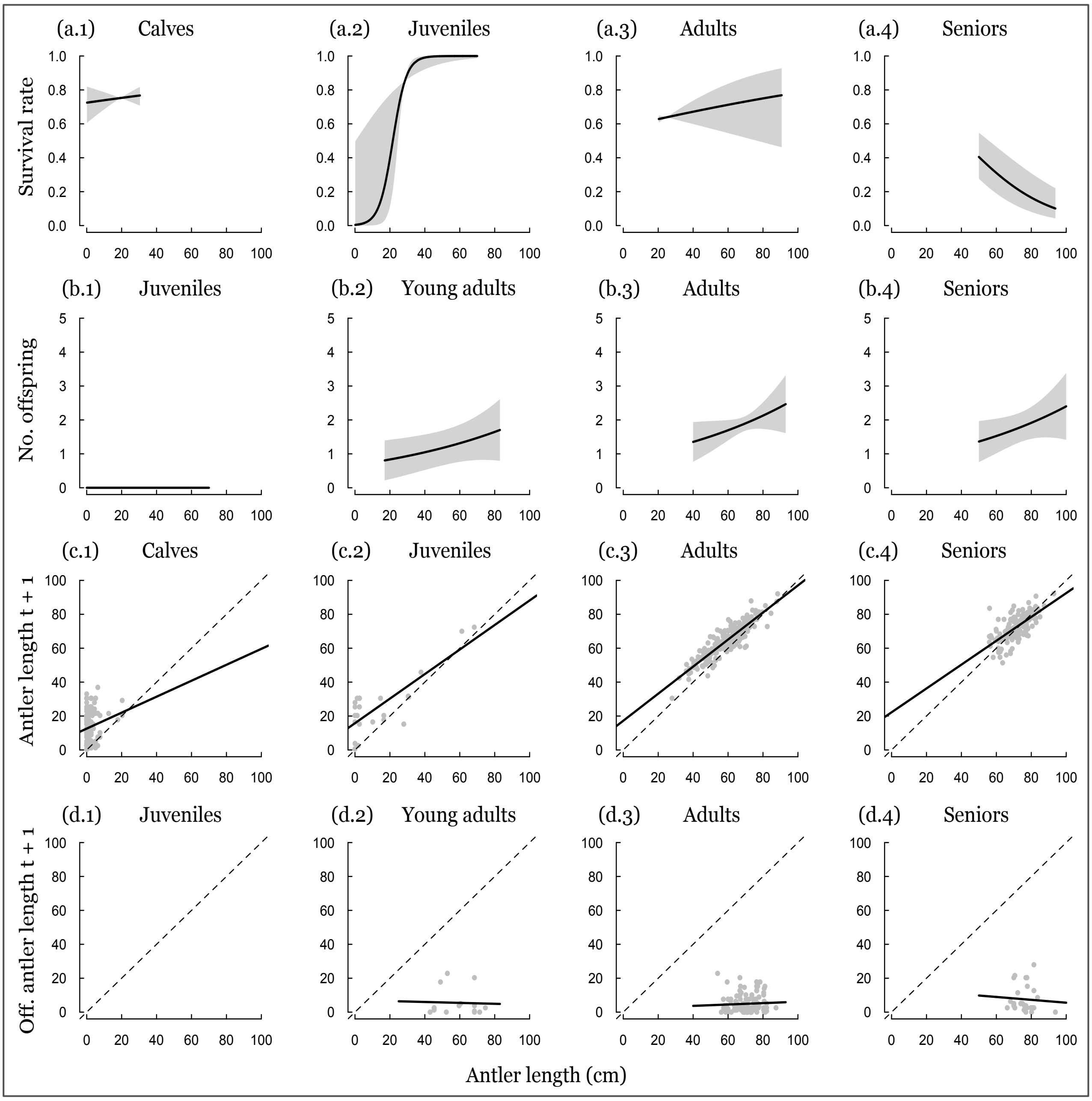

Figure 2. Relationship between antler length (cm) of red deer on the Isle of Rum, Scotland, 1972–2012 and 4 fundamental demographic processes: a) survival, b) recruitment, c) antler growth (antler length at *t* vs. antler length at *t* + 1), and d) inheritance (as a function of offspring (Off. in row d) antler length at time step *t* + 1). Survival and antler growth age classes consist of calves (0–1 yr), juveniles (2–3 yr), adults (4–8 yr), and seniors (>9 yr). Reproductive and inheritance age groups consist of juveniles (1–3 yr), young adults (4–6 yr), adults (7–11 yr), and seniors (>12 yr). In all panels shaded areas indicate the 95% confidence intervals. In rows c and d, dashed lines represent the x=y function and grey dots the raw data. Antler length is positively correlated with survival and recruitment, except for senior individuals. Antler growth rate was found to decline with antler size, and no correlation was found between antler length and inheritance. Since juveniles do not reproduce, no relationship was obtained for b.1 and d.1.

We also tested for an effect of age on detection probability. We fitted models using program E-SURGE (Choquet and Nogue 2011) and used standard maximum likelihood procedures to obtain parameter estimates (Lebreton et al. 1992). Model selection for the MR analysis and each fundamental function of the IPM were based on Akaike's Information Criterion (AIC; Akaike 1973). We retained the model with the lowest AIC value for subsequent analysis. We used R v3.0.1 for all statistical analysis (R Core Team 2014).

We used estimates for the intercept and slope from the best model to parameterize the survival function of the IPM:

$$S(a,l) = \frac{1}{1+ e^{-(\alpha_{s,a}+ \beta_{s,a}\ l)}}, \qquad \text{Equation 3}$$

where an individual from age class a and antler length l at time t has a probability of survival of $S(a,l)$. Here, $\alpha_{s,a}$ and $\beta_{s,a}$ denote the intercept and slope per age-class, respectively.

Effects of antler length on recruitment.—We used generalized linear models (GLM) to estimate male fertility (R_F; the probability for an individual to reproduce or not in a given year) and the number of recruits produced per male (R_N) once he reproduces, each as a function of antler length and age class. We estimated R_F from a GLM with a binomial error and logit link function and it had the same structure as $S(a,l)$ but with $\alpha_{F,a}$ and $\beta_{F,a}$ representing intercept and slope for fertility, respectively.

$$R_F(a,l) = \frac{1}{1+ e^{-(\alpha_{F,a}+ \beta_{F,a}\ l)}} \qquad \text{Equation 4}$$

We modeled R_N using a Poisson error structure and a log link function because of the count nature of our data. The R_N function within the IPM takes the following form:

$R_N(a,l) = e^{-(\alpha_{N,a} + \beta_{N,a} \times l)}$ Equation 5

This function describes the number of offspring that individuals from age group a, and of antler length l, will recruit conditional on reproduction into the population at time t. In equation 5, $\alpha_{N,a}$ and $\beta_{N,a}$ are the intercept and slope of recruitment per age-class, respectively.

If R_F is the number of individuals that reproduce per age group in the population and R_N is the number of offspring that individuals that do reproduce contribute per age group, the final equation for the recruitment function corresponds to the product of both:

$R(a,l) = R_{F,a} \times R_{N,a}$ Equation 6

Effects of antler length on growth.— We combined 2 sources of information to determine the ontogenic development of antler length. First, we used a linear model to fit regression lines per age class within both age group classifications (i.e., survival and reproduction) between measures from males sampled at time step $t+1$, in relation to the same individual at time t. The expected (E) antler length at time $t+1$ for a given antler length at time t had the form $E(a,l') = \alpha_{g,a} + \beta_{g,a} \times l$, where $\alpha_{g,a}$ and $\beta_{g,a}$ are the intercept and slope relating to growth for individuals of age class a; l is antler length at time t, and l' is antler length at time $t+1$. We then squared the residuals from this first model and regressed them against the antler length in a second linear model. We obtained the following equation, $\sigma^2\,(a,l') = \alpha_{gv,a} + \beta_{gv,a} \times l$, in which the growth variance (gv) intercept and slope per age group are represented by $\alpha_{gv,a}$ and $\beta_{gv,a}$ respectively. Finally, to estimate G in the IPM, we incorporated both functions in the following equation:

$$G(l'|\,l) = \frac{1}{\sqrt{2\pi\sigma^2(l,a)}}\, e^{-\left(l-E(l,a)\right)^2 / 2\sigma^2\,(l,a)} \qquad \text{Equation 7}$$

Effect of antler length on inheritance.—We compared the antler length of male offspring that survived from birth to their first census ($t + 1$), with that of their respective fathers at the time when the offspring was sired (t). We collected 1,992 repeated antler measurements from the field between 1970 and 2012, representing 869 unique males. Of these, 388 had known male offspring at time step $t + 1$, with spike length measured on 29 of the latter. We used these available data to predict the spike length at age 1 of adults for which this measurement had not been taken, but which had been observed in later life stages (n = 143 out of 388). Offspring that died before age 1 and were not seen in later life stages could not be included in this analysis because it was not possible to estimate their spike length.

We used 2 linear models to estimate the inheritance function: one to regress antler length of offspring at time $t + 1$ against antler length of the males that sired them at time t (i.e. the mean); and another to determine the relationship between squared residuals and average antler length in the population (i.e. the variance). The final equation for D followed a Gaussian distribution in the IPM:

$$D(l'|\,l) = \frac{1}{\sqrt{2\pi\sigma^2(l)}}\, e^{-(l'-(\alpha_d+\,\beta_d*l))^2 / 2\sigma^2\,(l)} \qquad \text{Equation 8}$$

The model for D did not consider age classes because we did not find a statistical difference between age groups for this function (Table 1). We therefore did not obtain intercepts and slopes per age class as in S, R, and G. We used only 1 intercept (α_d) and 1 slope (β_d) from the first linear model, and

1 intercept (α_{dv}) and 1 slope (β_{dv}) from the variance model (i.e. $\sigma^2(l) = \alpha_{dv} + \beta_{dv} \times l$) to predict $D(l' \mid l, t)$ in the IPM.

Table 1. Summary of model selection with Akaike's Information Criterion (AIC) evaluating relationships of antler length with 4 demographic processes of red deer on the Isle of Rum, Scotland, 1972–2012. The model column indicates explanatory variables included in each fundamental function. Antler length and male age classes are represented by length and age, respectively. Delta AIC (ΔAIC) shows the difference between each model and the best model selected for our analysis. *K* is the number of parameters considered in each model.

Function	Model	AIC	ΔAIC	*K*	Model weight
Survival	length × age	5340.1	0	8	0.170
	length + age	5347.4	7.3	5	0.004
	length	5520.9	180.8	2	0
	null	5525.5	185.4	1	0
Growth	length + age	3320.1	0	5	0.170
	length × age	3321.8	1.7	8	0.073
	length	3338.1	18.0	2	0
	null	4767.9	1447.8	1	0
Recruitment	length + age	917.9	0	5	0.170
	length × age	920.5	2.6	8	0.046
	length	953.9	36.0	2	0
	null	1310.6	392.7	1	0
Inheritance	null	1098.1	0	1	0.170
	length + age	1099.2	1.1	5	0.098
	length	1099.6	1.5	2	0.080
	length × age	1102.8	4.7	8	0.016

Numerical implementation.— To construct the matrix approximation for the IPM, we first discretized a range of values for antler length between the minimum (0 cm) and maximum (93.8 cm). We considered values between 0 and 100 to create 200 bins separated by an interval of 0.5 cm. We used the midpoint rule (Ellner and Rees 2006) in numerical approximation of the integrals to implement the IPM. We constructed a projection kernel from the 4 fundamental functions. We then discretized the latter to obtain a matrix model from which we calculated parameters of interest by eigen analysis, which in turn provided us with eigenvectors. These demographic parameters corresponded to the stable antler size distribution and the reproductive value. Because we did not include females in our analysis, we standardized reproductive value over all males (i.e. male population reproductive values summed to 1) for the entire study period.

Elasticity Analysis

We performed an elasticity analysis to examine how stable antler size distribution and reproductive value responded to perturbation of parameters in the model. We independently increased each of the age class coefficients (i.e. intercepts and slopes) by 1%, meaning that we multiplied positive and negative values by 1.01 and 0.99, respectively. After each perturbation we re-ran the IPM, returning to the original coefficients before altering the next parameter. This process is a conventional way of assessing how demographic parameters of interest are influenced by small perturbations (Easterling et al. 2000; Coulson et al. 2010). By perturbing each parameter, we aimed to understand how that specific value affected transition rates in the sub-matrices within and between age groups, and how this change ultimately altered stable antler size distribution and reproductive value. If we observed no changes in the demographic parameters of interest (i.e. stable antler size distribution and reproductive value) between perturbed and unperturbed models, we concluded there was no association between antler size and the model predictions calculated from the IPM (Coulson 2012).

Harvesting Analysis

To investigate the effects of harvesting on the male component of the red deer population, we simulated the removal of males under 2 scenarios: trophy hunting and uniform culling. For the purpose of this study, uniform culling was defined as the removal of a certain percentage of the population of males, regardless of antler length. In contrast, trophy hunting is a non-random process whereby humans select individuals to be removed based on 1 or several phenotypic traits (Festa-Bianchet 2003; Mysterud 2011). For the trophy hunting simulation, 3 proportions of males with antlers above a threshold length were removed from the population: 10%, 20%, and 50%. We focused on these 3 harvesting values because these are known to represent an unusually low hunting off-take (10%), a threshold above which male red deer population size is known to decrease (20%; Clutton-Brock and Lonergan 1994), and an over-intensive harvest quota (50%; Clutton-Brock and Lonergan 1994; Clutton-Brock et al. 2002). Because trophy-hunting stalkers generally avoid shooting calves and juveniles, we fixed trophy harvest as a decrease in survival rates of individuals >4 years (i.e. adults and seniors).

We implemented the trophy hunting approach by targeting only individuals with antler lengths that were above the mean antler length of antlered deer, which we calculated from the unharvested male population. Accordingly, we multiplied the probabilities of survival for antler sizes above this threshold by 0.9, 0.8, and 0.5. For each of these, we re-calculated stable antler size distribution and reproductive value from the IPM. We then calculated what harvest rates would have to implemented in the uniform culling approach to obtain identical values of mean antler length and reproductive value as those obtained with trophy hunting. To do this, we obtained values of mean antler length and mean reproductive value for a range of uniform culling rates (0–50%). We then regressed harvest rate against mean antler length, and mean reproductive value and used the resulting equation to derive the required uniform harvest rate values for the whole population of males that have antlers. In addition, we also investigated potential reproductive compensatory responses of smaller antlered males once the biggest trophies were removed through trophy hunting (see Supporting Information, available online at www.onlinelibrary.wiley.com). To simulate this, we multiplied the probabilities of recruitment of individuals with antler size below the threshold remaining in the population by 1.1, 1.2, and 1.5 respectively. For each of these, we re-calculated reproductive value from the IPM. Finally, we standardized the resulting reproductive value to better represent males' contribution per age group within the population.

Results

Fundamental Functions

Antler length had a positive influence on survival and recruitment rates (Table 1; Fig. 2, rows a & b) with the exception of senior survival rates, which decreased with antler length. Survival in younger age groups (i.e., calves and juveniles) was positively correlated with antler length, although this relationship was stronger in juveniles (Fig. 2, a.2). Adults with longer antlers were more likely to survive than those with shorter ones (Fig. 2, a.3). For seniors, increasing antler length was associated with a decrease in survival (Fig. 2, a.4).

The number of male offspring recruited per adult or senior male followed similar trends across age classes that were reproductively active (i.e., young adults, adults, seniors; Fig. 2, row b). Within reproductive age groups, the probability of recruiting offspring into the population increased with antler length.

Growth, measured as the association between antler length at years t and $t + 1$ (Table 1) showed positive trends (Fig. 2, row c). However, the regression lines crossed the zero-growth line for all age classes, indicating that antler growth rate declines with antler size (Fig. 2). In calves and juveniles, mean antler growth presented great variation around the regression line. For calves especially, mean antler size at $t + 1$ was as much as 35 times the size at t. Regression lines showed a much tighter fit in adults and seniors, reflecting a consistent growth of antlers for these age groups.

The inheritance function is understood as the correlation between father's antler length at siring to offspring antler length when recruited to the population (Table 1). As expected, the slope value for D was close to 0 (Fig. 2, row d).

IPM Demographic Parameters

The stable antler size distribution was characterized by a high proportion of males with small antlers (0–30 cm), representing the high percentage of calves and juveniles that grow small antlers during their first and second year (or do not grow them at all). Representation in the population decreased with antler size (Fig. 3a), with very few individuals possessing antlers over 90 cm. The estimated mean antler length for adult and senescent males was 56.58

cm, which is similar to the average antler size calculated from the raw data (56.08 cm).

The relative reproductive value estimated by the IPM increased in relation to antler size (Fig. 3b). However, the reproductive potential for age groups in which antler length increases rapidly (1–3 years old) showed higher slopes than older age groups at equivalent antler sizes. Thus, the relative reproductive value decreased proportionally in older individuals (>8 years old; Fig. 3b).

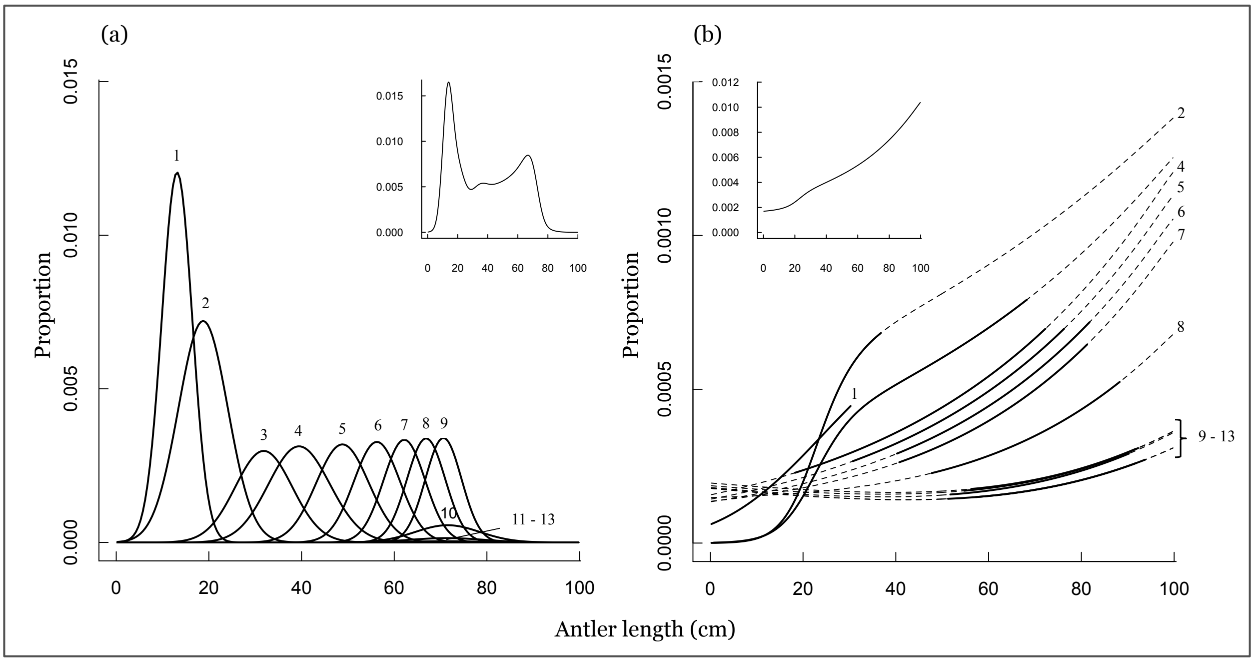

Figure 3. a) Stable antler size distribution (SAD) of antler length per age class for red deer on the Isle of Rum, Scotland, 1972–2012. Each line represents the antler size distribution associated with ages 1 to 13 (see numbered labels). The inset plot shows the additive SAD for the whole population. b) Relative reproductive value (rRV) as a function of antler length per age class. Each line represents the antler size distribution attributed to ages 1 to 13 (see numbered labels). Solid lines denote rRV distributions within age group antler length ranges, and dashed lines represent distributions predicted from the integral projection model for antler lengths out of age group ranges. The inset plot shows rRV for the whole population. The stable antler size distribution is characterised by a high proportion of males with small antlers, and few individuals with antlers over 90 cm. The estimated mean antler length was 56.58 cm. Relative reproductive value increased in relation to antler size, and decreased proportionally in older individuals (i.e. ages classes over 8 years old).

Elasticity Analysis

Population mean antler length and mean reproductive value were sensitive to function parameters (Fig. 4). The upward change in the intercepts and slopes of the survival and growth functions had stronger effects on mean antler length and mean reproductive value than changes in any other function. Both were extremely elastic to changes in juvenile survival parameters (Fig. 4, a.1 and b.1); this is not unexpected given that the effect of antler length on juvenile survival was significant. Perturbations to the growth function showed consistent positive effects on mean antler length. Antler length was primarily determined by changes in the adult group (Fig. 4, a.2). Mean reproductive value was particularly elastic to perturbed parameters associated with calf and adult antler growth (Fig. 4, b.2) and to an upward change in adult parameters for the recruitment function (Fig. 4, b.3).

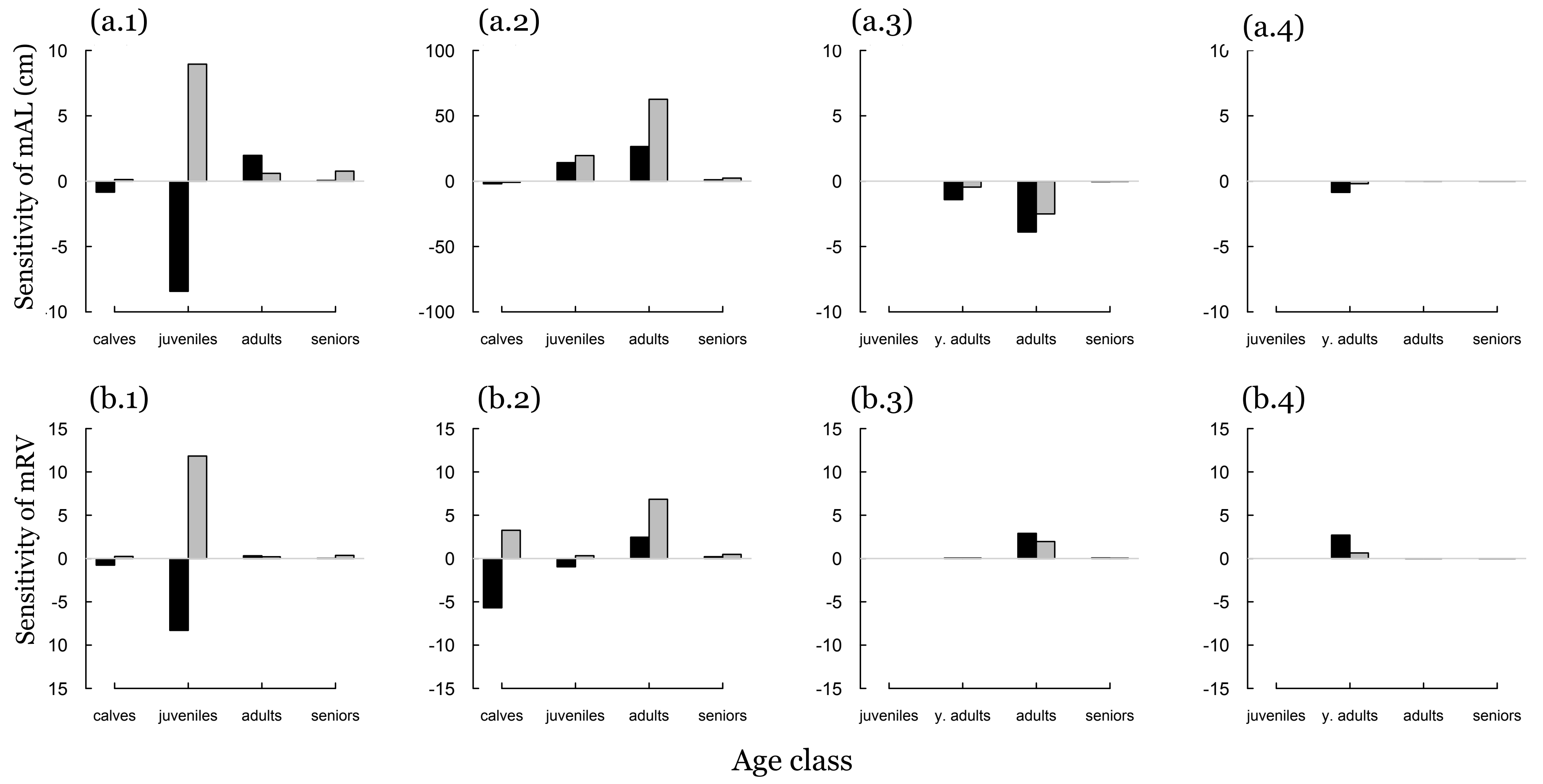

Figure 4. Elasticity of population mean antler length (mAL) and mean reproductive value (mRV) to perturbation of integral projection model function parameters for red deer on the Isle of Rum, Scotland, 1972–2012. Black and grey bars represent the change in mAL or mRV following perturbation to intercepts and slopes, respectively. Age classes for survival (a.1 and b.1) and growth (a.2 and b.2) functions are represented by calves (0–1 yr), juveniles (2–3 yr), adults (4–8 yr), and seniors (>9 yr). Age classes for the recruitment (a.3 and b.3) and inheritance (a.4 and b.4) functions are defined as juveniles (1–3 yr), young (y.) adults (4–6 yr), adults (7–11 yr), and seniors (>12 yr). Survival and growth functions had stronger effects on mAL and mRV than changes in any other function. Although mAL and mRV were elastic to changes in juvenile survival, antler length was determined mainly by changes in the adult group.

Harvesting Analysis

For simulated trophy hunts of 10%, 20%, and 50% of males with antler length greater than the population mean, the values for mean antler length were 55.90, 55.19, and 53.17 cm, respectively, and corresponded to uniform culling rates of 11.9, 21.5, and 49.5%, respectively. The same trophy hunting resulted in population mean reproductive values of 4.47, 4.20, and 3.42, respectively. These were equivalent to uniform culling rates of 35.3, 53.8, and 72.7%. As expected, the simulation of trophy hunting quotas of 10%, 20%, and 50% in our modified IPM skewed the stable antler size distribution towards individuals with smaller antlers (Fig. 5a). In contrast, changes in mean antler length appeared to be very small.

Under the same harvesting simulation, the relative reproductive value of individuals with antler length above the population mean experienced a rapid decrease (Fig. 5b). The removal of 10%, 20%, and 50% of males in the population also showed proportionally higher relative reproductive value for individuals with shorter antlers (Fig. 5b). Overall, after the harvesting simulation, the mean relative reproductive value decreased with higher quotas of trophy hunting for adults and seniors (Fig. 6). In addition, we ran an IPM in which we included the compensatory responses of smaller antlered males remaining in the population after harvesting quotas were simulated (see Supplemental Material). However, we found no evidence of a significant effect of compensatory responses (Fig. S2, Supporting Information).

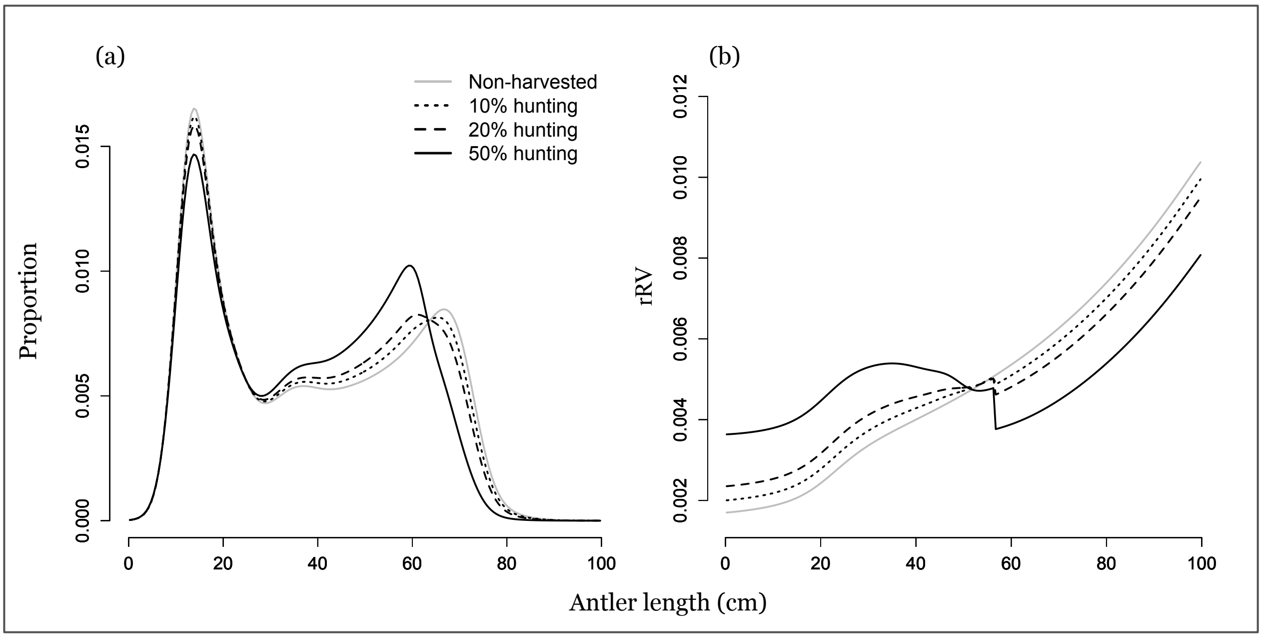

Figure 5. Harvesting effects on a) the stable antler size distribution (SAD) and, b) the relative reproductive value (rRV) of male red deer on the Isle of Rum, Scotland, 1972–2012. Grey lines represent a non-harvested population. Dotted, dashed, and full black lines represent trophy hunting regimes of 10%, 20%, and 50%, respectively. No significant change in the shape of either distribution (SAD and vRV) was detected unless 50% of the male population was hunted.

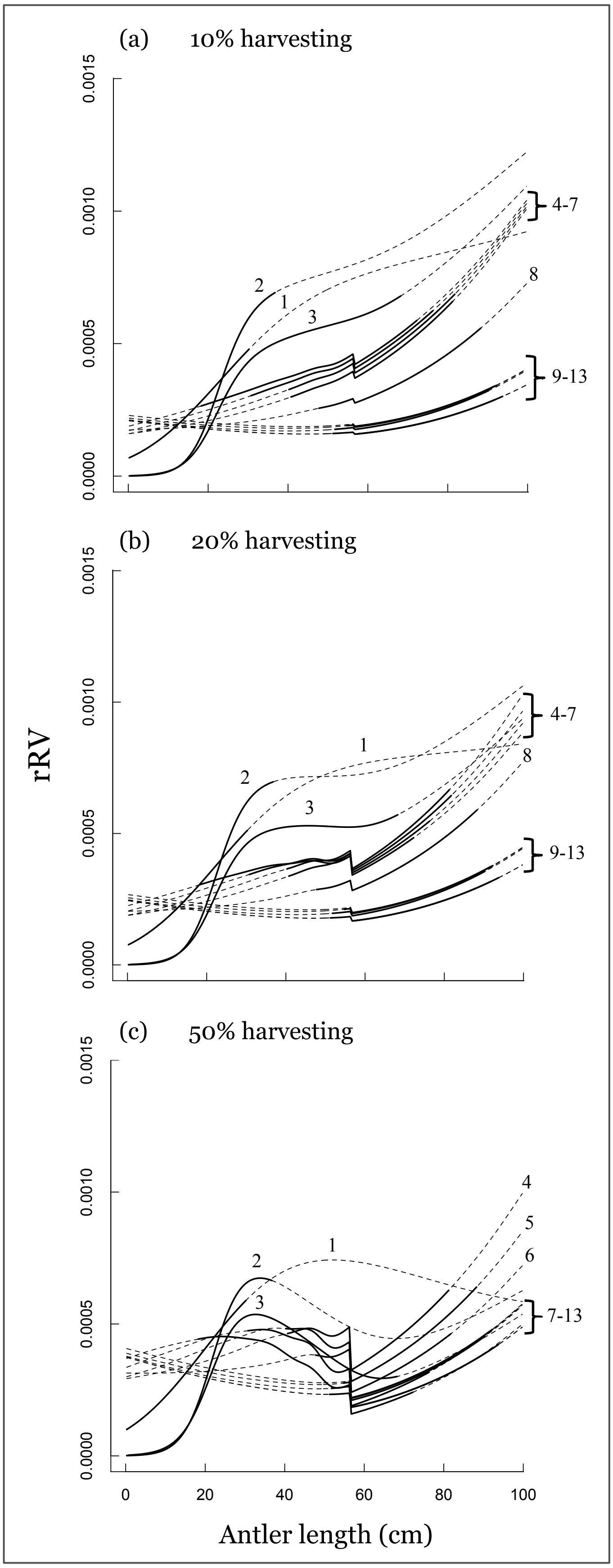

Figure 6. Change in relative reproductive value (rRV) per antler length and age class following different trophy hunting rates for red deer on the Isle of Rum, Scotland, 1972–2012. Numbered lines represent antler size distributions associated with ages 1 to 13. We ran simulations of 10% (a), 20% (b), and 50% (c) of harvesting. Simulation of trophy hunting quotas of 10%, 20% and 50% decreased the rRV for adults and

Discussion

The demographic consequences of selectively harvesting wild ungulates remain uncertain in spite of trophy hunting being a popular recreational activity worldwide (Milner et al. 2007, Palazy et al. 2011). The literature suggests that harvesting of males in mammals does not affect population dynamics significantly (Mysterud et al. 2002). In other words, the population dynamics of males is determined primarily by the number of females. However, the phenotypic attributes of males in future populations are determined by the reproductive value of males, and the fidelity with which antlers are passed from parents to offspring. In addition, males are typically culled by fee-paying hunters and generate more income than females (Clutton-Brock et al. 2002). Taken together, these insights have led to the suggestion that harvesting of adult male ungulates for antler trophies may represent a sustainable conservation tool. The approach we present here, despite some limitations, has shown how IPMs can be used to gain an understanding of the consequences of hunting on male reproductive value, a measure of relative fitness, and the distribution of antler sizes within the population.

Under unmanaged conditions, the fundamental functions of our IPM revealed, for some age classes, a noteworthy relationship between antler length and key demographic processes. Adults with larger antlers were more likely to survive and recruit individuals into the population, a finding that is consistent with the notion that antler size reflects the health of an individual (Hamilton and Zuk 1982; Andersson 1994; Malo et al. 2005*b*), and confers higher reproductive success (Clutton-Brock 1988; Andersson 1994; Kruuk et al. 2002). A stag's ability to defend a harem is closely related to its ability to win fights (Clutton-Brock et al. 1979; Clutton-Brock 1981, 1988), and it can be expected that individuals with smaller antlers have a higher risk of being evicted from potential territories, and thus, a reduced probability of holding harems (Carranza et al. 1990), or being injured during rut. Although we exclusively considered demographic processes as influences of antler size, Kruuk et al. (2002) reported the same relationship between antler size and breeding success for males of the same population after accounting for environmental effects. Given these pronounced associations, trophy hunting has the opportunity to impose considerable impact on the male component of the population. However, our study revealed that this was not always the case.

Inheritance in the IPM (i.e., the correlation between the parental trait at age *a* and the offspring trait at age 1) was low. This function should not be confused with heritability (Coulson 2012). Previous studies have reported that antler size has a low heritability within this red deer population (Kruuk et al. 2002, 2014). It is important to stress that the inheritance function in our study was particularly susceptible to measurement error resulting from the estimation of spike length for some individuals. Additional biases may also have arisen from male calves failing to survive to later ages. However, we do not believe our results to be strongly affected by these potential biases because the responses of mean antler size and reproductive value to changes in the inheritance function parameters were relatively small.

Our results show that mean antler size is highly elastic to parameters in the growth function. This is unsurprising because to evolve a larger or smaller trait, it is necessary to alter how long an individual develops the trait for, or the speed at which the trait develops. In contrast, the reproductive value of individuals was most elastic to the survival function. In a long-lived species like deer, population growth rate, a measure for population-level fitness, is usually most sensitive to survival rather than fertility (Coulson et al. 2004). Similarly, we report that relative reproductive value and mean antler sizes are sensitive to selective harvesting only when culling rates are as high as 50%. These results suggest that lower levels of trophy hunting are unlikely to have a large effect on key aspects (i.e. survival and reproduction) of hunted populations and are in agreement with conclusions from previous studies (Mysterud 2011; Traill et al. 2014).

We obtained results from a simple model. First, we did not include the female component of our study population. This precluded us from studying aspects of population dynamics in a system that is largely female dominant. Females do not develop antlers and no maternal effects have been found to significantly influence antler size (Kruuk et al. 2002, 2014). Therefore, we did not explicitly model this aspect of our study system. Because of the above, we do not expect our focus on males to be entirely inappropriate.

Our model did not include the effects of density dependence or environmental stochasticity, both of which are known to play important roles in shaping population dynamics (Coulson et al. 2004) and antler development. The nutritional consequences of increased population density are influential in determining antler size in red deer (Clutton-Brock and Albon 1989; Kruuk et al. 2002; Schmidt et al. 2007). In deer species, habitat quality influences not only the absolute but also the relative size of antlers (Ramanzin and Sturaro 2014), and males are more susceptible to bad weather conditions than females (Pelletier et al. 2012). Selective culling experiments have reported that reductions in female density often lead to increases in male numbers (Clutton-Brock et al. 2002). However, for sexually dimorphic species, it remains unclear whether males are sensitive to either female or male densities, or a combination of both (Bonenfant et al. 2009). Therefore, and because the focus of our study was to investigate purely demographic effects of selective hunting on mean antler length and reproductive value, including density dependence and environmental stochasticity would have limited our ability to attribute our results to hunting exclusively. Nevertheless, we are aware these are important variables in determining demographic parameters in wild populations and suggest that future models should include them to obtain results more illustrative of the effects of trophy hunting on wild populations of red deer.

Integral projection models offer a powerful tool for understanding the phenotypic and life-history consequences of harvesting (Bunnefeld and Keane 2014; Traill et al. 2014). Our study offers valuable insights into how trophy hunting may influence reproductive value and mean antler size in red deer at unusually high hunting quotas (>50%). Our findings lead us to the tentative conclusion that a trophy hunting rate between 10% and 20% is unlikely to have a substantial impact on mean antler size.

Acknowledgements

We are thankful to the Red Deer Project and to the Scottish Natural Heritage Isle of Rum National Nature Reserve for making use of the long-term dataset possible. We are equally grateful to all fieldwork assistants and volunteers who have contributed to data collection on individual red deer over the past 35 years and to C. Walling and J. Huisman who constructed the red deer population genetic pedigree. Finally, we thank T. H. Clutton-Brock, J. P. Pemberton, and L. E. B. Kruuk for managing and funding the long-term red deer study on Rum, and members of the Eco-Evolutionary and Demography group (E2D) from the Department of Zoology, University of Oxford, for valuable ideas and comments. This project was funded by grants from the Natural Environment Research Council (NERC) the European Research Council (ERC), and the National Commission for Scientific and Technological Research (CONICYT)'s International Doctorate program (Chile).

Supporting Information

Data Formatting

The data used in this project was individual-based information on males from the red deer population of the Isle of Rum, Scotland. Each row in the dataset corresponded to information of an individually identified male in a particular year of study between 1972 and 2012 (see Table S1 as an example). The information per individual was organized similarly to Coulson (2012).

Table S1. Example of data structure for 2 individuals of male dataset from the Isle of Rum.

Code[a]	Cast year[b]	Age[c]	Survival[d]	Reproduce[e]	No. males[f]	Antler length (cm)[g]
EID01	2000	9	1	1	5	80.4
HRM90	2009	9	1	0	0	70.9

[a] unique combination of names and numbers to individually identify males from the population.

[b] deer year running from 1 August to 31 July that indicates time t at which an individual cast its antlers.

[c] an integer representing the year of the male at time t. For instance a calf born in May 2000 (i.e., time t) would be 1 year old anytime after August 2000 (i.e., time $t + 1$). Thus, when the same male cast his antlers in April 2004 (i.e., time $t + 4$), he was considered to be 4 years old.

[d] survival of an individual using 1 when a particular male was seen alive, and a 0 when the male was seen dead. This data was gathered between 1 August of year t and 31 July at year $t + 1$.

[e] individual denoted with a 1 when it produced a live male offspring and with a 0 when no male offspring were identified for the male at year t.

[f] number of male offspring recruited by a single individual at year t that survived to recruit to the population in August of year $t + 1$.

[g] the length of antlers (cm) collected during the casting season (Mar–May) at year t.

Complementary results

We simulated reproductive compensatory responses of smaller males once larger trophies were removed from the population at 10%, 20% and 50% rates. To do this, we multiplied the probabilities of recruitment of individuals with antler size below the threshold remaining in the population by 1.1, 1.2 and 1.5 respectively. For each of these, we re-calculated RV from the IPM. We standardized the resulting RV to better represent males' contribution per age group within the population.

Results of compensatory responses of smaller males are shown in figure S1.

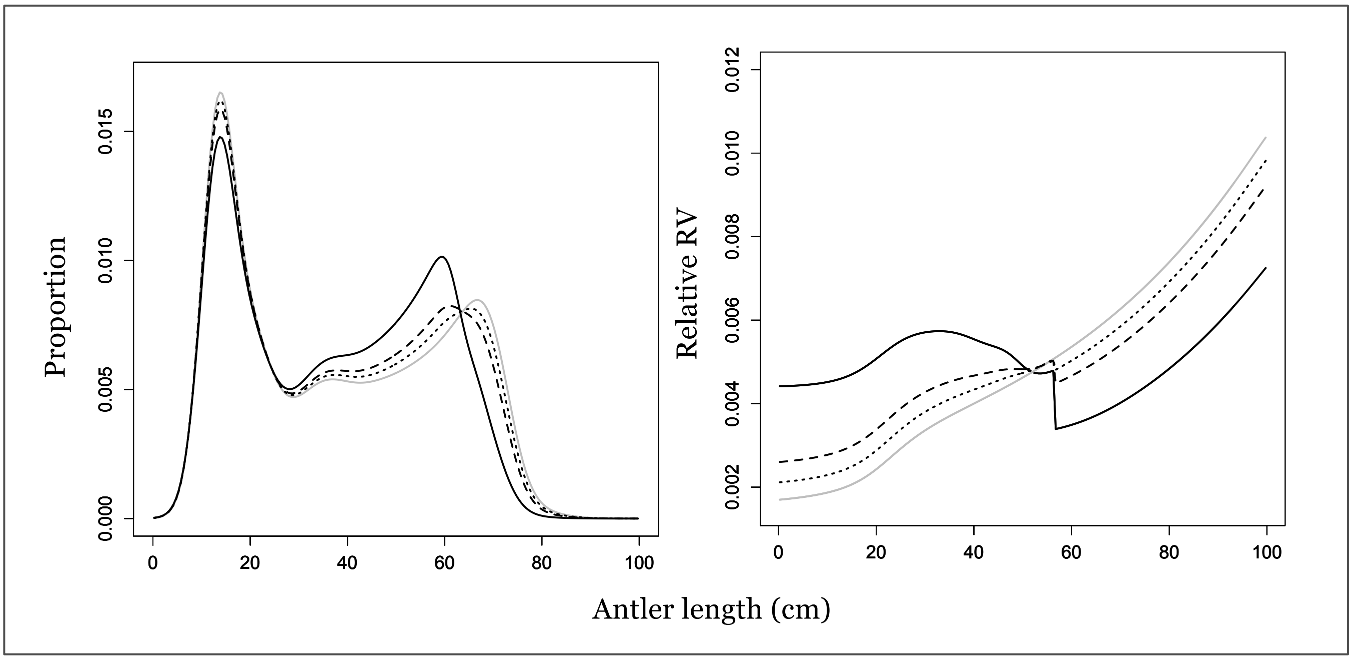

Figure S2. Harvesting effects on a) the stable size distribution (SAD) and, b) the relative reproductive value (rRV) once compensatory responses of smaller red deer males remaining in the population were included. Grey lines represent a non-harvested population. Dotted, dashed and full black lines represent trophy-hunting regimes of 10%, 20% and 50%, respectively.

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Chapter 6

Discussion

To respond to the challenges caused by rapid human population growth, conservation research and implementation need to work collaboratively in order to develop efficient and realistic strategies to tackle and predict emerging human-wildlife impacts. These are certainly varied and complex, and when developing into conservation conflicts they require a multidisciplinary approach at the appropriate scale to identify impacts and develop flexible management frameworks on the ground. Throughout this thesis, I have examined two of the preliminary steps involved in developing efficient approaches for planning long-lasting solutions in conservation conflicts: the gathering of ecological data (Chapters 2 and 3) and the testing of the efficiency and consequences of conservation management options before they are applied in the field (Chapters 4 and 5). In this discussion, I briefly evaluate the importance and applicability of my findings. Specifically, I look at three general questions that cover the main insights gained from my thesis and the general implications for future work in this area.

Are temporal and spatial scales important when studying conflicts in conservation?

The short answer is, yes. When conflicts arise the first step is to identify them. But what does this mean? When does an interaction between human activities and wildlife become a conflict? Who does this specific conflict affect? The answer to all these questions relate to different aspects of human-wildlife impacts, but most of them encompass time and space. For instance, throughout this thesis, I used the case study of conflicts due to crop-raiding by African elephants (Chapters 2-4), which has tended to increase across the continent over the last decade. Yet, elephant crop-raiding is not a new problem. Since the pre-colonial period, wild elephants have raided people's crops causing food shortages, displacing settlements and/or preventing agricultural activities (Game Department of Uganda 1924; Naughton-Treves et al. 1999). So why do the current levels of competition for resources seem to be a problem between people and elephants? There is no simple answer to this question, but the temporal period over which we frame conflict development says a lot about the impacts we face nowadays. Clearly, human population density, agricultural expansion, the protection of elephants (i.e. Appendix I, CITES), the illegal trade in ivory, and local policies are aspects that nowadays have increased the level of conflict, or the perception of conflict, relative to pre-colonial times. Therefore, the time frame over which we study conservation conflicts is important not only in helping us determine when interactions develop into negative impacts but also allowing us to identify the relevant stakeholders involved (Redpath et al. 2015).

In Chapter 2, I found that the drivers of conflict and predictions for future trends were dependent on the temporal scale used, and that although the levels of conflict perceived in the study area had risen in the last decade (Songhurst 2012), the number of crop-raiding incidents in the region had decreased. These findings provide valuable information for future studies as well as potential management options in the Eastern Panhandle. It is important to be clear about how people represent an issue in terms of a particular scale before interventions take place (Young et al. 2013), because management decisions can be controversial and stakeholders from different groups often seek to move the decision-making process to a scale that favours them (Linnell 2015). In my case study, depending on the temporal scale used, stakeholders with different interests could claim that crop-raiding by elephants is likely to increase, decrease or stay the same in future years.

Furthermore, in Chapter 2 I found that the reduction in the number of raiding incidents over the last eight years was related to the agricultural land allocated to people. Our results concur with other studies that found conflicts in conservation are a spatial phenomenon (e.g. Sitati et al. 2003), highlighting the relevance of considering interactions between temporal and spatial scales when looking at approaches to tackle conservation conflicts. The importance of considering the consequences of spatiotemporal interactions also became clear in Chapter 3. For example, elephant space-use patterns changed depending on the period of the year or day considered (i.e. dry, wet and crop-raiding seasons versus day/night times), and therefore if mitigation methods are applied in the field time and space should be taken into account. Without a clear understanding of the spatial scale at which conflicts occur inadequate conservation management strategies can be put into practice. There has been evidence of ‘mis-framing’ conflicts, when local conflicts may be linked to larger scales and patterns of political relationships and biodiversity used

(Meadowcroft 2002). In our study system, it may be that elephants use corridors and do not move away from fenced areas only in the eastern Panhandle, but then behave different in the rest of the country. Equally, people in the eastern Panhandle have only shared resources and space with elephants during the last 20 years, and therefore in other parts of the country local communities may show more tolerance towards elephants if they have been living around them for longer. Therefore, applying the same management criteria across Botswana is unlikely to be effective at mitigating this conflict. A single spatiotemporal framework is unlikely to provide the solution. Rather, multiple spatial and temporal scales need to be considered in socio-ecological systems (Kok and Veldkamp 2011) when deciding on the appropriate management scale (Redpath et al. 2015). This will certainly avoid disappointment in conservation management and policy that may arise from the failure to take into account the spatial, temporal, social, political and cultural scale and cross-scale dynamics in human-environment interactions (Cash et al. 2006). Finally, we cannot forget that both ecological and social systems are flexible and in constant change. Consequently, considering spatial and temporal dimensions is an essential part of the management of conflicts, and particularly when monitoring conservation practices implemented in the past and adapting them to future challenges.

Why should the impact of conservation interventions be assessed?

As mentioned in the previous section, socio-ecological systems in which human-wildlife impacts take place are permanently evolving. To adapt to these changes, the first step is to test the effectiveness of potential solutions in the field through monitoring and experimentation. Ideally, after collecting all possible information about the conflict under study, conservation managers should evaluate potential mitigation methods thereby improving conflict understanding, reducing the level of uncertainty and adapting management approaches accordingly to evidence found in the field (Redpath et al. 2015). When developing my ideas for Chapters 4 and 5, I was surprised at how often the development of conservation management was “played by ear”.

Sutherland et al. (2000) pointed out that conservation practice is not well supported by background knowledge and is largely based on anecdotal evidence. This phenomenon is the result of the combined effects of inaccessible research for practitioners on the ground (Arlettaz et al. 2010), and the inertia of myth-based beliefs that prevent managers from adopting alternative practices (Sutherland et al. 2004). Practical implementation and the assessment of practices in conservation should be an integrated part of the scientific activity because in the absence of evidence, or access to it, conservation managers have been forced to rely on limited and often experience-based information (Pullin et al. 2004). For example, in Broadland (UK) – an international important wetland with the highest statutory protection under European law – more than 70% of information sources used were anecdotal (i.e. either ‘common sense’, ‘personal experience’ and ‘speaking to other managers in the region’; Sutherland et al. 2004), and only 2.4% of the information used was obtained from the scientific literature. There is an urgent need to use evidence-based conservation (Pullin and Knight 2001; Sutherland et al. 2004), and that conservation management needs to adopt a similar radical revolution than the one transformed medical practice in the 1970s’ (Sutherland et al. 2004). But conservation differs from medicine in several ways, starting from the fact that the socio-ecological systems involved in conservation are far more complex than human bodies involved in medical practice, and medical research is much better resourced than conservation science (Fazey et al. 2004; Sutherland et al. 2004; Stewart et al. 2005; Adams and Sandbrock 2013). Also, there is a comparatively low quality of methodologies and a lack of access to relevant studies in conservation in comparison to medical research (Stewart et al. 2005; Pullin and Knight 2001). Consequently, it is not surprising that evidence is often lacking in many areas of conservation biology, and therefore evidence-based frameworks are challenging to employ in natural systems (Stewart et al. 2005).

In Chapters 3 and 4 I highlight the importance of assessing conservation – specifically conflict-related – interventions and informing them, because in both cases (as in countless fields of science) I obtained unexpected results. In the first case, chilli-briquettes modified elephant behaviour but only in the short-term and did not change population numbers in areas of interest; and in the case of male red deer I found that selective harvesting had to remove 50% of the population before significant impacts on trophies and reproduction were detected. Without testing the effectiveness and impacts of these methods it would be difficult and probably ineffective to apply them in the field, surely management decisions would differ from others previously tested, and the consequences of non-assessed trial would probably be mistaken in the ground. Additionally, without sharing these findings it would be hard for future trials to modify those components that could be improved because without an experimental or modelling design helping us to identify the different steps at which we can detect failures in mitigation methods, it is certainly difficult to progress in the use of conflict mitigation strategies.

Because of the above, I strongly support assessing conservation interventions and communicating them, so that as scientists we can increase available evidence and make it accessible for conservation managers. I likewise acknowledge that formal scientific evidence is not always available or not sufficient, in which case a good alternative could be to adopt Adams and Sandbrook's (2013) proposal of expanding the concept of 'evidence-based conservation' to 'evidence-informed conservation'. The latter recognises other sources of useful knowledge for practitioners (e.g. indigenous knowledge) and reflects the idea that conservation decisions should be always based on the best information available. In either case, I argue that communication is a key aspect of conservation research, and in particular of conservation conflicts that appear to be a new branch in conservation science. Conservation actions are rarely documented (Pullin et al. 2004), and neither are research results that are not routinely reviewed nor actively disseminated (Sutherland et al. 2004). Sharing knowledge not only enables informed decisions, but also allows us to standardise the use of non-scientific information (e.g. education programmes, management reports, etc.) and, most importantly, adapt to constantly improving management frameworks. In the field of conflicts in conservation, this has undoubtedly contributed to successful approaches (Cope et al. 2005).

What else is needed to approach and manage conflicts?

The gathering of ecological data and the testing of mitigation strategies is just the beginning of a long and complex process of negotiation, research and feedback between numerous stakeholders with different interests, backgrounds, cultural beliefs, expectations and budgets trying to find a common ground to decrease negative impacts between people and wildlife.

Throughout this thesis I mentioned several times the need for an interdisciplinary approach to tackle conservation conflicts, and the aim of my work was not to cover all of these disciplines. Although the four research chapters I have presented here are a very important to the successful management of conflicts, gathering data and testing mitigation methods for adapting management frameworks represent only a small fraction of the whole process. Redpath et al. (2015) clearly describe the principles and steps towards collaborative conflict management from mapping to managing conflicts in conservation. One aspect not covered in this thesis relates to the social component of conservation conflicts (e.g. people's attitudes, cultural believes and livelihoods). As I hope the reader has noticed throughout this thesis as well as in the several examples I used in it, in most cases conservation conflicts are not issues between people and a certain species but between different groups of people that differ in their interests. Therefore, social sciences and humanities are principal components in approaching conservation conflicts (Manfredo and Dayer 2004) and both crucial to finding ways for people and wildlife to co-exist. Equally, the role of economics is more and more relevant to conflicts when looking at alternatives to reduce or prevent human-wildlife impacts by, for example, returning benefits to local communities that bear the costs of living with wildlife or attributing cost to those who enjoy its benefits (Van Dyke 2008).

I have no doubt that I have probably omitted other important areas of knowledge to approach conservation conflicts, and that many more disciplines are likely to play a fundamental role in future studies. Nevertheless, conflicts in conservation are a serious and growing problem for wildlife and people. Minimising them could not only offer a very valuable contribution towards reducing the loss of biodiversity worldwide, but also support local communities and their way of life in the process.

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Appendix

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

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The demographic consequences of elephant poaching: insights from rapid population assessments across space and time

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

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Q 1

Abstract Crop losses to foraging elephants are one of the primary obstacles to the coexistence of elephants and people, and one of the causes of elephant population decline. Understanding if some individuals in a 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' livelihoods. We used camera traps to study the crop foraging behaviour of African elephants *Loxodonta africana* in farmland adjacent to the Udzungwa Mountains National Park in southern Tanzania during |October 2010–August 2014. Camera traps placed on elephant trails into farmland detected elephants on 336 occasions during the study period. We identified individual elephants for 126 camera-trap detections. All were independent males, and we identified 48 unique bulls aged 10–29 years. Two-thirds of the bulls identified were detected only once by camera traps during the study period. 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, although young males dispersing from maternal family units also consume crops in Udzungwa. We found a large number of occasional crop-users (32 of the 48 bulls identified) and a smaller number of repeat crop-users (16 of 48), suggesting that lethal control of crop-using elephants is unlikely to be an effective long-term strategy for reducing crop losses to elephants.

Keywords Crop foraging, HEC, human–elephant coexistence, PAC, problem animal control, Tanzania, Udzungwa Mountains

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Introduction

The population decline of African elephants *Loxodonta africana*, categorized as Vulnerable on the IUCN Red List (Blanc, 2008), is one of the most pressing conservation issues currently facing sub-Saharan Africa (Maisels et al., 2013; Wittemyer et al., 2014; Wasser et al., 2015; Chase et al., 2016). Another challenge for elephant conservation in the long term is coexistence with people, in particular where elephants consume or damage crops (Hoare, 2015). Given their large ranges and long-distance movements (Graham et al., 2009), elephants spend considerable time outside 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 property, death of livestock, and injury (and in some cases death) of people (Thouless, 1994; Ngure, 1995; Kangwana, 1996; Lahm, 1996). These impacts on people and their livelihoods can lead to retaliatory and legal killing of elephants under Problem Animal Control policies (Hoare, 2000, 2015). 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 to 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 is a high-risk, high-gain strategy for male elephants to maximize their nutrient intake while minimizing the time spent and distance travelled while foraging (Sukumar & Gadgil, 1988; Chiyo & Cochrane, 2005). Crop foraging has also been observed in males of other polygamous species, including at least nine species of African primates (Trivers, 1985; Davenport et al., 2006; Wallace & Hill, 2012). In contrast, females may not exhibit this behaviour as often as males because of the potential risk to dependent offspring in agricultural landscapes (Sukumar & Gadgil, 1988). This is not always the case, however, 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, as they commonly rely on interviews with farmers, who are usually not formally trained in sexing and ageing elephants (Smith & Kasiki, 2000).

Repeat or habitual crop use by African elephants has been reported previously (Hoare, 2001; Chiyo & Cochrane, 2005; Chiyo et al., 2011, 2012). A study in Amboseli, Kenya, found considerable variation in crop use among individuals (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; for example, 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 investigate behaviour that could be challenging to study using direct observations (Griffiths & van Schaik, 1993); however, they have not previously been used to study crop foraging behaviour in elephants.

We used camera traps to investigate patterns of crop use and to establish the number, sex and age structure of crop-using elephants along the boundary between Udzungwa Mountains National Park and adjacent farmland in south-central Tanzania during October 2010–August 2014. We discuss the implications of our results in the context of current policies for managing crop losses to elephants at our study site in Tanzania, and more generally across Africa where elephants and people co-occur.

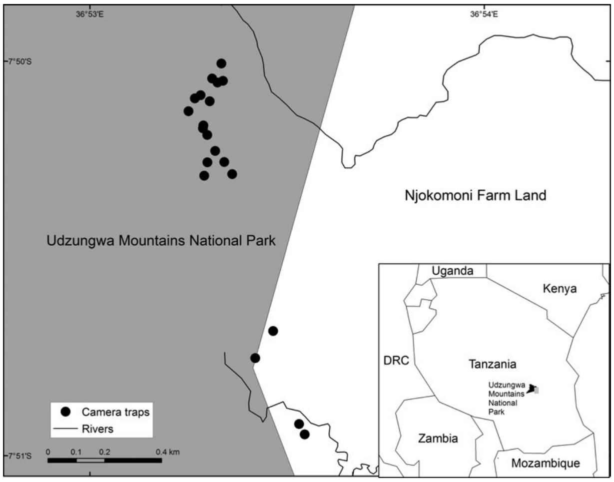

FIG. 1 The study area in Udzungwa Mountains National Park and the adjacent farmland of the Njokomoni area, Tanzania.

Study area

The study site is in Njokomoni, a small area of farmland (c. 2.5 km^2) directly adjacent to the Udzungwa Mountains National Park 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 savannah elephants (Nowak et al., 2009). After heavy poaching between the 1960s and 1980s led to the near extinction of elephants in the Udzungwa Mountains, this 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 people from the villages known as Mang'ula A and Mang'ula B, both located along the east-facing escarpment of the Udzungwa Mountains (Fig. 1). The vegetation along the eastern side of the Park comprises lowland rainforest and miombo woodland, which extend to the Park boundary. Crop losses to 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 comprises > 120 farms of 0.25–2 ha. Over 30 crops are cultivated in a mixed intercropping system (Joram, 2011). The wet season spans November–May, and the dry season June–October (Lovett & Wasser, 1993). Farming activity occurs year-round, with rain-fed farming during the wet season and irrigated farming during the dry season, facilitated 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 Park identified Njokomoni as a hotspot of elephant crop use, as $> 75\%$ of verified reports of crop losses came from farmers in Njokomoni (Joram, 2011). The major reason for high levels of elephant activity in this area is the lack of a buffer zone between the Park and adjacent farms (Joram, 2011).

Methods

Camera trapping

During October 2010–August 2014 a total of 23 camera-trap sites were monitored along a c. 1 km stretch of the eastern boundary of Udzungwa Mountains National Park. Effort and coverage were variable over this period, with 1–10 camera traps active each night during October 2010–April 2012, 1–3 during August 2012–January 2013, and 10 during July 2013–August 2014 (Supplementary Table S1). Heat and motion camera traps (Cuddeback Capture, Cuddeback, De Pere, USA) were placed along known elephant pathways to and from farms, and were shifted according to elephant activity, as indicated by the presence of elephant dung and tracks. Given the limited number of cameras available, only one camera trap was placed per trail. To obtain suitable portrait photographs for individual identification, camera traps were mounted on trees at a height of 3 m and oriented downwards to 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 s (the minimum possible for the model). Batteries were replaced and SD cards downloaded every 2 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 the farmland area or back into the Park). In addition, images were categorized according to whether or not they were suitable for individual identification. For those images that were deemed suitable, the elephant's sex and, when possible, age were determined, and individuals were identified based on unique characteristics of their pinnae and tusks (Moss, 1996). The sexing and ageing of elephants was carried out by JS following training at the Amboseli Elephant Research Project, Kenya, on elephants of known age.

Monitoring crop losses to elephants

Monitoring of crop losses to elephants in the focal area was carried out following a modified protocol developed by the African Elephant Specialist Group of IUCN (Parker et al., 2007). Two local enumerators employed by the Southern Tanzania Elephant Program responded to calls from farmers reporting crop loss incidents, and surveyed farms within the study area 6 days per week for additional unreported incidents. They recorded the date and location of the incident, the types 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 for analysis: the entire study period and the final year of monitoring (July 2013–August 2014). We ran a temporal analysis comparing the timing of camera-trap captures of elephants travelling 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, as temporal activity at the scale of a single night is unlikely to be affected by inconsistent camera-trap effort. Image time stamps were grouped into 24 one-hour bins (0–23), resulting in a frequency distribution spread over 24 hours.

We also tested for a significant association between the detection of an elephant by any of the camera traps in operation (absence = 0, presence = 1) and the recording of a crop loss incident in the Njokomoni farmland on the following day by enumerators (absence = 0, presence = 1), using data collected during July 2013–August 2014. We arranged corresponding frequencies in a 2 × 2 contingency table and performed a Pearson's χ^2 test of independence to investigate whether observed frequencies were more or less than those expected by chance. We used data from the final year of monitoring, 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 incidence, we correlated the proportion of days in the month for which at least one elephant photograph 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 entire study period and the final year based on individuals identified from camera-trap images (for photographs of two bulls detected multiple times, see Supplementary Plate S1). We also assessed the number of nights that individual bulls had been detected by camera traps, and used this as an indicator of the relative likelihood of a bull visiting 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 (Supplementary Fig. S1).

We investigated the sex and age structure of individuals identified over the 4-year study period. We grouped elephants identified in camera-trap photographs into four age categories (Moss, 1996): 10–14, 15–19, 20–24 and 25–29 years (we did not observe any individuals > 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 clearly visible

Fig. 2 - B/W online, B/W in print

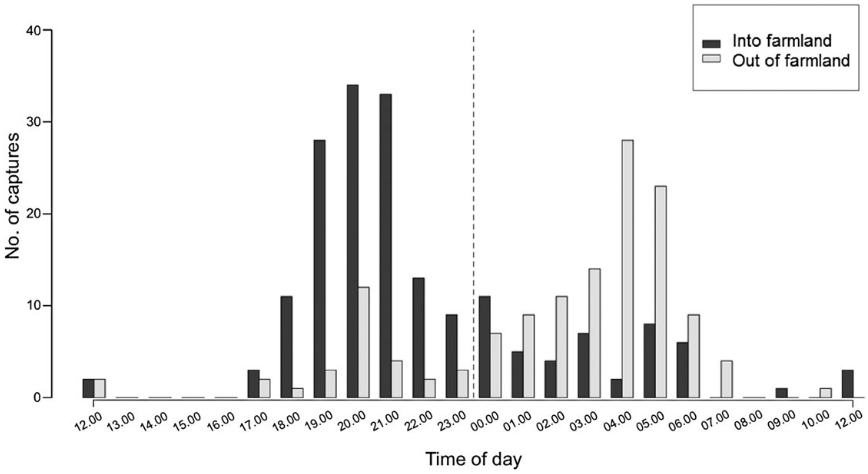

FIG. 2 Temporal pattern of elephant *Loxodonta africana* detections at camera traps placed along the eastern border of Udzungwa Mountains National Park (Fig. 1).

on camera-trap photographs. The head of a male elephant increases in size with age, and takes on a pronounced hourglass shape around the age of 25 (Moss, 1996). For full-body photographs we also used height and body size for ageing. For images of bulls representative of the four age classes used, see Supplementary Plate S2. *R v. 3.0.1* (R Development Core Team, 2014) was used for all statistical analysis.

Results

We obtained 443 photographs of elephants over 5,314 trap-nights, 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 travelling into the farmland predominantly during 18.00–00.00 (median = 19.00) and back into the Park during 00.00–07.00 (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 (Supplementary Fig. S1). During the final year of the study we found that camera-trap data and crop loss incidents as recorded by enumerators co-occurred more than expected by chance ($n = 39$, $\chi^2 = 13.6$, df = 1, $P < 0.001$). Nonetheless there was still a high number of instances when crop losses were reported but no elephants were photographed ($n = 98$), and 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).

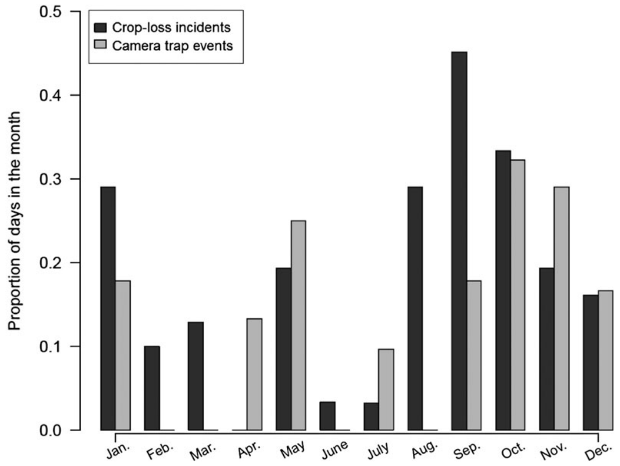

Fig. 3 - B/W online, B/W in print

FIG. 3 Proportion of days in the month for which crop loss incidents were reported, and on which elephants were detected by camera traps along the eastern border of Udzungwa Mountains National Park (Fig. 1).

We were able to identify individual elephants in 37% ($n = 126$) of the 336 camera-trap events. All of the 48 individuals identified were males (Fig. 4). Most of the bulls identified were detected only once by camera traps during the study period (66.7%; Fig. 5), and this pattern was also found during the final year of the study, when camera-trapping effort was constant (70.6%; Fig. 5). A skew towards single detections was also found when we considered only those camera detections of bulls associated with crop loss incidents (Supplementary Fig. S2).

Sixteen individuals were photographed multiple times during the study period (Fig. 5), with one individual detected > 30 times. Five of the 17 bulls identified in the final year of the study were captured on camera multiple times (Fig. 5). The majority of the 48 bulls identified from camera-trap images during the study period were 25–29 years old (Fig. 6). Bulls who were detected multiple times were also primarily of this age group, followed by younger

Fig. 4 - B/W online, B/W in print

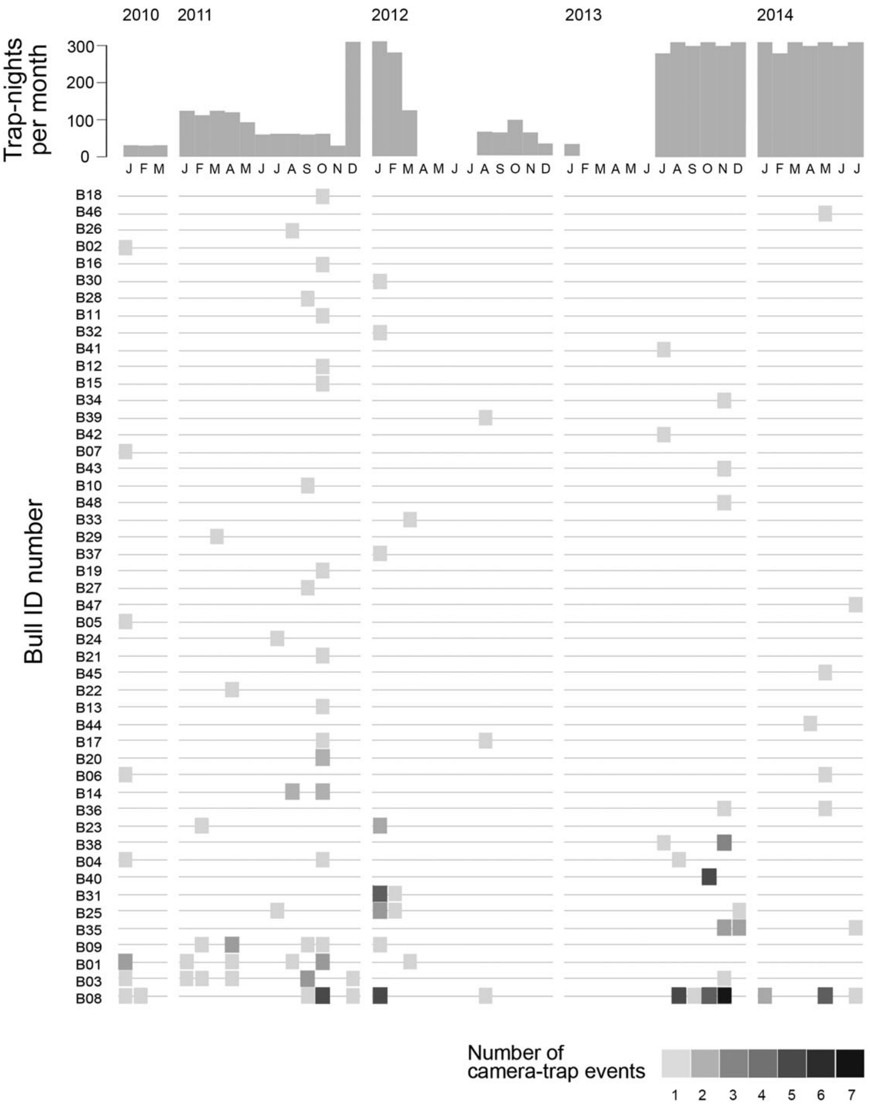

FIG. 4 Camera-trap detection rates for 48 identified bull elephants, in ascending order (from top to bottom) of frequency of detection during the study period (October 2010–August 2014). The histogram shows the sampling effort in trap-nights per month.

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 largely because of the inconsistency in 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 2 consecutive days, and 43% of re-captures occurred within 7 days.

Discussion

In a test of 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 adjacent farmland in south-central Tanzania, we found a distinct pattern of elephant activity, with elephants entering farmland at night and returning to the Park early in the morning, along regular trails. This is consistent with previous findings of avoidance of farmers by elephants, and a propensity for nocturnal crop foraging behaviour (Smith & Kasiki, 2000; Graham et al., 2010; Chiyo et al., 2012; Gunn et al., 2014; Wilson et al., 2015). The evidence that elephants use these trails for the purpose of entering farms and consuming crops is strengthened by the significant pattern of co-occurrence between camera-trap records of elephants, 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 (i.e. bulls photographed while entering farmland did not always consume crops, as they may have encountered risks 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

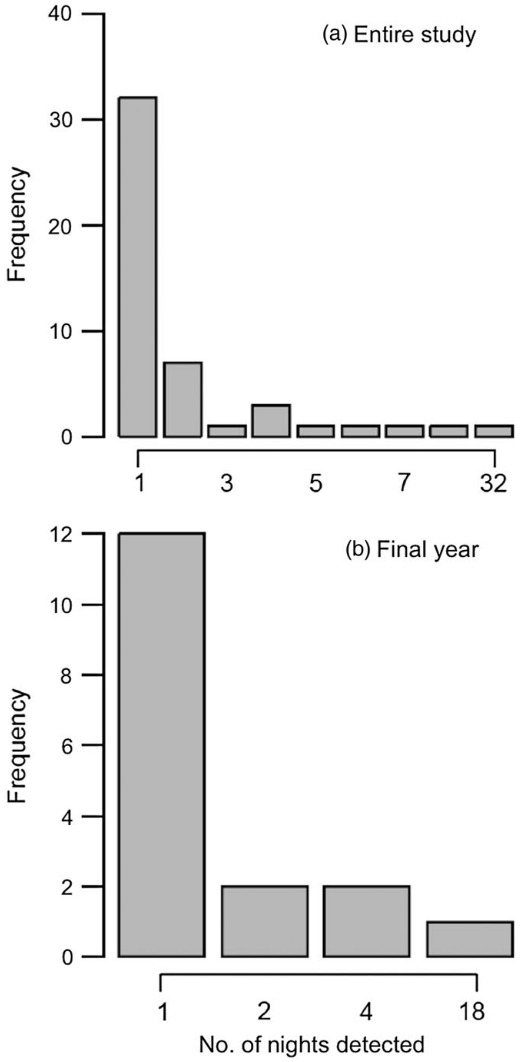

Fig. 5 Frequency distributions of the number of nights on which identified bulls were detected by camera traps (a) for the entire study period, and (b) for the final year only.

Fig. 5 - B/W online, B/W in print

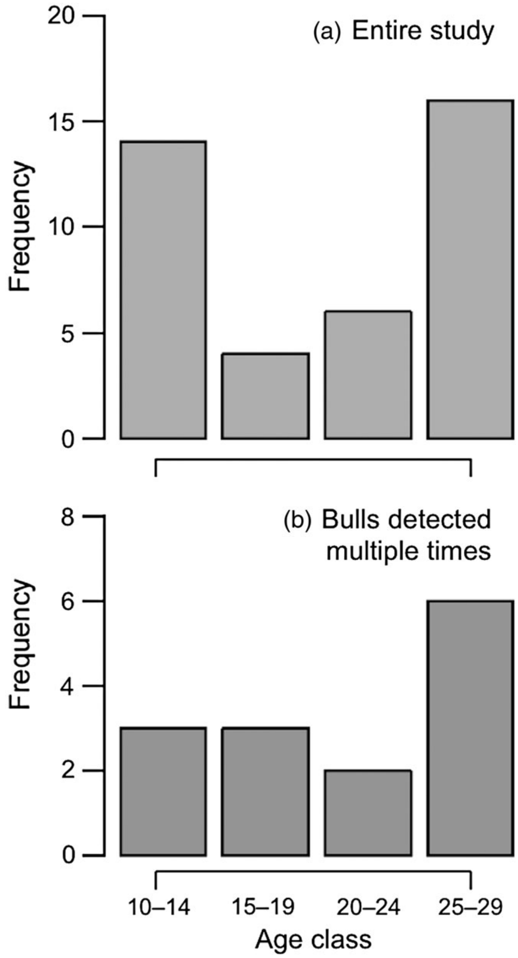

Fig. 6 Age structure of (a) 40 of the 48 bull elephants identified over the entire study period, and (b) 14 of the 16 bull elephants who were detected multiple times during the study period.

Fig. 6 - B/W online, B/W in print

behaviour. Additionally, it may be that bulls occasionally used routes to farmland that were not sampled by our camera traps. Therefore, camera trapping may not be suitable for studying temporal patterns in crop losses to elephants. Nevertheless, we consider camera trapping and enumeration of crop losses to be 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 (Von Gerhardt et al., 2014).

Using standard ways of identifying individual elephants on the basis of tusks and ears, we identified a minimum of 48 bulls in our study area during the 4-year study period. However, reliable individual identification was possible from only c. 37% of the camera-trap detections. 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 felids (Kelly et al., 2008; Harihar et al., 2010).

Most of the bulls identified were aged 20–29 years (55%), followed by younger bulls aged 10–14 (34%) and 15–19 (11%) years, which raises 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 years old, suggesting that crop use may be initiated during male dispersal (Chiyo & Cochrane,

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

Age (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

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 $>$ 40% of crop-using bulls were $>$ 30 years old (Chiyo et al., 2012), whereas we did not identify any bulls over the age of 30 in Udzungwa. This probably reflects the history of poaching in Udzungwa, 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 by camera traps only once during the study period, and the same pattern was evident for the 17 bulls identified in the final year of the study. This suggests that a large number of bulls are occasional crop-users. Sixteen bulls were detected multiple times (2–32) on camera during the study period, suggesting these individuals may be repeat crop-users. There was considerable variation in detection rates of repeat crop-users, with one bull detected four times more frequently than any other repeat crop-user. These are likely to be conservative numbers, and we acknowledge that many elephants may have gone undetected because of the small number of cameras available, the large proportion of photographs from which individual identification was not possible, and the likelihood of cameras failing to record 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, where almost half of the repeat crop-users were bulls aged 25–29 years. Similarly, studies in Kibale and Amboseli 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 that were detected multiple times was highly variable (range 0–681 days, median 13.5 days). Although inconsistent camera-trapping effort complicates the picture, it is possible that some of these potentially repeat crop-users had breaks in visits to the study area. For three of the bulls, the time between successive detections was a year or longer. These results bear some similarity to visitation patterns of forest elephants in the Dzanga Bai, in Dzanga-Ndoki National Park, Central African Republic (Turkalo et al., 2013). Long-term monitoring of the Dzanga Bai indicated 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 implications for strategies to mitigate crop losses to elephants, particularly the legal killing of animals considered to be pests under Problem Animal Control policies, which have been applied across elephant range in Africa and Asia in an attempt to reduce crop losses to elephants (Hoare, 2001; Puyravaud et al., 2016). 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, 2015). Although we found evidence of repeat crop use by elephants, the much larger pool of occasional crop-users supports the argument 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 (a hotspot of elephant crop use; Joram, 2011) suggests that high levels of crop loss at such hotspots do not result from the activity of a few habitual crop-users. Lethal elimination of crop-users carries the risk of misidentifying individual elephants, and can also be used as justification for elephant poaching or ivory accumulation under the pretext of Problem Animal Control (Masunzu et al., 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, 2015), and therefore our findings are 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

TJ, KN and JS conceived the study and collected and analysed data. RP and JC conducted data analysis. All authors contributed to writing the article.

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The demographic consequences of elephant poaching: insights from rapid population assessments across space and time

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SUMMARY

1. Illegal killing for ivory is a huge threat to the survival of the African elephant (*Loxodonta africana*) across its current range. Poaching targets older bulls and females for their larger tusks, thereby disrupting the reproductive potential and social structure of a given population. Quantifying the resulting changes in population structure is key to understanding and detecting the effects of poaching.

2. We analyse data collected using a rapid demographic assessment (RDA) method implemented in six sites across Tanzania to examine the likely impacts of poaching on population structure, as well as on the level of tusklessness. We examine whether populations experiencing contrasting levels of poaching in 2009 show significant differences in their age structure, operational sex ratio (i.e. adult males to adult females), calves to adult female ratio at the group level, and proportion of tuskless individuals. We then compare similar metrics between populations sampled in Ruaha National Park in 2009 and again in 2015 following a suspected increase in poaching.

3. Samples from elephant populations experiencing medium and high levels of poaching in 2009 were characterised by fewer calves and old individuals, a reduced number of adult males for the number of adult females, and a lower ratio of calves to adult females within groups. We also find a higher proportion of tuskless individuals in these populations (> 6 %).

4. Changes in age structure in the Ruaha population between 2009-15 were similar to those observed across sites in 2009.

5. The demography of poached populations in the present study is consistent with previous work documenting how the loss of older individuals suppresses recruitment and survival of elephant calves. These changes are likely to compound the challenge of recovery even after poaching is reduced.

6. *Synthesis and applications* – Poached African elephant populations have clear and consistent demographic signatures including fewer infants and old individuals, and higher tusklessness. Our study demonstrates the use of the RDA technique as a cost-effective method to compare the structure of animal populations across space and over time, and thereby monitor and evaluate the demographic consequences of illegal harvesting.

Key words: age structure, operational sex ratio, rapid demographic assessment, Ruaha National Park, Tanzania, tusklessness

INTRODUCTION

The illegal killing of African elephants (*Loxodonta africana*) for ivory is leading to population declines across the African continent (Wittemyer *et al.* 2011; Maisels *et al.* 2013; Wittemyer *et al.* 2014; Chase *et al.* 2016). In this long-lived species exhibiting a slow reproductive rate and strong social bonds (Lee 1987; Archie, Moss & Alberts 2006), the loss of older bulls and matriarchs – preferentially targeted for their larger tusks (Poole 1989; Mondol, Mailand & Wasser 2014) – has important demographic and behavioural consequences (Poole & Thomsen 1989; Slotow *et al.* 2000; Chiyo *et al.* 2011; Archie & Chiyo 2012; Shannon *et al.* 2013). In particular, recent studies have highlighted disrupted kin-based associations (Gobush, Kerr & Wasser 2009), reduced female reproductive output (Gobush, Mutayoba & Wasser 2008), earlier age of reproduction (Owens & Owens 2009), and longer calving interval (Gobush, Mutayoba & Wasser 2008; Oyango & Lesowapir 2016; Turkalo, Wrege & Wittemyer 2016), all of which are likely to influence population structure (Moss 2001). Quantifying changes in the latter is thus key to understanding and monitoring the effects of poaching on demographic processes (Wittemyer *et al.* 2009; 2013; Rughetti 2016).

Demographic assessments of wild populations are often based on long-term, individual-based datasets, which typically track the survival, productivity and mortality of study individuals (Langvatn & Loison 1999; Moss 2001; Milner, Nilsen & Andreassen 2007; Clutton-Brock & Sheldon 2010; Wittemyer *et al.* 2013). Although hugely valuable, such studies are scarce and rarely carried out on populations experiencing varying levels of legal or illegal harvesting, as well as other types of disturbance. When long-term datasets are not available, comparative studies may still be carried out using data derived from rapid population surveys carried out over short periods of time, yet this approach is rarely implemented (Tella *et al.* 2013). In the case of elephants, so-called rapid demographic assessments (RDAs) were first devised and implemented by Poole (1989) to assess the impact of poaching on the structure of four east African elephant populations. The RDA approach attempts to sex and age as many individuals as possible within a given population, with the overall aim of providing a snapshot of population structure at a given point in time (Ferreira & Van Aarde 2008, Kioko *et al.* 2013). Despite being logistically more feasible than long-term monitoring, few studies since Poole (1989) have promoted the RDA as a tool to characterise changes in elephant population structure, and relate these to poaching activities.

In this study, we use RDA data collected in 2009 across six elephant populations in Tanzania to examine the likely impacts of poaching on population structure, as well as on the level of tusklessness. Recent elephant censuses have highlighted alarming population declines in Tanzania (Chase *et al.* 2016), a country that was also shown to be one of the main poaching hotspots in Africa (Wasser *et al.* 2015; Thouless *et al.* 2016). More specifically, we examine whether populations experiencing low, medium and high levels of poaching prior to 2009 show significant differences in their age structure, operational sex ratio (i.e. adult males to adult females), calf to adukt female ratio at the group level, and proportion of tuskless individuals. We then compare similar metrics between populations sampled in Ruaha National Park (hereafter, Ruaha) in 2009 and in 2015 following a suspected increase in the level of poaching. Although Ruaha holds one of the largest populations of elephants in Tanzania, it has been highlighted as a centre for poaching post-2011 (Wasser *et al.* 2015). Based on our findings, we discuss the value of comparative studies based on RDA data collected over space and time for characterising the effects of poaching on elephant population demography.

MATERIALS AND METHODS

Study sites

Demographic data were collected on elephant populations in six study sites across Tanzania (Fig. 1). Four out of the six populations were surveyed within designated national parks (NPs; Tarangire, Serengeti, Ruaha and Katavi NPs) that allow for photographic tourism only, whilst two populations were surveyed within game reserves (GRs) designed for both photographic tourism and trophy hunting (Selous and Ugalla GRs). All study sites are characterised by distinct wet and dry seasons, which generally occur between November-April and May-October, respectively. Annual rainfall across the study sites in 2009 ranged from 439.6 mm in Ugalla GR to 707.6 mm in Selous GR (Fig. 1).

Poaching levels

Historical patterns of poaching intensity across Tanzania are unreliably documented and primarily anecdotal (Mduma et al. 2010). Although all of the elephant populations considered in this study experienced poaching in the 1970s and 80s (Poole & Thomsen 1989), recent and current poaching levels vary considerably from one site to another (Thouless *et al.* 2016). As a result, we classified study populations as experiencing low, medium and high levels of poaching based on population trends in the three years prior to the 2009 surveys (Fig. 2). Following this, populations in Tarangire and Serengeti were categorised as undergoing low levels of poaching as they demonstrated rapid growth between 2006 and 2009 (Fig. 2, but see also Hilborn *et al.* 2006; Foley & Faust 2010). In contrast, populations in Ruaha and Katavi were found to be stable between 2006 and 2009, respectively, with suspected but unreliably documented poaching occurring at both sites (Gobush, Mutayoba & Wasser 2008; Martin & Caro 2012; Fig. 2). As a result, these populations are classified as experiencing a medium level of poaching. Lastly, elephant populations in Selous and Ugalla underwent dramatic declines between 2006 and 2009 (Mduma *et al.* 2010; Thouless *et al.* 2016; Fig. 2), due to high levels of illegal killing (Wasser *et al.* 2009; Wilfred & MacColl 2014; Bennett 2015).

Data collection

An RDA survey was carried out at each of the six study sites considered during 2009-10 (Fig. 1) following the method described by Poole (1989). Observers (TJ and PB) were trained in ageing and sexing elephants on the well-known northern sub-population of Tarangire NP, which has been the focus of a continuous study since 1993 (Foley & Faust 2010). Observer accuracy and inter-observer consistency were tested until they had reached a satisfactory level (>90% accuracy on known individuals). The observers then surveyed each study site for two to four weeks, with the exception of Tarangire NP, where elephants were surveyed over three days.

The primary aim of RDA surveys is to record the age, sex and unique physical attributes (e.g. presence/absence of tusks or wounds) of as many different elephants in a given population as possible, as well as record the size of the group they belong to (Poole 1989). Selection of survey areas within study sites followed local advice on where elephants were most likely to be encountered. Importantly, search area was shifted by at least 10 km each survey day. Moreover, all recorded individuals were geo-referenced using a Global Positioning Satellite (GPS) system, and whenever possible, portrait photos and/or identification notes were taken. Together these data were used to ensure no double counting of individuals had occurred (i.e. an individual recorded more than once). Wherever possible, a minimum sample size of 300 individuals was sought.

Elephants were approached to within 20-50 m in the field using a motorized vehicle. Observed individuals were sexed and assigned to one of seven age classes (0-4, 5-9, 10-14, 15-19, 20-24, 25-39 and 40+; inclusive of the last age shown) based on shoulder height, back length, head and body shape, and size of tusks (Poole 1989;

Moss 1996). Individuals under 10 years of age were sometimes difficult to sex, and their gender was recorded as “unknown” when this was the case. Following Moss (1996), an elephant group was defined as “any number of elephants moving together with no individual farther away than the distance that is equal to the diameter of the coordinated body of the group at its greatest point”. Lone individuals occurring outside of groups were recorded as being solitary.

Demographic data pertaining to the Ruaha population in 2015 were collated from monthly road transect surveys and opportunistic monitoring by three observers (TJ, JS and LM) between May and October 2015 (Fig. 1). Observers followed the same protocol for approaching and ageing elephants as that used in the 2009 surveys. Data were collected as part of an ongoing elephant monitoring study implemented by the Southern Tanzania Elephant Program (STEP), which operates an elephant ID database for Ruaha containing >1000 individually identified elephants. Each individual is identified from a unique ID code, and its sex, age, and identifying features are known from direct visual observation and portrait photographs. The Ruaha 2015 dataset comprises all unique elephants sighted between May and October 2015 in the same geographic area as surveyed in 2009 (Fig. 1).

The analyses described below only consider groups in which every member older than 10 years of age was accurately assigned to an age class. Owing to the uncertainty associated with the sexing of individuals younger than 10 years (especially females), we split all individuals falling into the 0-4 and 5-9 age classes according to a 1:1 ratio. In a 30-year study of elephant population demography in Amboseli NP, Moss (2001) documented a sex ratio in new-born calves that was not significantly different to 1:1 (see also Gough & Kerley 2006).

Data analysis

Sensitivity of age structure to sampling effort

To assess the degree to which the observed age structure of a given population was sensitive to the number of individuals sampled, we performed a subsampling exercise whereby a reduced number of observations – ranging from 1 to the observed sample size – was randomly selected to estimate a "pseudo" age structure. The latter was then compared to the observed age structure by way of a chi-square test, and the resulting P-value used to determine whether the two distributions were significantly different from each other. Resampling was carried out without replacement to simulate the avoidance of double counting. For each level of effort, we produced N=1000 subsamples, and derived a probability of obtaining an age structure that was significantly different to the observed by dividing the number of iterations resulting in $P < 0.05$ by N. In doing this, we were interested in assessing whether a small reduction in the number of individuals sampled rapidly increased the probability of deriving a different age structure for a given population.

Multi-site comparison

For the purpose of this study, we consider the Tarangire NP population in 2009 as relatively undisturbed by poaching, and use it as a reference sample against which to compare the demography of other sampled populations. Following a ban on ivory trade in 1990, poaching in Tarangire was reduced to a very low level, and the elephant population has since shown a rapid recovery (Foley & Faust 2010). We thus compared age class frequencies obtained for the Serengeti, Ruaha, Selous, Katavi and Ugalla populations (hereafter, test populations) to those observed for the reference Tarangire population. More specifically, for each test population, we performed separate chi-square tests based on all sampled individuals, males only and females only, and used the proportion of individuals obtained in each age class for the Tarangire population as expected probabilities. For each comparison and age class, we calculated the standardised residual (*SR*) between the observed (O) and expected (E) frequencies as $SR = (O - E)/\sqrt{E}$. Negative and positive *SR* values denoted observed frequencies that were less or more than expected, and we used these to assess age-class specific patterns across sampled populations.

For each population, we also calculated the ratio of adult males (individuals > 25 years) to adult females (individuals > 10 years) following Poole (1989), which we hereafter refer to as the operational sex ratio. We interpret the latter as the number of adult males available to adult females for the purpose of reproduction. We expected the operational sex ratio to decrease with the level of poaching, a pattern that has been highlighted in previous studies (Poole & Thomsen 1989; Dobson & Poole 1998; Mondol, Mailand & Wasser 2014). We also investigated whether the ratio of calves (individuals < 5 years) to adult females measured at the group-level was affected by the level of poaching experienced by the population. To do this, we modelled the calf to adult female ratio as a function of study site using a one-way ANOVA, after checking for homogeneity of variances using Bartlett's test ($K^2 = 8.8$, df = 5, P = 0.117) and normality of errors through visual inspection of the QQ plot. We interpret the IFR as the number of calves an adult female is able to recruit, and expect a decrease in this ratio with increased poaching. Lastly, we estimated the proportion of all individuals older than 5 years of age that were observed to be tuskless in each population.

Temporal comparison in Ruaha

To highlight the decline in elephant numbers in the Ruaha-Rungwa ecosystem (which contains Ruaha), we built a time series of elephant density using estimates of population size derived from Systematic Reconnaissance Flight (SRF) censuses carried out in 2006, 2009, 2013 and 2015 (Mduma *et al.* 2010; TAWIRI 2013; 2015). Since the area surveyed differed across years, we divided the estimate of population size by the total area surveyed in the corresponding year. Estimates and associated standard errors were derived following Norton-Griffiths (1978). For the same time period, we also plotted the trend in the proportion of illegally killed elephants (PIKE) reported by the Monitoring the Illegal Killing of Elephants (MIKE) program in Ruaha-Rungwa (CITES 2016), which we consider here as an index of poaching pressure (Wittemyer *et al.* 2014). The PIKE index is calculated as the number of illegally killed carcasses divided by the total number of carcasses reported for a given year (including natural, legal and illegal deaths).

In a similar way to the multi-site comparison, we compared the age class frequencies of the Ruaha elephant population sampled in the dry season of 2015 to that sampled in dry season of 2009. We used the proportion of individuals obtained in each age class in 2009 as expected probabilities for 2015. We also compared the operational sex ratio, the calf to adult female ratio, and the level of tusklessness between the two years using the same tests as for the multi-site comparison. All analyses were carried out in R version 3.2.1 (R Core Team 2016), with statistical significance based on an alpha level of 0.05.

RESULTS

Details pertaining to populations sampled in 2009-10, as well as in Ruaha in 2015, are summarized in Table 1 and Fig. S2. Only the age structure of the Ugalla population was sensitive to a reduction in the number of individuals sampled (Fig. S2). Indeed, the probability of obtaining a significantly different age structure started increasing upon removal of one individual from the Ugalla population sample, whereas it remained at zero after removal of a much larger number of individuals from the other study populations (Fig. S2). We view this result as an indication that the sample sizes for all but one of the study populations were adequate to derive reliable age structures.

Multi-site comparison

Comparison of age class frequencies revealed no significant difference between the age structures of the Tarangire and Serengeti populations in 2009-10, regardless of whether all individuals, males or females were considered (Table 2). In contrast, populations experiencing medium and high levels of poaching showed consistent differences in age structure relative to the Tarangire population (Table 2, Fig. 3). More specifically, these populations showed a lower proportion of calves (aged 0-4) and adults above 40 years of age, and a higher proportion of individuals in the age classes 15-19 and 20-24 (Fig. 3a). Other age classes (5-9, 10-14 and 25-39) showed both positive and negative standardized residuals depending on the sampled population. The proportion of males in age classes 15-19 and 20-24 was greater in all sampled populations experiencing medium to high poaching than those with low levels of poaching, with the exception of the Ugalla population, which showed no difference in the proportion of males aged 20 to 24 (Fig. 3b). It must be noted that the latter population was also characterized by a small sample size overall (Fig. S2), but for males in particular (n = 46, Table 1). There were also fewer males aged 25 to 39 in populations with medium to high poaching. This was not the case for females, which showed higher proportions of individuals in the 20-24 and 25-39 age classes in the same populations (Fig. 3c).

The ratio of adult males to adult females reflected the suspected level of poaching in test populations, with populations experiencing low levels of poaching showing highest operational sex ratios and those more affected by poaching exhibiting the lowest (Fig. 4a). A similar trend was found for the calf to adult female ratio, with a significant decrease for populations in Katavi, Selous and Ugalla, relative to the reference population in Tarangire (Fig. 4b, Table 3). Sampled populations in Tarangire, Serengeti and Ruaha did not differ in their calf to adult female ratio (all were above 1), although the Serengeti population did show a higher ratio than that sampled in Tarangire. Lastly, the proportion of tuskless individuals was markedly higher in populations classified as experiencing medium to high poaching (Ruaha: 7.0 %; Katavi: 6.3 %; Selous: 6.3 %; Ugalla: 9.7 %) relative to those experiencing comparatively low levels (Fig. 4c).

Temporal comparison in Ruaha

Elephant density in Ruaha-Rungwa showed a marked decline between 2006 and 2015, which was concurrent with an increase in the PIKE index reported by the MIKE program between 2009 and 2012 (Fig. 5). It must be noted that carcass sample size for years prior to 2009 was too low (< 20) to provide meaningful insights into the level of poaching in the Ruaha-Rungwa area (Table S1). Comparison of age class frequencies obtained during the dry seasons of 2009 and 2015 revealed significantly different age structures in Ruaha ($\chi^2 = 30.7$, $P < 0.001$, Fig. 6a). In particular, the sampled population in 2015 presented a lower proportion of calves (0-4 years of age), a pattern that appeared driven primarily by a notable decrease in the proportion of male calves

(χ^2 = 16.6, $P < 0.05$, Fig. 6b); although it must be noted that this pattern is dependent on the chosen 1:1 ratio for individuals younger than 10 years of age. Overall, there was a loss of individuals in older age classes, with lower proportions of females aged 25 and above (χ^2 = 15.7, $P < 0.05$, Figure 6c) and males aged 40 and above. With the exception of the 10-14 age class, age categories between 5 and 24 years of age showed increased proportions relative to the population sampled in 2009.

The operational sex ratio of the Ruaha population showed a very slight increase between 2009 and 2015 from 0.120 to 0.133. This was the result of a decrease in the number of adult females (from 100 to 90), with the number of adult males encountered remaining the same at 12 individuals. Average calf to adult female ratio at the group-level did not differ significantly between the two years (1.177 ±0.093 for 2009 and 1.155 ±0.125 in 2015, P = 0.860), whilst the proportion of tuskless individuals showed a small increase from 7.0 % in 2009 to 7.5 % in 2015.

DISCUSSION

The present study, which builds on the work of Poole (1989), highlights clear and consistent differences in the structure of elephant populations experiencing contrasting levels of poaching pressure in Tanzania. Although these levels were based on population trends measured between 2006 and 2009, we feel confident they provided a reasonably accurate description of recent illegal harvesting activities. In a first instance, such sustained and dramatic population declines as those observed in Selous and Ugalla GRs are unlikely to have been caused by climatic factors (e.g. drought; see Foley, Pettorelli & Foley 2008) or repeated methodological biases, and likely reflect true population crashes as a result of documented poaching (Wasser 2009). Secondly, PIKE data collected in Ruaha and Katavi NPs between 2006 and

2009 indicate an increasing number of illegal carcasses encountered at both sites, and this despite suspected unreliable reporting (Martin & Caro 2013). Lastly, our assumption that poaching was less intense in both Serengeti and Tarangire NPs is supported by a prolonged increase in the density of elephants at both sites over the past decade, which has been linked to more effective anti-poaching measures (Hilborn et al. 2006, Foley & Faust 2010).

With this in mind, we found that elephant populations classified as experiencing medium to high levels of poaching between 2006 and 2009 were characterised by fewer calves and old individuals, a reduced number of adult males (defined as > 25 years of age) for the number of adult females (> 10 years), and a lower ratio of calves (< 5 years) to adult females within groups. These patterns reflect the demographic consequences of poaching highlighted by previous studies, whereby loss of older individuals – and males over 25 years in particular (Mondol, Mailand & Wasser 2014) – suppresses recruitment into the population (Barnes & Kapela 1991; Dobson & Poole 1998). The latter may be the result of fewer breeding opportunities for females (Ishengoma *et al.* 2008) and/or reduced survival of calves owing to disrupted groups with a loss of leadership from older matriarchs and increased stress levels (Dublin 1983; Gobush, Mutayoba & Wasser 2008; Archie & Chiyo 2012). The loss of old and young individuals was also characteristic of the Ruaha population in 2015, with observed patterns mirroring those described by Barnes & Kapela (1991), who highlighted that intense poaching in the late 1970s and early 1980s had “affected both ends of the age distribution” of the Ruaha population. Furthermore, the reduction in the proportion of individuals younger than five years of age observed in medium to highly poached populations mirrors the pattern found in Mikumi NP by Poole (1989).

It is worth noting the absence of significant changes in the operational sex ratio and group-level calf to adult female ratio over time in Ruaha, and particularly how this contrasts with the pattern observed across populations in 2009. The Ruaha population age structure from 2009 indicates that the proportion of males older than 25 years of age was already low (8.3% of all males versus 14.8 % for Tarangire, 12.5 % for Serengeti, and approximately 20 % for the Amboseli population in 1996; see Fig. 3 in Moss 2001). Thus, it is possible that between 2009 and 2015, poachers preferentially targeted females over 25 years of age, thereby leading to a reduction in the proportion of the corresponding age classes (Mondol, Mailand & Wasser 2014). This is supported by observation of a slight increase in the operational sex ratio in 2015. The concurrent reduction in the proportion of calves may therefore be a direct consequence of the decrease in the number of experienced adult females, which would not affect the calf to adult female ratio in this case. This contrasts with differences in calf to female ratios measured across populations in 2009, which are likely the result of both the loss of older matriarchs and the long-term disruption of social bonds (Gobush, Mutayoba & Wasser 2008).

The higher proportion of tuskless individuals was another consistent feature of poached populations sampled in 2009. This finding is in agreement with previous studies that have highlighted increased tusklessness in local elephant populations subject to heavy illegal harvesting (Poole 1989; Jachmann, Berry & Imae 1995; Whitehouse 2002), and also concurs with a recent study showing a decline in tusk size in recovering populations (Chiyo *et al.* 2015). In comparison to the relatively undisturbed elephant population of Amboseli NP, which shows a proportion of tuskless adults of less than 1 % (Poole 1989; Steenkamp, Ferreira & Bester 2007), a proportion of 6-8 %, as found in populations experiencing medium to high poaching in 2009 and in the Ruaha population in 2015, is unusually high (Poole & Thomsen 1989). We believe that the behavioural and evolutionary implications of tusklessness in poached elephant populations represent key avenues for future research.

Although the present study demonstrates the value of the RDA as a method for cross-site and temporal comparisons of elephant population structure, it is important to realise its limitations. The method is unlikely to be reliable if elephant density is too low or population size too small to achieve meaningful sample sizes, if vegetation is too dense to allow sightings of all individuals in observed groups (for operational sex ratio and calf to female measures), or if shyness and flight behaviour in response to observers does not enable good demographic records to be taken (Graham *et al.* 2009; Mduma *et al.* 2010; Goldenberg *et al.* 2016). In these cases, other methods such as estimating population structure from dung or spoor surveys may offer more robust alternatives (Morrison *et al.* 2005).

Moreover, RDAs rely on accurate sexing and aging of individual elephants, which can only be achieved by suitably trained observers. Even then, inconsistencies or unexplained results can occur. For instance, the 5-9 age class observed in Ruaha in 2015 showed higher proportions than expected relative to the population sampled in 2009, while the 10-14 age class showed lower proportions. This could be due to undocumented historical mortality events (e.g. drought) ten years previously, which we do not account for, and which would have affected the survivorship of individuals in the 0-4 age class (Foley, Pettorelli & Foley 2008), thereby leading to a lower representation of 10-14 year olds in 2015. In addition, all of the populations considered underwent a period of heavy poaching from the late 1970s to the early 80s, the effects of which might still be reflected in age structures observed in 2009. More generally, knowledge of poaching history is clearly important to the interpretation of

RDA data, and we recommend that comparisons between populations be assessed with due regards to potential differences in historical poaching levels.

Although our study focuses on elephant populations in Tanzania, we believe rapid demographic assessments could be extended to a wide range of species, for which aging and sexing is feasible in the field. Not only would such an approach represent a cost-effective alternative to individual-based monitoring programs when funding is limited or uncertain, but also facilitate the monitoring of poorly known populations and provide insights into possible demographic processes that might affect recovery (Rhuggeti 2016). As a case in point, with a hypothetical growth rate of 4.2 % per annum in the absence of illegal killing (Wittemyer *et al.* 2014), the Ruaha elephant population sampled in 2015 would take more than two decades to return to its estimated population size in 2009. However, our demographic monitoring has shown that poaching is likely to compound the challenges facing the population through loss of experienced female leaders, absence of prime breeding males, and reduced recruitment and survival of calves. In this context, long-term security will be key to ensuring the recovery of the elephant population in Ruaha.

AUTHORS' CONTRIBUTIONS

TJ, AL, SM and CF conceived the ideas and designed methodology; TJ, JS, LM and PB collected the data; JC, RP and TJ analysed the data; JC, RP, TJ and JS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA ACCESSIBILITY

Data used in this study will be made available via the Dryad repository upon acceptance.

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TABLES

Table 1. Number of individuals sampled in each of the six elephant populations considered.

Dry season	Population	# individuals sampled	# males	# females	# gender unknown
2009	Tarangire NP	443	182	261	195
	Serengeti NP	364	151	213	130
	Ruaha NP	329	145	184	114
	Katavi NP	413	170	243	105
	Selous GR	347	123	224	124
	Ugalla GR	153	46	107	39
2015	Ruaha NP	312	145	167	33

Table 2. Age class frequencies for six elephant populations experiencing different levels of poaching pressure. $\chi 2$ and P values relate to Pearson's chi-square tests between age class frequencies of the corresponding population and those of the Tarangire population. Note that the Ruaha population was surveyed in both 2009 and 2015. Due to aging uncertainty, number of male and female individuals for age classes 0-4 and 5-9 were derived using a sex ratio of 1:1 following Moss (2001).

Population	Individuals considered	Age class							$\chi 2$	P-value
		0-4	5-9	10-14	15-19	20-24	25-39	40+		
Tarangire NP	All	181	74	53	20	17	75	23	-	-
	Males	90	37	21	3	4	23	4	-	-
	Females	91	37	32	17	13	52	19	-	-
Serengeti NP	All	143	60	42	19	22	60	19	5.3	0.502
	Males	71	30	18	6	7	17	2	10.0	0.125
	Females	72	30	24	12	15	43	17	2.5	0.872
Ruaha NP (2009)	All	120	47	48	22	30	56	6	39.1	< 0.001
	Males	60	23	23	13	14	10	2	93.5	< 0.001
	Females	60	24	25	9	16	46	4	15.6	< 0.05
Ruaha NP (2015)	All	94	60	34	36	40	46	2	123.3	< 0.001
	Males	47	30	16	22	18	12	0	244.6	< 0.001
	Females	47	30	18	14	22	34	2	35.9	< 0.001
Katavi NP	All	116	81	67	24	50	69	6	111.1	< 0.001
	Males	58	40	23	10	25	14	0	155.8	< 0.001
	Females	58	41	44	14	25	55	6	38.6	< 0.001
Selous GR	All	125	28	35	25	70	60	4	276.3	< 0.001
	Males	62	14	14	13	13	6	1	110.3	< 0.001
	Females	63	14	21	12	57	54	3	216.1	< 0.001
Ugalla GR	All	38	15	27	23	23	26	1	111.6	< 0.001
	Males	19	7	10	8	1	1	0	79.0	< 0.001
	Females	19	8	17	15	22	25	1	82.0	< 0.001

Table 3. Differences in the ratio of calves (individuals < 5 years) to adult females (individuals > 10 years) (IFR) across the six elephant populations sampled in 2009, as measured using a one-way ANOVA.

Population	# Groups sampled	Mean IFR	One-way ANOVA coefficients		
			Estimate	SE	*P*
Tarangire NP	43	1.365	-	-	-
Serengeti NP	24	1.530	0.166	0.146	0.259
Ruaha NP	30	1.177	-0.187	0.137	0.172
Katavi NP	34	1.027	-0.338	0.122	<0.01
Selous GR	46	0.890	-0.475	0.132	<0.001
Ugalla GR	7	0.548	-0.816	0.234	<0.001

FIGURES

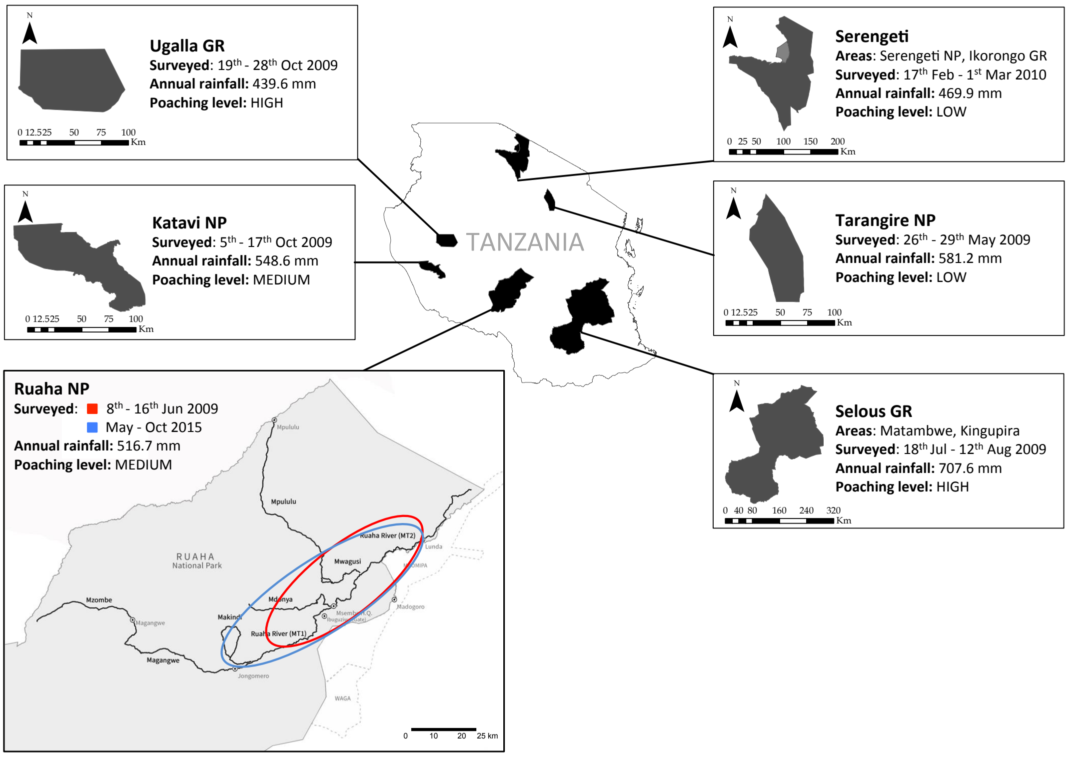

Figure 1. Description of the six study sites in terms of the areas sampled, the dates of the corresponding survey, the annual rainfall estimate for the year 2009, and the level of poaching (see text). For Ruaha, areas surveyed within the National Park in 2009 (red) and 2015 (blue) are shown together with the road network (black lines). Annual rainfall estimates were derived from the Tropical Rainfall Measuring Mission's 3B43 dataset (https://trmm.gsfc.nasa.gov/).

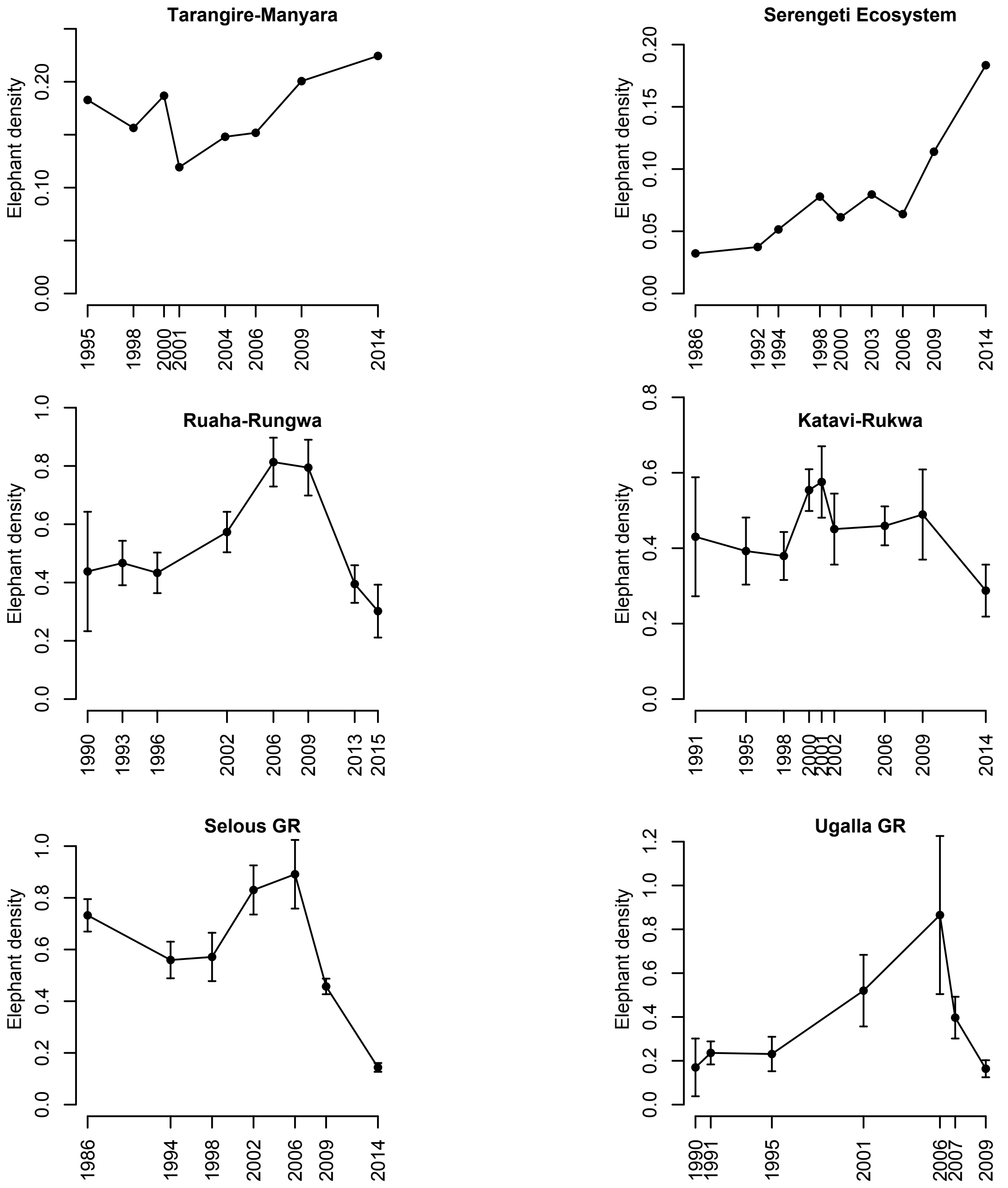

Figure 2. Elephant density trends in six ecosystems containing the sites considered in this study, over the period 1986-2015. For each ecosystem, we collated population size estimates derived from total counts (Tarangire-Manyara and Serengeti) and Systematic Reconnaissance Flight (SFR) surveys (Ruaha-Rungwa, Katavi-Rukwa, Selous and Ugalla) carried out by the Tanzania Wildlife Research Institute (TAWIRI). Density estimates (black dots) and their associated standard errors (error bars) were obtained by dividing population size estimates by the total area surveyed during corresponding flights.

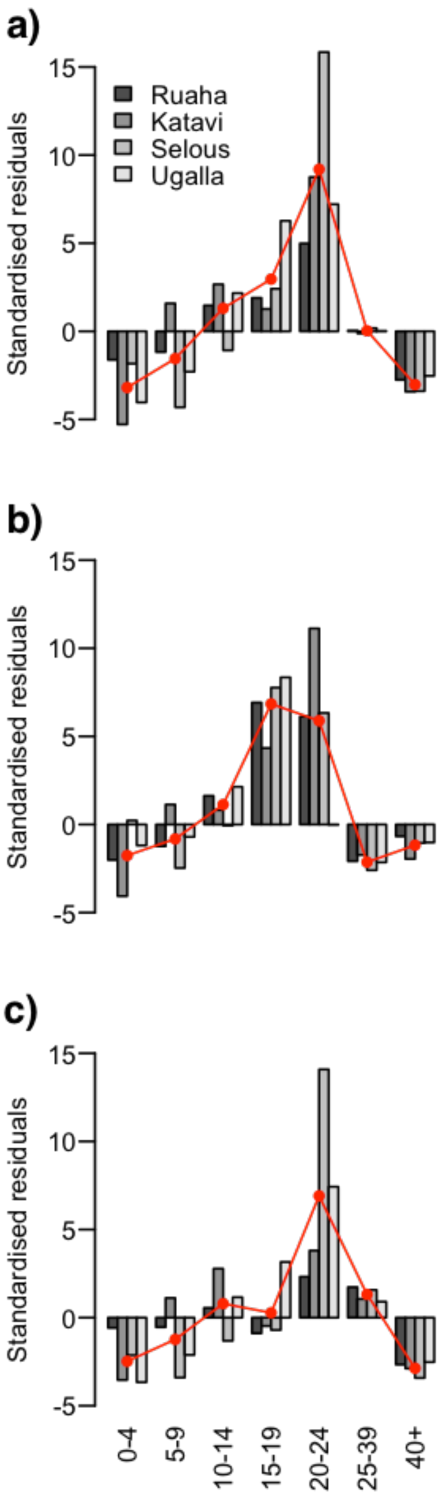

Figure 3. Standardised residuals from chi-square tests comparing the age class frequencies of four poached elephant populations to that of the population sampled in Tarangire NP. Age class frequencies were compared based on all sampled individuals (a), males only (b), and females only (c). Red dots denote mean standardised residual value across sites for a given age class.

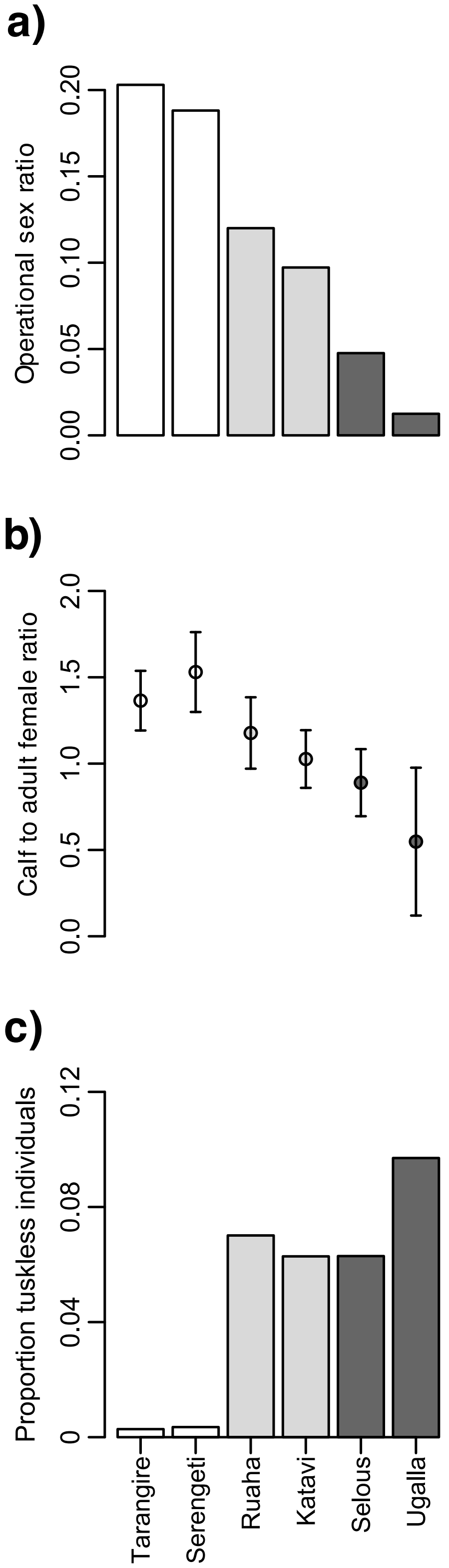

Figure 4. Comparison of the operational sex ratio (a), the ratio of calves to adult females in a group (b), and the proportion of tuskless individuals (c) across six elephant populations sampled using the rapid demographic assessment method in 2009-10. White, light grey and dark grey colours indicate low, medium and high levels of poaching (see text).

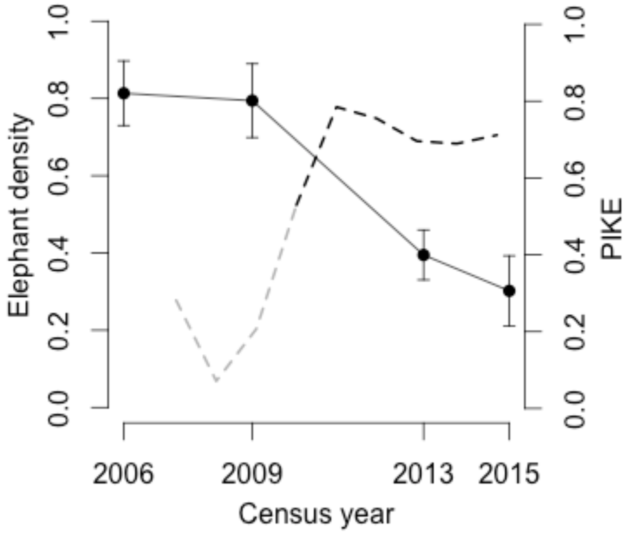

Figure 5. Time series of elephant population density (black dots and associated standard errors) and proportion of illegally killed elephants (PIKE, dashed curve) reported for Ruaha-Rungwa between 2006 and 2015. Density estimates were derived by dividing population size estimates obtained from SRF surveys by total area surveyed (see text). The dashed curve represents a local polynomial model fitted to PIKE data collected between 2007 and 2015 (see Table S1). The grey section of the PIKE curve reflects years for which the total number of observed carcasses was < 20 and from which inferences on the level of poaching are unreliable.

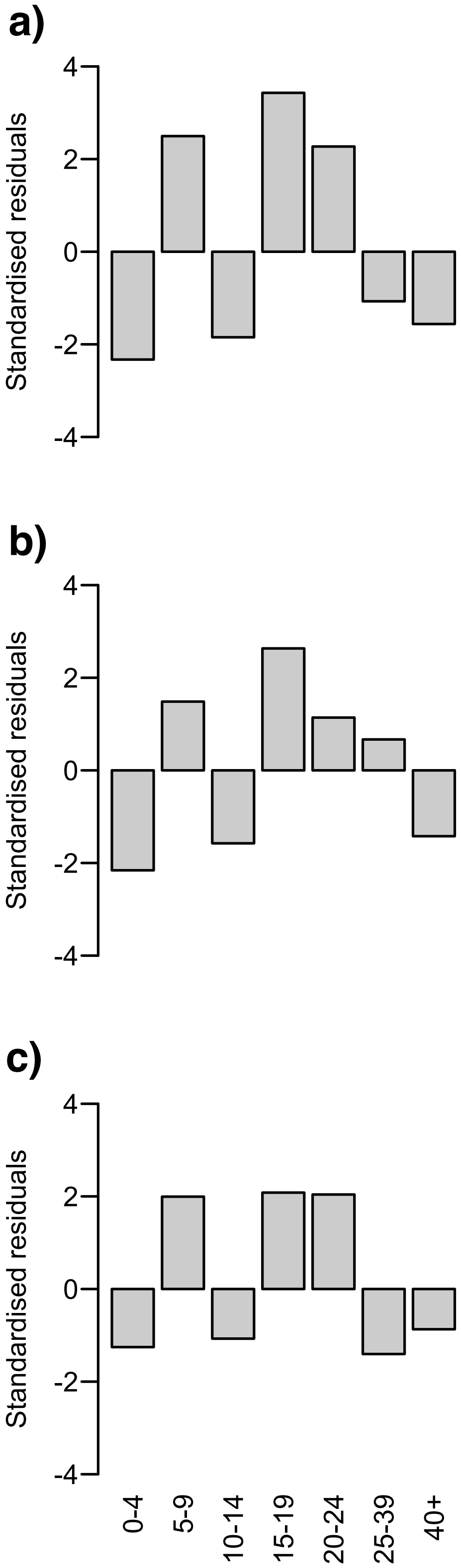

Figure 6. Comparison of the Ruaha elephant population age structure between the dry seasons of 2009 and 2015, as derived from all sampled individuals (a), males only (b) and females only (c). For each plot, bars represent the standardized residuals obtained from a chi-square test with age class frequencies of 2015 as observed values and age class frequencies of 2009 as expected.

SUPPORTING INFORMATION

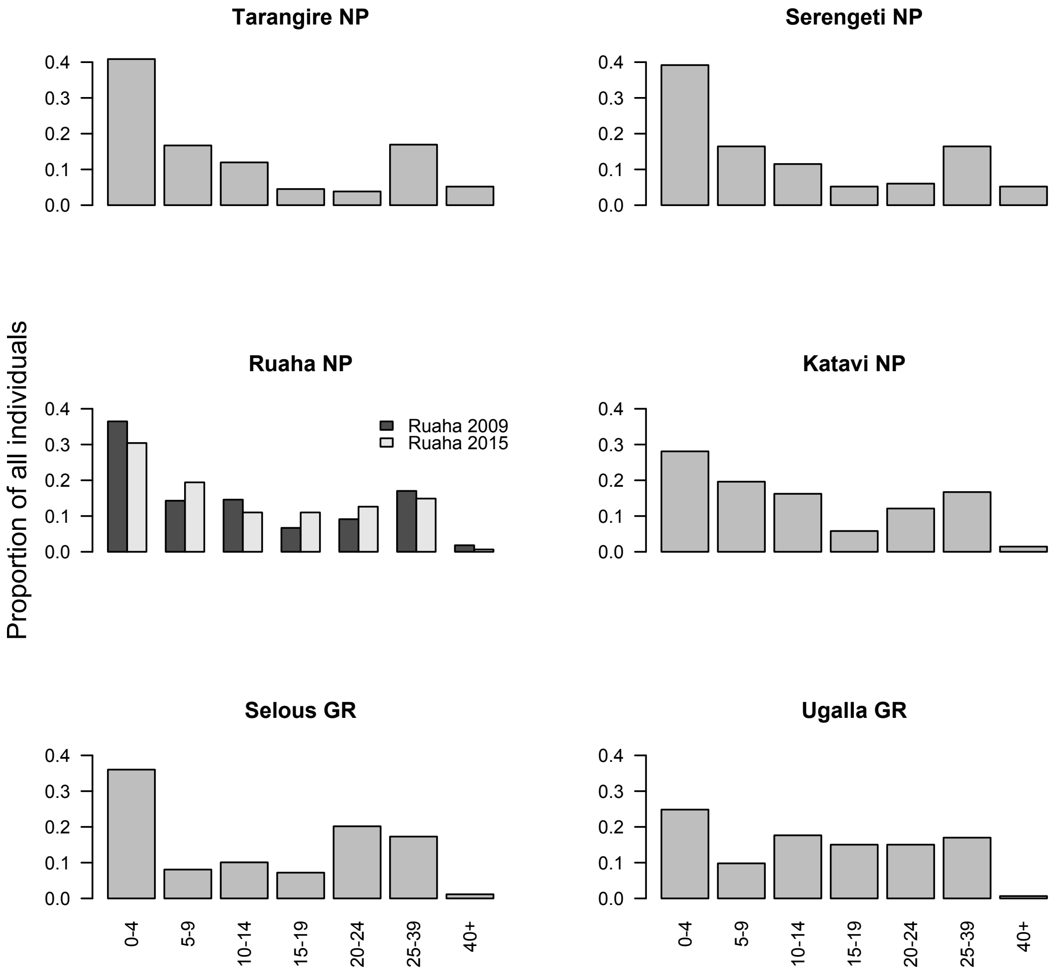

Figure S1. Age structure of elephant populations in the six study sites, as derived from rapid demographic assessments carried out in the dry season of 2009 and, for Ruaha National Park, the dry season of 2015.

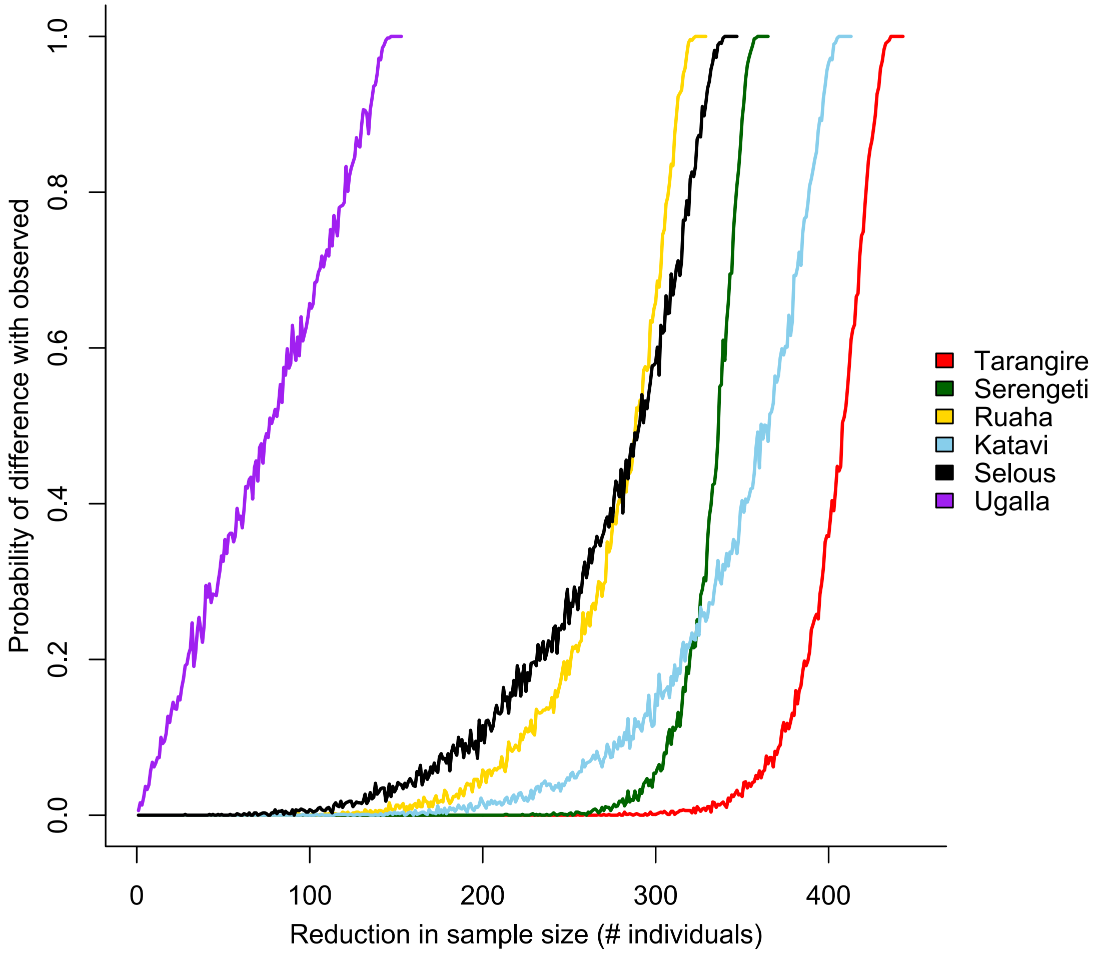
Probability of difference with observed
0.0
0.2
0.4
0.6
0.8
1.0
0
100
200
300
400
Reduction in sample size (# individuals)
Tarangire
Serengeti
Ruaha
Katavi
Selous
Ugalla

Figure S2.

Table S1. Number of carcasses reported by the Monitoring the Illegal Killing of Elephants (MIKE) program in Ruaha-Rungwa between 2007 and 2015, including total and illegal counts. MIKE records were accessed from https://cites.org/eng/prog/mike/data_and_reports.

	Number of elephant carcasses	
Year	Total	Illegal
2007	2	0
2008	3	2
2009	3	1
2010	28	16
2011	34	32
2012	110	73
2013	57	48
2014	50	29
2015	47	35