Understanding how land-use change in the Trans Mara District, Kenya is driving human-elephant conflict and elephant movement

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I am dedicating this thesis to Peter de Bourcier, a truly remarkable man, who, through a chance encounter, has changed my life. I met Peter in 2012 while I was working on an elephant behaviour project in a remote part of Thailand. One evening in the local hotel bar, I was giving a talk about elephants to some project volunteers. Peter happened to be listening to my talk and afterwards we got talking. I told Peter about the work I did and my passion for elephants. He said that he funded PhD students and that he would like to fund me. I was in shock and could not quite believe it. After a few hours of talking, we said our goodbyes and the last thing Peter said was that "you will never forget this moment in your life"; and, true to his words, I never have, as 10 months later, in September 2013, I started my PhD at DICE, funded by Peter. Words will never be sufficient to describe how grateful I am to Peter, as his incredible generosity has enabled me to pursue my career working with elephants.

Tragically, Peter passed away in February 2017 and never got to read this thesis. I hope I would have made him proud.

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Some of my field team and my fantastic supervisor (far right) Bob Smith in the Trans Mara District, Kenya.

Author's declaration

All chapters in this thesis were written by L.N. Tiller with comments and editorial suggestions provided by my supervisors R.J. Smith (all chapters) and T. Humle (chapters 2-4). Chapters 2-4 include collaborations with other researchers, both within and external to the University of Kent. All research was approved by the School of Anthropology and Conservation Ethics Advisory Group, University of Kent.

Chapter 2: L.N. Tiller and R.J. Smith conceived the idea and designed the sampling strategy. L.N. Tiller conducted the data analyses and wrote the manuscript. N. Sitati, N. Leader-Williams, M. Walpole and M. Goss provided data for the scenario modelling. All authors provided feedback and commented on the text.

Chapter 3: L.N. Tiller, R.J. Smith and T. Humle conceived the idea. L.N. Tiller designed the sampling strategy, conducted the data analyses and wrote the manuscript. The field data were collected by L.N. Tiller and field scouts in Kenya. N. Sitati, N. Leader-Williams and M. Walpole provided historical data. N. Deere assisted with coding the Generalised Additive Models. All authors provided feedback and commented on the text.

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Abstract

Human-wildlife conflict is a global problem, due to habitat destruction and fragmentation, and it severely impacts the livelihoods of people and leads to the persecution and retributive killing of wildlife. In Kenya, human-elephant conflict is one of the most serious and challenging conservation issues. To successfully reduce conflict, management strategies and land-use planning must be informed and underpinned by robust evidence-based research. This thesis focused on understanding how land-use patterns and change in the Trans Mara District, Kenya, is driving human-elephant conflict and elephant movement. The aims of this thesis are to: (1) determine the implications of agricultural expansion on human-elephant conflict; (2) understand the seasonal, temporal and spatial drivers of crop raiding over time; and (3) investigate elephant pathway use and their role in human-elephant conflict. Methods used included risk mapping, landcover change scenario modelling, human-elephant conflict monitoring, fine scale spatial analysis of crop raiding using Generalised Additive Models, camera trapping, elephant sign surveys, qualitative focus groups and quantitative household surveys.

The findings from this thesis show that the extent of agriculture land in the Trans Mara has increased by 42.5% between 2000 and 2015 and scenario modelling suggests that even with high future deforestation levels, large areas will remain susceptible to elephant crop raiding. The results also indicate that temporal, seasonal and spatial conflict trends are becoming less predictable, as crop raiding occurs throughout the year and affects crops at all stages of growth. This crop raiding has increased in frequency by 49% since 1999-2000 but has decreased in damage per incident by 83%, and increasingly involves a new group type consisting of elephant family units plus bulls. Results from this thesis also show that elephants used pathways between the Trans Mara and Masai Mara National Reserve at night, and that elephants preferred paths that had a high percentage of forest cover and were closer to farms, saltlicks and forest in the Trans Mara. In light of changing patterns of human-elephant conflict and landcover, land-use planning is crucial to balance the needs of humans and wildlife.

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1. Introduction

1.1. Global biodiversity loss

The global human population in 2017 was 7.6 billion and it is estimated that, before 2100, this figure will reach over 11 billion (United Nations, 2017). Human activities have modified and transformed over half of the global land surface (Chapin et al., 2000), causing extensive habitat loss and fragmentation, and leading to a global decline in species (Butchart et al., 2010; Pimm and Raven, 2000; Sala et al., 2000). We are now witnessing the beginning of a sixth mass extinction, with extinction rates 1000 times higher than pre-human background levels (Barnosky et al., 2011; Pimm et al., 2014). In the last 500 years, 332 species of terrestrial vertebrates have become extinct (Dirzo et al., 2014) and nearly 13,000 species of animals have been classified as threatened with extinction (IUCN, 2017). This human-induced modification of the planet and mass extinction has been termed anthropocene defaunation (Dirzo et al., 2014).

Agricultural expansion is one of the main human activities threatening biodiversity, as it is a driver of pollution, habitat loss and fragmentation (Foley et al., 2005; Maxwell et al., 2016; Rockström et al., 2009). Croplands and pastures now represent the largest land-use on the planet, covering 38% of the surface (FAOSTAT, 2015). Agriculture uses the greatest amount of freshwater compared to any other industry and the intense use of fertilizers has severely polluted water systems and fisheries and altered the nutrient cycle (Canfield et al., 2010; Tilman et al., 2001). Biodiversity is crucial for the maintenance of ecosystems, which underpins numerous ecosystem services vital for humans (Cardinale et al., 2012; Hooper et al., 2005). Despite the vast benefits that biodiversity provides for humans, habitat loss on a global scale continues to accelerate, particularly in the tropics (Butchart et al., 2010; Phalan et al., 2013).

1.2. Human-wildlife conflict

Habitat loss and fragmentation have also extended the interface between farmland and natural habitats, creating agricultural frontiers that increase interactions and resource competition between humans and wildlife populations (Madden, 2004; Nyhus, 2016; Woodroffe et al., 2005). The resultant human-wildlife conflict can have important negative impacts on people through crop damage, loss of livestock and potential loss of life (Naughton-Treves, 1997; Thirgood et al., 2005). This can elicit fear and anger towards wildlife, leading to retributive killings (Choudhury, 2004; Linkie et al., 2007). Human-wildlife conflict is a complex issue and one of the greatest challenges facing conservationists today (Inskip and Zimmermann, 2009; Nyhus, 2016; Woodroffe and Ginsberg, 1998; Woodroffe et al., 2005). This is reflected by the exponential growth over the last 20 years of the number of research articles across disciplines (social and natural sciences) published on human-wildlife conflict (Nyhus, 2016) (Figure 1.1).

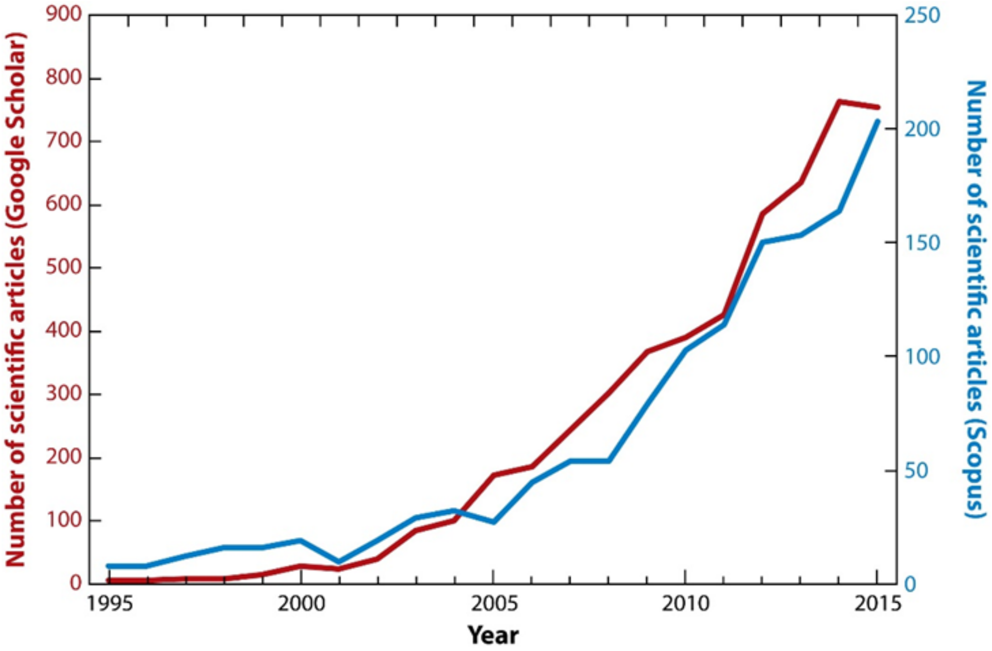


Figure 1.1. The number of research papers from natural and social sciences looking at human-wildlife conflict between 1995 and 2015. The red line shows the number of citations using the exact words `human-wildlife conflict' in Google Scholar and the blue line shows any combination of the terms `human' and `wildlife' with `conflict' in the scientific database Scopus (from Nyhus, 2016).

1.2.1. Defining human-wildlife conflict

Human-wildlife conflict has been described as "the situation that arises when behaviour of a non-pest, wild animal species poses a direct and recurring threat to the livelihood or safety of a person or a community and, in response, persecution of the species ensues" (Inskip and Zimmermann, 2009). In recent years, however, some scholars have argued that the term is problematic, as it is misleading and may exacerbate the problem (Hill, 2015; Madden, 2004; Peterson et al., 2010; Pooley et al., 2017; Redpath et al., 2014). These scholars think that the term does not clearly distinguish between human-wildlife impacts and the manifestation of underlying human-human conflicts between authorities and local communities, or between different cultures of people (Redpath et al., 2014). Moreover, human-human conflict can be more important in driving conflict than wildlife itself (Dickman, 2010). It is also argued that the term `human-wildlife conflict' portrays wildlife as conscious human antagonists when they are exhibiting natural behaviours (Hill, 2015; Peterson et al., 2010). However, finding an alternative term has proven difficult as many researchers contributing to the literature have not adjusted to the proposed terminology (Hill, 2015), such as `human-wildlife coexistence' (Madden, 2004; Peterson et al., 2010), `human-human conflicts' (Marshall et al., 2007), `conservation conflicts' (Redpath et al., 2013), and `human-wildlife interactions'. This thesis will use the term `human-wildlife conflict' as it is used in the majority of the literature.

1.2.2. Impacts of human-wildlife conflict

Human-wildlife conflict affects many people all across the world and involves a variety of wildlife including insects, reptiles, birds and mammals (Nyhus, 2016; Woodroffe et al., 2005). Much of the literature has focused on species of conservation concern, as a major challenge for conservationists is balancing the protection of threatened species with the needs of local communities (Woodroffe et al., 2005). Owing to the range of species that can be involved, there are different types of conflict that can occur, as described below.

1.2.2.1. Crop raiding

Crop raiding is the consumption of, and/or damage to, crops. It is the most common form of human-wildlife conflict and can cause significant costs for local communities, especially for subsistence farmers (Gillingham and Lee, 2003; Naughton-Treves, 1998; Thirgood et al., 2005). For example, chimpanzees (*Pan troglodytes*) and *Cercopithecus* monkeys were responsible for incurring a food replacement cost of 10–20% for local households in western Rwanda (Mc Guinness and Taylor, 2014). Costs due to crop raiding are not limited to the developing world, as each year white-tailed deer (*Odocoileus virginianus*) in Wisconsin, USA, cause $34 million in crop damage (Naughton-Treves and Treves, 2005).

1.2.2.2. Livestock depredation

Another widespread form of human-wildlife conflict is livestock depredation, particularly by large carnivores, which can have devastating impacts on people (Inskip and Zimmermann, 2009). For example, in Bhutan National Park, livestock depredation by tigers (*Panthera tigris*) and leopards (*Panthera pardus*) cost people over two thirds of their income (Wang and Macdonald, 2006). In general, livestock loss through disease or theft is higher than depredation by carnivores (Dar et al., 2009; Loveridge et al., 2010). However, even low levels of depredation can impose significant costs on poor households. In India, depredation of 1.6 head of livestock costs households 50% of their per capita income (Bagchi and Mishra, 2006). For some traditional rural communities, the loss of livestock may not only incur economic costs but also cultural costs, as livestock are often important sociocultural assets. Thus, their loss can affect social status (Sillero-Zubiri and Laurenson, 2001).

1.2.2.3. Attacks on people

From a human perspective, attacks on people represent the most negative form of conflict as they can lead to human injury or loss of life. Around the world, attacks on humans by large cats, bears, wolves and elephants have been reported for centuries (Quigley and Herrero, 2005). Although a lot of information on attacks is anecdotal and difficult to verify, there is now a large body of evidence that suggests thousands of people are killed by wildlife each year (Quigley and Herrero, 2005). For example, each year in India, elephants (*Elephas maximus*) kill 100-200 people (Veeramani, 1996), and tigers kill 100 people (Sanyal, 1987). In Tanzania, between 1990-2004, lion attacks lead to injury or death of over 800 people (Packer et al., 2005). This can also have a profound influence on the attitudes and tolerance towards wildlife of people not directly affected (Conover, 2002; Thirgood et al., 2005), and fear of attack by wildlife, as opposed to actual attacks, can lead to pre-emptive killing of wildlife and intensify conflict (Kaltenborn et al., 2006).

1.2.2.4. Indirect costs

There are a number of indirect costs that human-wildlife conflict inflicts on people. These indirect costs can be higher than the actual costs of crop damage or livestock predation and can severely impact tolerance towards wildlife and intensify conflict (Barua et al., 2013). Indirect costs include: (1) increased need to guard fields or livestock enclosures that can create labour bottlenecks in certain seasons; (2) disruption to education, as children may have to help guard crops and livestock; (3) loss of sleep from guarding; (4) increased exposure to diseases such as malaria due to guarding at night; (6) restriction of movement; (7) behavioural and psycho-social impacts of living with dangerous wildlife (Barua et al., 2013; Hill, 2000; Thirgood et al., 2005).

1.2.2.5. Retributive killing of wildlife

The result of wildlife damaging crops, killing livestock and attacking people can lead to retributive killing, where wildlife are killed both legally and illegally by individuals or governments (Woodroffe et al., 2005). Such killing can severely affect local wildlife populations and, in more serious cases, cause range collapse. For example, in the 1900s, prairie dogs were perceived as vermin that competed with livestock. As a consequence, they were subjected to a mass poisoning campaign by the government. Subsequently, prairie dog range reduced to <2% by the end of the twentieth century (Reading et al., 2005). Retributive killing can also lead to local extinctions. One study found that retributive killing contributes more to the extinction of large carnivores isolated in small reserves than do stochastic processes (Woodroffe and Ginsberg, 1998). A systematic review of human-felid conflict found that 47% of cheetah, 46% of Eurasian lynx and up to 50% of tiger mortality has been attributed to retaliatory killing in certain regions across the world (Inskip and Zimmermann, 2009).

1.3. Key determinants of conflict

Human-wildlife conflict is complex as there is no simple linear relationship that exists between damage, attitudes and actions. While the most important underlying drivers are increasing human populations and associated impacts (Nyhus, 2016; Woodroffe et al., 2005), conflict is influenced by multiple and diverse factors. These can be spatial, ecological, biological or human-social in form and are discussed in more detail below (Dickman et al., 2013; Inskip and Zimmermann, 2009; Nyhus, 2016; Woodroffe et al., 2005).

1.3.1. Spatial determinants

The spatial distribution of humans and wildlife can affect the occurrence and intensity of conflict. Identifying spatial trends can help identify ‘hotspots’ and help predict where future incidents of human-wildlife conflict are likely to occur, which can guide conservation management. Numerous studies on livestock depredation by felids have found that rates of depredation tend to increase with greater proximity to natural habitats that provide suitable cover for felids. Rates decline with increasing proximity to human habitation (Inskip and Zimmermann, 2009). For wildlife species that cause crop damage, studies have found that crop raiding may be influenced by the amount of land under cultivation, (Pozo et al., 2017; Sitati et al., 2003) and/or the location of fields in relation to landscape features such as water availability, protected areas, and wildlife habitat (Chen et al., 2016; Graham et al., 2010; Guerbois et al., 2012; Hill, 1997; Linkie et al., 2007; Smith and Kasiki, 2000; Wilson et al., 2013). Other factors have also been found to affect the amount of damage a field receives, including season, amount of guarding, human density, hunting, isolation of fields and crop types available (Graham et al., 2010; Hill, 2000; Naughton-Treves, 1998).

1.3.2. Ecological and biological determinants

The availability of food, as well as other ecological factors, influences the distribution and abundance of conflict. At certain times of the year when wild prey is less abundant, or in areas where prey populations are hard to find, livestock depredation rates are generally high (Bagchi and Mishra, 2006; Johnson et al., 2006; Polisar et al., 2003). However, this is not always the case, as in France and Norway depredation by Eurasian lynx (*Lynx lynx*) on livestock is high despite there being an abundance of prey (Stahl et al., 2001).

There can also be considerable variation within a population of animals as to whether individuals or groups are involved in human-wildlife conflict (Hoare, 2012). Age can affect the likelihood of involvement, as high nutritional requirements of older individuals may drive them to crop raid or kill livestock (Chiyo et al., 2012). Sex is another factor which can determine involvement in conflict. For example, bull elephants in some areas are primarily responsible for crop raiding, due to their high nutritional requirements for mating success (Chiyo and Cochrane, 2005; Hoare, 1999; Sukumar and Gadgil, 1988), and male felids kill more livestock than females as they have larger home ranges (Loveridge et al., 2010). It has also been reported that social learning may have an influence on the acquisition of conflict behaviour among some species. In Amboseli National Park, Kenya, bull elephants who associate with crop raiders are more likely to become crop raiders themselves (Chiyo et al., 2012).

1.3.3. Human social determinants

Human-wildlife conflict intensity can be shaped by people’s attitudes and tolerance towards wildlife, which can be influenced by a combination of complex social factors (Dickman, 2010; Dickman et al., 2013). Thus, an understanding of this human dimension of conflict is a crucial requirement for developing effective mitigation (Loveridge et al., 2010; Manfredo and Dayer, 2004; Pooley et al., 2017). There are different social factors at an individual and societal level which can influence human-wildlife conflict. A few examples of these factors are briefly discussed below.

1.3.3.1. Individual level

Human behaviour is complex and can be affected by attitudes, values and beliefs, which all interact with one another (Dickman et al., 2013; Manfredo and Dayer, 2004). Attitudes and tolerance towards wildlife can form and change quickly. They do not exist in isolation, as they are influenced by numerous factors such as values, personal experiences, emotions, education and wealth (Manfredo and Dayer, 2004). Values are broad-based beliefs about desirable goals and modes of conduct such as honesty and obedience (Manfredo and Dayer, 2004; Manfredo, 2008). People acquire values early in life which take time to form and are difficult to change (Bright and Manfredo, 1996). These values influence attitudes which directly determine human behaviour (Manfredo, 2008).

Personal experience can determine the level of hostility towards wildlife. For example, in a study looking at spearing and poisoning of lions by Maasai people in Kenya, 75% of the respondents who said that they would kill a lion had previously suffered from depredation to their livestock (Hazzah et al., 2009). Emotions, which are linked to personal experiences, also play an important role in decision making in humans. People who are fearful of wildlife are usually more antagonistic towards them (Roskaft et al., 2007) and deep seated fear is probably a key driver of hostility towards wildlife (Berg, 2001).

Education is an important variable which can affect conservation outcomes (Kideghesho et al., 2007), as it can be valuable for raising awareness and creating advocacy for wildlife. Knowledge can lead to more positive attitudes towards wildlife (Ericsson and Heberlein, 2003) and wealth can influence education as well as other social factors. For instance, wealth can act as a buffer against the impacts of crop loss and depredation, making households less vulnerable to the potential risk of wildlife. Greater wealth should lessen the impacts of conflict, as this increases access to capital and enables people to afford more efficient protective strategies (Naughton-Treves and Treves, 2005).

1.3.3.2. Societal level

Social norms are behaviours that individuals perceive to be acceptable by others. Social norms can motivate action by offering potential rewards or punishments for engaging or not engaging in a particular behaviour (Dickman et al., 2013). For example, in the Pantanal, 25% of ranchers justified their approval of jaguar killing on the basis of tradition (Marchini and Macdonald, 2012). Social norms are linked with social identity, as certain behaviours can be central to a social group. This is evident in some groups of Maasai who are traditional pastoralists in East Africa and where killing lions is central to their culture. Young Maasai men or warriors are expected to kill a lion as a sign of manhood and are thus encouraged to do so (Hazzah et al., 2009).

Religion and folklore can also influence how people feel about wildlife. Carnivores in many stories are portrayed as frightening characters, which may influence negative, long-lasting perceptions towards wildlife. (Marchini and Macdonald, 2012). Equally, religious beliefs may make people more tolerant towards wildlife. Buddhists in Manang, Nepal, are particularly tolerant of snow leopards despite them killing livestock. Killing is not part of their religious beliefs and these cats are considered sacred (Ale, 1998).

Sources of income can also affect human-wildlife conflict, but it is not a conclusive predictor of conflict related tolerance. On the one hand, people who solely rely on farming or livestock can be severely impacted by crop raiding or livestock depredation, and so they can be generally less tolerant of wildlife. On the other hand, those who have income from other sources, such as wildlife tourism, often have more positive attitudes towards wildlife (Sillero-Zubiri and Laurenson, 2001). However, in some cases, income or wealth levels have actually been found to have no effect on tolerance towards wildlife. For example, rich cattle ranchers often pursue jaguars (*Panthera once*) more than poorer farmers with small holdings (Zimmermann, 2014).

1.3.3.3. Risk perception

Risk perception can play an important role in human-wildlife conflict as there is often a mismatch between people's perception and the actual degree of risk (Dickman, 2010). This is further complicated by the influence of different socio-cultural factors such as cultural values, histories and ideologies, intrinsic dread and novelty of risk (Dickman, 2010). For example, in Zanzibar the endangered red colombos (*Procolobus kirkiu*) were thought to have detrimental impacts on coconut harvests to the extent that people wanted them to be killed. However, studies found that the red colombos actually improved the harvest of coconuts due to a pruning effect that they had. Thus, the species actually benefitted crop production, contrary to farmers' beliefs (Siex and Struhsaker, 1999). Addtionally, some species that are large, highly visible and potentially dangerous, such as elephants, may generate disproportionate concern and antagonism even if other species cause more damage (Thirgood et al., 2005). In Kerinci Seblat National Park, Sumatra, wild boar were thought to be the worst crop raiders out of 11 species, when it was actually the pig-tailed macaque which caused the most damage to farmers crops. This blaming of wild boar may have been due to them being more conspicuous than macques, leading to this inacuarate view by farmers. It has also been reported that people often over-report the scale of conflict (Gillingham and Lee, 2003; Linkie et al., 2007), leading to an inaccurate view of the situation (Gillingham and Lee, 2003; Linkie et al., 2007; Sekhar, 1998; Siex and Struhsaker, 1999).

1.4. Managing conflict

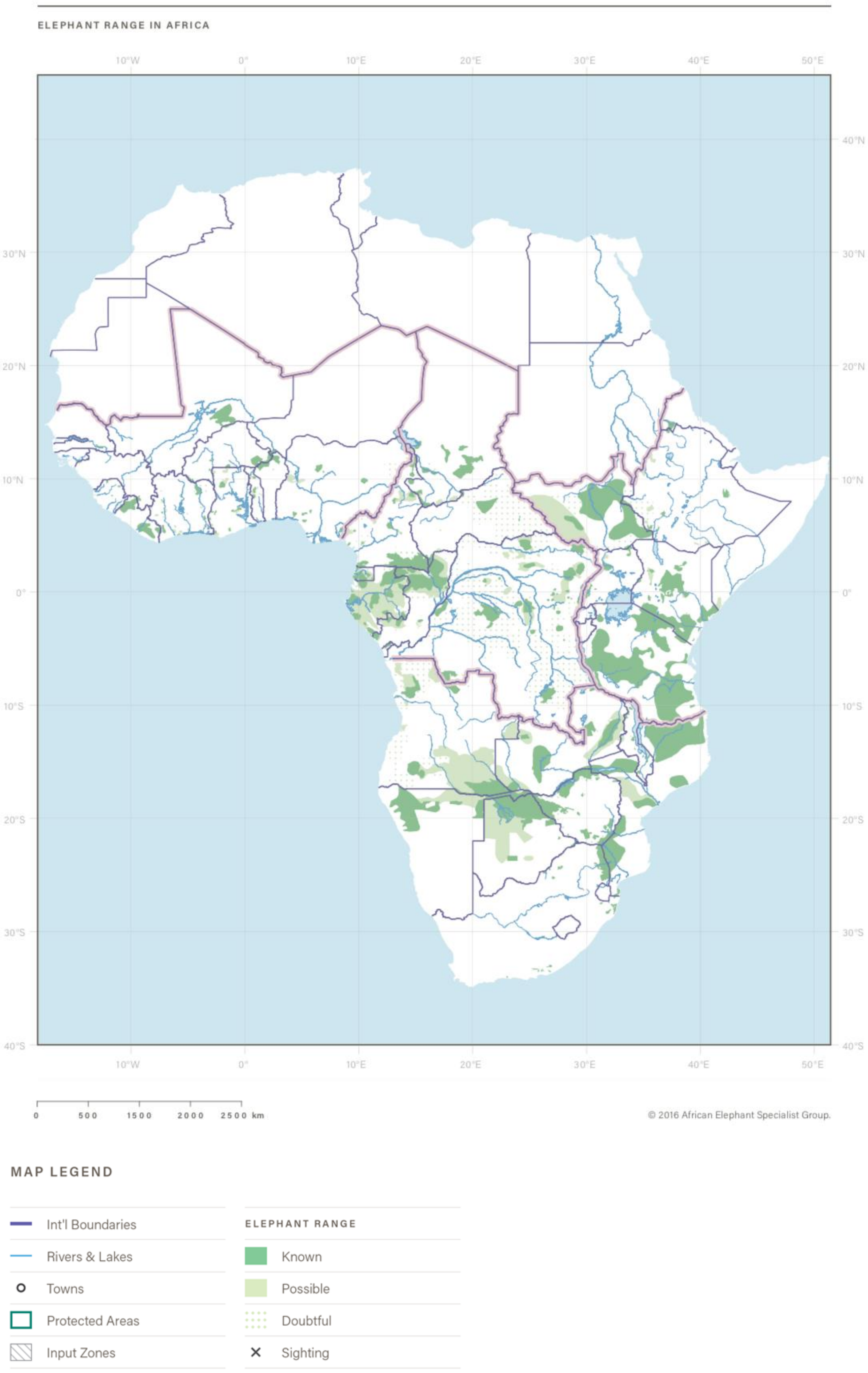
A range of lethal and non-lethal approaches have been developed to try to reduce the magnitude of human-wildlife conflict (Table 1.2). In some cases, mitigation measures have been successful (Balme et al., 2009; King et al., 2017; Marker et al., 2005), although many interventions only provide short term solutions or simply shift the problem elsewhere (Goswami and Vasudev, 2017; Hoare, 2012). A longer-term approach to address the broader issues of land-use change is needed, as well as the human dimensions of conflict.

1.5. African elephant conservation

The African elephant (*Loxodonta africana*) is the world's largest land mammal. Their historic range covered the whole of Africa from the northern Mediterranean coast to the southern tip. However, their distribution has declined to Sub-Saharan Africa, so that they currently exist in 37 countries (Blanc et al., 2007), with a range of approximately 3.1 million km² that includes large areas of continuous range in parts of Central, Eastern and Southern Africa (Figure 1.2), although many areas are becoming increasingly fragmented (Thouless et al., 2016). Elephants play a crucial role in the ecosystem, are an important species for conservation campaigns and they can also generate significant returns from wildlife-based tourism which can be an important source of income for local communities (Litoroh et al., 2012). Elephants are keystone species, as they maintain ecological community structure and processes (Dublin, 1995; Shoshani, 1993; Western, 1989). For example, elephants are seed dispersers and in some areas are responsible for spreading seeds further than any other species (Blake et al., 2003; Campos-Arceiz and Blake, 2011). Some plant species depend entirely on savannah elephants for their dispersal such as the plant '*Balanites Wilson*' in Uganda where no other animal can perform this function (Babweteera et al., 2007). In forest ecosystems, elephants also play an essential role in opening up dense vegetation by creating forest gaps. These gaps enable light to reach the forest floor which result in a more varied and productive ground layer, thus benefitting other ground species such as forest hogs, gorillas, bush pigs and buffalo (Western, 1989).

Elephants are also referred to as an umbrella species as their conservation depends on large areas of their ecosystems being conserved. This therefore serves the objective of wider biodiversity conservation (Epps et al., 2011). In addition, elephants are a flagship species that are commonly used to serve as a rallying point for fundraising and raising awareness about conservation issues (Barua et al., 2011). Owing to their appealing aesthetics, such as their large body size, elephants appeal to international audiences and are often used as a key fundraising species by international non-government organisations (Smith et al., 2010). However, this approach has been criticised as less well-known species lose out on the money raised from these campaigns (Smith et al., 2012).

African elephants are currently listed as Vulnerable (IUCN, 2017) due to variability in their population trends. Elephants are severely threatened by the recent surge in the illegal ivory trade (CITES Secretariat, 2016; Wittemyer et al., 2014) and by human-elephant conflict, which is becoming a pervasive problem due to habitat loss and fragmentation (Thouless et al., 2016). On a global scale, elephant population numbers have declined, as the recent population estimate was 415,428 ± 20,111 (Thouless et al., 2016), down by about 104,000-114,000 in 2007. Elephant populations across central and western Africa are in peril as populations have plummeted by 78-81% in the last 10 years (Poulsen et al., 2017). However, in some countries, such as South Africa, elephant populations appear to be overabundant, increasing and threatening other species and their habitats (Blanc, et al., 2005; Lombard et al., 2001; Van Aarde and Jackson, 2007). Conservation biologists are therefore faced with the dilemma of managing a species in urgent need of protection over most of its range, while being in need of population control or reduction in certain areas.



Source: Thouless et al., (2016). IUCN SSC African Elephant Specialist Group.

Figure 1.2. Current elephant range in Africa

1.6. Human-elephant conflict

Elephants require large amounts of space and resources due to their physiology and energy requirements (Owen-Smith, 1988; Ruggiero, 1992; Sukumar, 1990). To meet these nutritional requirements, elephants often range outside boundaries of protected areas (Thouless et al., 2016). However, increasing human populations and changing land-use patterns have increased competition for space and resources between people and wildlife (Hoare, 2000; Sitati et al., 2003; Woodroffe et al., 2005). This human-elephant conflict is among the most emotive and political form of human-wildlife conflict (Lee and Graham, 2006). Internationally, elephants have an iconic status, are widely loved and, in conservation terms, are regarded as threatened, and are therefore protected (Barua, 2014; Lorimer, 2010). Thus, they are often the focus of conservation campaigns. However, locally, elephants may be feared and resented due to their ability to cause significant damage to crops and people (Choudhury, 2004; De Boer and Baquete, 1998; Gillingham and Lee, 1999; Naughton-Treves, 1997).

Despite the variety of wildlife involved in crop raiding, African elephants have received particular attention as they can cause severe localised damage and, more seriously, cause human injury or loss of life (Naughton-Treves, 1998; Naughton-Treves et al., 1999; Thirgood et al., 2005). A review of the top pest species in Africa found that elephants actually accounted for less than 10% of crop loss and were ranked relatively low compared to the other species (Naughton-Treves et al., 1999). However, elephants can also cause substantial indirect costs (see section 1.2.2.4) which can be higher than the actual amount lost from crop damage. The combination of direct and indirect costs make elephant crop damage one of the most significant causes of human–wildlife conflict in Africa, and elephants are widely perceived as a major threat to people’s livelihoods (Thirgood et al., 2005). Thus, human-elephant conflict can elicit violent responses from people. For example, in northern Tanzania, six elephants were killed by being chased over a cliff by villagers. This was a result not only of a desire for retribution for crop or property damage, but also of a wider, underlying resistance to authority over land issues and disempowerment (Mariki et al., 2015).

For the future co-existence between humans and elephants, understanding seasonal, temporal and spatial trends of elephant crop raiding are integral to developing effective mitigation strategies (Naughton-Treves, 1998).

1.6.1. Temporal and seasonal patterns of human-elephant conflict

To understand patterns of crop raiding, researchers have described elephant behaviour in terms of 'optimal foraging theory', based on the principle that individuals seek to gain the most energy for the lowest cost (Stephens and Krebs, 1986). Crops are attractive to elephants as they are highly nutritious and palatable (Sukumar and Gadgil, 1988), and elephants can obtain 38% of their daily forage intake from crops in 10% of the time they spend foraging on wild plants (Chiyo and Cochrane, 2005). Crop raiding has often been related to rainfall patterns as the quality of natural forage declines during the dry season at the same time that crops ripen (Chiyo et al., 2005; Goswami et al., 2015; Gubbi, 2012; Osborn, 2004; Webber et al., 2011). Temporal patterns are generally thought to be more driven by risk-avoidance behaviour, as studies have shown that elephants will generally crop raid during the night to avoid being detected by humans (Graham et al., 2010, 2009).

1.6.2. Spatial trends of human-elephant conflict

Risk-taking behaviour is also thought to predict the spatial distribution and intensity of human-elephant conflict. Once again, this is often context specific, but there are some general trends that relate to elephants avoiding areas where they are most likely to be detected by farmers. Crop raiding tends to occur more frequently closer to forest edges and protected areas, further from roads and in areas of low human density (Barnes et al., 2005; Chen et al., 2016; Goswami et al., 2015; Graham et al., 2010; Guerbois et al., 2012; Sitati et al., 2003; Wilson et al., 2013).

One approach that has been used to analyse spatial trends of crop raiding is a GIS-based analysis. For example, Smith and Kasiki (2000) used administrative boundaries as sampling units to look at crop raiding in Tsavo, Kenya. They found that crop raiding incident density in sampling units were negatively related to distance to permanent water, elevation and protected area frontage. More recent studies have used grid cells (of 1 x 1 and 5 x 5 km^2) as sampling units and found that crop raiding can be predicted by area under cultivation (Graham et al., 2010; Sitati et al., 2003).

These spatial relationships are complicated by multiple factors relating to food availability, such as farm location, farmer mitigation effort, number and types of crops and availability of food and water. In addition, understanding the factors that determine crop raiding depends on analysing the data at an appropriate scale. Previous analyses often used coarse-scale approaches, mostly to avoid the problems of spatial autocorrelation that occur when studying this type of spatially clustered data. However, these coarse scales may not be sufficient to explain the complexity of spatial drivers of crop raiding (Songhurst and Coulson, 2014).

1.6.3. Sexual composition of elephant groups

Crop raiding is a high-risk, high-gain strategy and, in some areas, only male elephants have been reported to crop raid (Hoare, 1999; Osborn, 2004; Sukumar and Gadgil, 1988; Sukumar, 1990). This risk-taking behaviour of males could have evolved as a result of strong sexual selection for large body size and condition-dependent mating success in males (Chiyo et al., 2011). Crop raiding can lead to gains in body size for elephants, as cultivated food crops are highly nutritious (Chiyo et al., 2011). Male elephants' annual reproductive performance is positively correlated with musth duration (Hollister-Smith et al., 2007; Poole, 1989) and musth is dependent on body condition, body size and age of individual males. Males with access to reliable, easily digested and high energy human crops experience longer musth episodes, while those with limited energy are less likely to experience musth (Poole, 1989; Sukumar, 2003). Thus, the larger a male elephant, the greater its reproductive success (Hollister-Smith et al., 2007; Moss, 1983; Poole, 1989). However, in other areas, female elephants have also been reported to crop raid (Graham et al., 2010; Sitati et al., 2003; Smith and Kasiki, 2000) and, in some cases, are responsible for the most incidents (Smith and Kasiki, 2000). The differences in elephant group types involved in crop raiding highlight the fact that crop raiding behaviour can vary across sites, depending on food availability, risks and the behaviour of people towards elephants.

1.7. HEC mitigation

A number of field interventions have sought to mitigate crop raiding and resulting conflict via lethal (e.g., shooting of problem animals) and non-lethal approaches (e.g., translocation, barriers, guarding and repellents). Recent studies assessing the effectiveness of mitigation have found that a combination of simple early warning systems to detect elephants before they have entered farms, combined with a communal approach to guarding using simple tools, is an effective method for reducing human-elephant conflict (Davies et al., 2011; Gunaryadi et al., 2017; Osborn and Parker, 2002; Sitati and Walpole, 2006). Examples of these tools are torches, flashing LED lights, fire and firecrackers.

The increasing problem of human-elephant conflict and varying levels of success with many mitigation methods have led to increased investment in electrified fences. For example, in Kenya, the Kenya Wildlife Service estimates that there is a total of 1245 km of electrified fencing in the country, with an additional 1000 km under the process of construction (KWS, 2017). Electric fences are erected to try to create hard boundaries and separate spaces for elephants and people. Electric fences are very expensive to set up and maintain (Hoare, 2012) and, in some cases, can exacerbate conflicts, causing human-human conflict which is shaped by different conflicting political interests within a region (Evans and Adams, 2016).

However, evidence suggests that many interventions only provide short term solutions as they can often be site specific and not encompass the whole landscape; they can be expensive to implement; there can be a lack of uptake by local communities; elephants can become habituated; and they can simply shift the problem elsewhere (Goswami and Vasudev, 2017; Hoare, 2012; Osipova et al., 2018). Short term approaches have also been described as "treating crop raiding elephants with aspirin" (Barnes, 2002), as they seek to reduce the symptoms of conflict, while failing to address the underlying causes of conflict such as land-use change and political ecology. Extensive habitat destruction has transformed the planet (Butchart et al., 2010; Chapin et al., 2000; Maxwell et al., 2016; Pimm et al., 1995) and led to increased competition between humans and wildlife for natural resources (Nyhus, 2016; Woodroffe et al., 2005). However, there is very little research showing the impacts of this land-use change on human-wildlife conflict patterns and trends. The political ecology between different stakeholders can often exacerbate conflict, which is more appropriately termed human-human conflict (Redpath, 2013) . For example, conflict can be fuelled by the underlying resistance to conservation management pratices that marginalise and disempower people (Evans and Adams, 2016).

1.8. Elephant movement and pathway use

Elephants have large home ranges that commonly go beyond the existing network of protected areas (Blanc et al., 2007). Thus, understanding how elephants move in increasingly human-dominated landscapes is crucial for maintaining the long-term viability of elephant populations. Elephant movement is non-random (Loarie et al., 2009; Wittemyer et al., 2008) and is driven by the need for resources such as food, water and minerals (Chamaille-Jammes et al., 2007; Harris et al., 2008; Murwira and Skidmore, 2005; Wittemyer et al., 2007). Elephants may travel vast distances when resources are scarce. For example, in Namibia, home ranges of elephants have been recorded up to 12,800 km^2 (Leggett, 2006) and in Mali up to 24,000 km^2 (Blake et al., 2003). Movement can be triggered by the cessation of major rain events, with the timing and duration of their movement matching the greening and senescing of vegetation (Bohrer et al., 2014; Cushman et al., 2005). In areas of high human densities, elephants may alter their behaviour and adopt risk avoidance strategies such as travelling at night and moving faster in these areas (Cushman et al., 2005; Douglas-Hamilton et al., 2005; Graham et al., 2009).

Elephants also develop pathways by repeatedly following the same routes when travelling between favoured habitat patches. (Blake and Inkamba-nkulu, 2004; Shannon et al., 2009; Vanleeuwe and Gautier-Hion, 1998; Von Gerhardt et al., 2014). Thus, pathways can act as least-effort routes to food resources (Blake and Inkamba-Nkulu, 2004), suggesting elephants use them to optimise their foraging strategy and gain the most energy for the lowest cost (Stephens and Krebs, 1986). Moreover, pathways play a particularly important role in human-dominated landscapes, where important habitat patches are increasingly isolated by the spread of agriculture. Therefore, there is a need to better understand the role of these pathways in human-dominated landscapes and how they influence patterns of human elephant conflict, which is important for land-use planning and human-elephant conflict mitigation (Adams et al., 2017; Smit et al., 2017; Songhurst et al., 2015; Von Gerhardt et al., 2014)

1.9. Conservation in Kenya

Kenya is home to more than 35,000 species of flora and fauna and the country has a variety of natural ecosystems that range from marine to mountains, grasslands and forests to savannas (Ojwang et al., 2017). Kenya's total land area covers about 582,646 km^2, while protected wildlife areas cover only 8% of land, and a significant proportion (>60%) of large herbivores reside outside protected areas (Ojwang et al., 2017; Western et al., 2009). However, Kenya is experiencing rapid land-use change which is driven by land sub-division, high human population growth (Homewood et al., 2001) and rapid agricultural expansion (Homewood et al., 2001; Serneels et al., 2001; Serneels and Lambin, 2001).

Protected areas in Kenya are becoming increasingly isolated and habitat connectivity is being lost through the spread of settlements, agriculture and high livestock densities (Ogutu et al., 2016). As a result, there has been a rapid decline in wildlife species and an increase in human-wildlife conflict incidents (Ogutu et al., 2016). Human-elephant conflict has also been highlighted as one of the most serious and challenging wildlife management and conservation issues in Kenya. As such, HEC research and mitigation have been highlighted as important activities by Kenya Wildlife Service in the Conservation and Management Strategy for the Elephant in Kenya 2012-2021 (Litoroh et al., 2012).

The future wildlife in Kenya cannot rely on protected areas alone. Thus, conservation requires range-wide planning and a landscape approach in which core protected areas are integrated with human-dominated areas into wider connectivity landscapes. This understanding has led to the development of the project ‘Securing Wildlife Migratory Routes and Corridors’, which is a joint initiative between Kenya’s Ministry of Environment and Natural Resources, Kenya Wildlife Service and numerous other institutions (Ojwang et al., 2017). This is a flagship project of the ‘Kenya Vision 2030’ programme, which was launched by President Mwai Kibaki in 2008 and aims to help transform Kenya into a "newly industrializing, middle-income (income exceeding World's average currently at US$10000) country providing a high quality of life to all its citizens by 2030 in a clean and secure environment”. The Kenya Vision 2030 was developed using a participartory stakeholder process from Kenyans all across the country and is based on three pillars: economic, social and political. Within each of these pillars there are numerous flagship projects which will aim to lead to macroecomomic stability, governance reforms, enhanced equity and wealth creation opportunities for the poor, infrastructure, energy, science and innovation development, land reforms, human resources development and security and public reforms (Vision 2030, 2018).

The Masai Mara Ecosystem is one of the six key and continuous habitats highlighted for protection in ‘Kenya Vision 2030 Flagship Project – Securing Wildlife Migratory Routes and Corridors’ (Ojwang et al., 2017). The Masai Mara is connected to the Serengti National Park and it is this connectivitiy that allows for the abundance and diverse assemblages of wild ungulates, and for the seasonal migration of approximately 1.2 million wildebeest, along with 0.6 million zebras and gazelles each year. (Sinclair and

Norton-Griffiths, 1979) Thus, this is a globally important transfrontier region for conservation. However, as with many wildlife areas across Kenya, it faces the various challenges related to land-use change.

1.10. Study site

The Trans Mara District is situated in South-West Kenya and borders the western portion of the Masai Mara National Reserve (Figure 1.3). The district is is part of Narok County and covers an area of 2,900 km^2, 76% of which is unprotected. Agriculture is the dominant landcover type, interspersed by a mosaic of afro-montane, semi deciduous and dry-deciduous forests and Acacia savanna woodlands. Rainfall is typically bimodal, falling in general in two seasons, the ‘long rains’ between February and June and the ‘short rains’ in November and December.

Natural pathways link the Trans Mara and Masai Mara through a steep escarpment, enabling movement of wildlife between the two areas (Sitati, 2003). The region is an important dispersal area for wildlife due to the rich resources such as food, water and minerals found in the forest there. The area has traditionally been home to a resident elephant population of 200-300 individuals and there is also a portion of the Masai Mara elephant population which migrates in and out (Sitati et al., 2003). The Trans Mara is also home to a diverse number of other mammals, birds, reptiles and invertebrates, reptiles (WWF, 2015), which is why studying this region is so important.

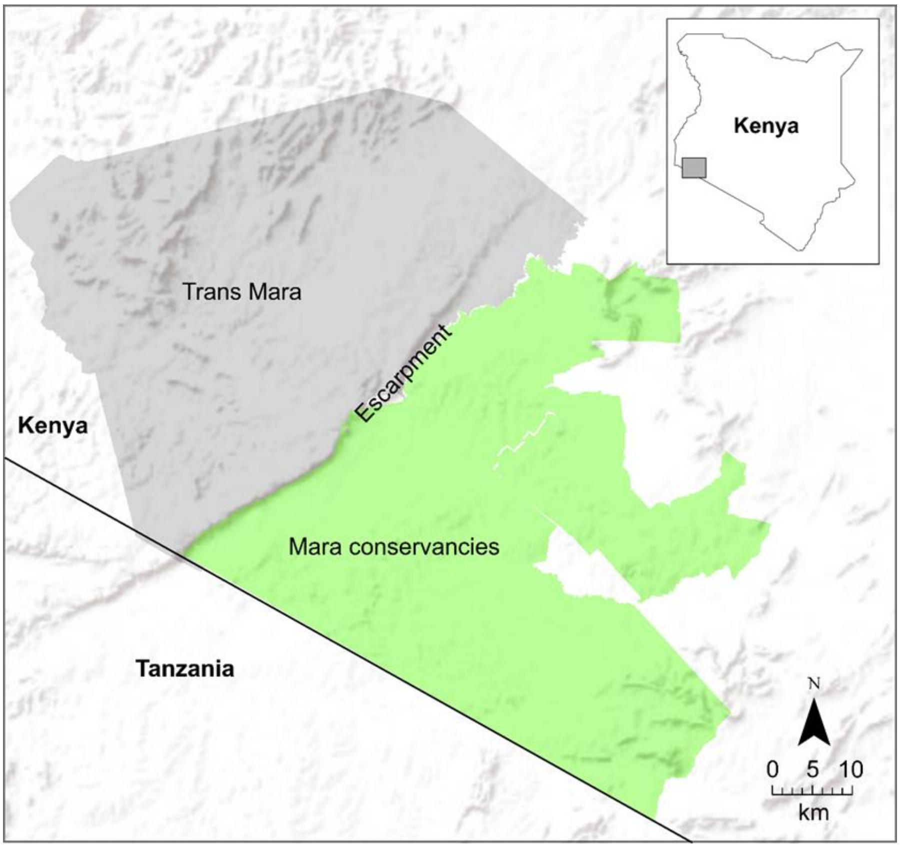


Figure 1.3. The Trans Mara District and Masai Mara ecosystem

The Trans Mara District is a classic example of what is occurring across much of Kenya and East Africa, as it is an area experiencing: (1) high human population growth (Sitati, 2003); (2) rapidly changing land-use, especially as people are shifting land-use pratices (Homewood et al, 2001) and; (3) high human-wildlife conflict. The region has been recognised as a human-elephant conflict hotspot within Kenya, due to the high number of incidents each year (Litoroh et al., 2012). Thus, these factors make the Trans Mara District an ideal study site, as the results from this thesis are likely to act as indicator of trends elsewhere. The fact that this thesis is comparing data to a historical data set provides a unique opportunity to see how land-use change is affecting human-elephant conflict over time, which is especially important in the context of climate change. Given the importance of human-elephant conflict in Kenya, robust research and monitoring is needed to guide conflict mitigation and land-use planning.

1.11. Thesis outline and objectives

Kenya Wildlife Service's long-term goal for the next ten years is to maintain and expand elephant distribution and numbers in suitable areas, enhance security to elephants, reduce human-elephant conflict and increase the value of elephants to people and habitat.

Knowledge of land-use change, the impact of large scale human influx into elephant areas, human-elephant conflict trends, elephant distribution numbers and movement patterns are crucial in order to achieve these long-term goals. This thesis was developed to be integrated into the 'Kenya Wildlife Service Elephant Strategy' by aiming to fill a number of knowledge gaps. Thus, the main aims of this thesis are to:

(1) determine the implications of agricultural expansion on human-elephant conflict;

(2) understand the seasonal, temporal and spatial drivers of crop raiding over time;

(3) investigate elephant pathway use and their role in human-elephant conflict;

This thesis comprises of the following data chapters, each of which is written as a stand-alone piece of research that can be submitted for publication:

Chapter 2 documents landcover change in the Trans Mara since 2000 and identifies current drivers of change. Combining landcover data and elephant movement data, it models the implications of landcover change on the areas vulnerable to human-elephant conflict and looks at different scenerios of forest loss over time. This was the first stage in understanding how land-use change can impact human-elephant conflict patterns and elephant movement.

Chapter 3 builds from the work of Chapter 2. Chapter 2 found that human-elephant conflict will continue to be an important issue in the Trans Mara. Thus, Chapter 3 sought to understand what specific factors are driving these trends and how they have changed over time. Specifically, I investigate temporal, seasonal and spatial patterns of human-elephant conflict in the Trans Mara and compare these results with historical data from 1999-2000.

Chapter 4 builds from the work of Chapter 3, as Chapter 3 shows that crop raiding is occurring at conservation boundaries. Thus, it is important to understand the use of elephant pathways in human-dominated landscapes, as they provide connection for elephants between the boundary of the National Park and the Trans Mara. Chapter 4 identifies specific elephant pathways in the Trans Mara and combines elephant sign survey data and camera trap data to examine seasonal and temporal trends of pathway usage to understand the fine-scale movements of elephants in this region. Chapter 4 also provides an in-depth investigation of the use of pathways and their role in human-elephant conflict.

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2. Modelling the implications of agricultural expansion in a human-elephant conflict hotspot

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2.1. Abstract

Agricultural expansion is one of the greatest threats to biodiversity and human-wildlife conflict is an escalating problem, but there is little research on the relationship between them. We investigated the implications of agricultural expansion on elephant crop raiding in the Trans Mara, Kenya, an area characterised by rapid land-use change and high conflict levels. We first mapped the spread of agriculture from 2000 to 2015 and, using logistic regression modelling, we identified that distance to existing farmland, and longitude and latitude best explained agricultural expansion patterns. Using this model, we then produced four forest loss scenarios, as patches of this important habitat type are used by elephants as refuges when crop raiding. Our scenarios identified areas most at risk, based on annual deforestation rates of 1%, 3%, 5% and 10% (the annual rate between 2000 and 2015 was 2.8%), and predicted up to 65% forest loss and a halving of forest patch number by 2025. Finally, we estimated the future area of farmland vulnerable to crop raiding, based on three different estimates of the distance that elephants could travel from forest patches to farmland. This analysis predicted that farmland vulnerable to crop raiding would decrease by between 33% and 67% for the worst deforestation scenario. Thus, our results predicted that even with high deforestation levels, many forest patches will remain to act as refuges, so large areas will remain susceptible to elephant crop raiding. Our results illustrate the value of landcover change scenario modelling to guide land-use decisions, and land-use planning for the long-term mitigation of human-wildlife conflict.

2.2. Introduction

Agricultural expansion is one of the biggest threats to terrestrial biodiversity (Maxwell et al., 2016), as increases in cropland, livestock farming and timber production have led to severe habitat conversion and increased extinction rates (Butchart et al., 2010; Green, 2005; Foley et al., 2005; Newbold et al., 2015; Tscharntke et al., 2012). Habitat loss and fragmentation have also extended the interface between farmland and natural habitats, creating agricultural frontiers that increase interactions and resource competition between humans and wildlife populations (Madden, 2004; Woodroffe et al., 2005). The resultant human-wildlife competition can have important negative impacts on people, through crop damage, loss of livestock and potential loss of life (Naughton-Treves, 1997; Thirgood et al., 2005). This can elicit fear and anger towards wildlife, leading to retribution killings (Choudhury, 2004; Linkie et al., 2007). This is a particular problem for large mammal species (Goswami et al., 2014), which are generally seen as more of a threat, and are often the focus of conservation campaigns, some of which are seen by local people as favouring wildlife over people (Dickman, 2010; Gillingham and Lee, 1999; Naughton-Treves, 1997; De Boer and Baquete, 1998). Unfortunately, this makes these charismatic megafauna particularly vulnerable to extirpation in these agricultural frontiers, as their large body size and slow population growth rates predisposes them to extinction (Cardillo et al., 2005).

Conserving large mammals in these agricultural landscapes depends on promoting co-existence with people, as these species generally have home ranges that are larger than most protected areas (Balme et al., 2010; Goswami et al., 2014; Woodroffe et al., 2007). A number of field interventions have sought to mitigate human-wildlife conflict via lethal (e.g., removal of problem animals) and non-lethal approaches (e.g., translocation, barriers, guarding and repellents). In some cases, such measures have been successful (Balme et al., 2009; King et al., 2017; Marker et al., 2005), but many interventions only provide short term solutions or simply shift the problem elsewhere (Goswami and Vasudev, 2017; Hoare, 2012). A longer-term approach is to address the broader issues of land-use change and land-use planning, as human-wildlife conflict is largely a landscape level problem. Such planning can involve developing wildlife corridors and refuges, implementing land-use and management zoning systems and creating hard or soft barriers (Linnell et al., 2005; Nyhus, 2016; Runge et al., 2014). Such plans need to account for the traits and behaviour of the relevant species but also need to consider patterns of landcover change (Goswami and Vasudev, 2017).

Mapping and modelling agricultural expansion is an important topic in conservation (Defries and Townshend, 1999; Green et al., 2013; Smith et al., 2008) and there have been recent advances in both remote-sensing and geospatial analyses to identify the predictors of land-use change. Such studies show rates of agricultural expansion are site and scale-specific and caused by multiple interactions that vary across regions (Geist and Lambin, 2002). However, there are a number of broad factors that predict rates and spatial patterns of agricultural expansion and these include accessibility to markets (Serneels and Lambin, 2001), topography (de las Heras et al., 2012; Green et al., 2013; Patarasuk and Fik, 2013; Pfeifer et al., 2012), distance to roads (Chomitz and Gray, 1996; Mann et al., 2010; Patarasuk and Fik, 2013; Pfeifer et al., 2012) and distance to villages (Serneels and

Lambin, 2001). However, these mapping and modelling approaches have not been incorporated into studies of human-wildlife conflict, even though habitat expansion is a well-known driver of biodiversity loss (Nyhus, 2016). Here we address this issue by presenting a case study from Kenya that used fine-scale logistic regression modelling of agricultural expansion to investigate the implications of different land-use change scenarios on human-elephant conflict.

African elephants (*Loxodonta africana*) are particularly prone to conflict with people because 70% of their home range lies outside protected areas, and they are often involved in incidents such as crop raiding, infrastructure damage and attacks on people (Blanc et al., 2007). A key factor in elephants' ability to live around agricultural frontiers is the presence of refuges, which are remaining patches of relatively undisturbed natural vegetation that allow animals to shelter and rest (Graham et al., 2010; Pittiglio et al., 2014). These refuges can range from small patches of dense vegetation, such as forest or thicket (Pittiglio et al., 2014; Wilson et al., 2013), to larger, more secure areas (Hoare, 1999). They also play an important role in determining where human-elephant conflict takes place, with studies from India and Kenya showing animals use refuges to avoid contact with humans before and after crop raiding (Graham et al., 2010; Wilson et al., 2013).

The Trans Mara, which neighbours the world famous Masai Mara National Reserve in Kenya, is a perfect example of a landscape where elephants and people interact during their daily activities. The region is an important area for elephants, because it has traditionally been home to a resident population and also acted as a dispersal area for individuals that spend most of their time in the National Reserve. Elephants use the Trans Mara because it contains important patches of forest, which provides key resources throughout the year, such as preferred plant species and salt licks (Dublin, 1996; Sitati et al., 2003). However, the area is also characterised by rapid land-use change, which is driven by land sub-division, high human population growth (Homewood et al., 2001) and shifting land-use from pastoralism to agro-pastoralism and cultivation (Nyariki et al., 2009; Maitima et al., 2009). This spread of agriculture has reduced the amount of elephant habitat and created an agricultural frontier, leading to many crop raiding incidents and other negative interactions between people and elephants. This situation is exacerbated by the presence of elephant refuges, as these animals have permanent protection in the

National Reserve and use small patches of forest within the Trans Mara as crop raiding staging posts (Sitati, 2003). This means any land-use planning aimed at reducing human-elephant conflict within the Trans Mara must account for both the predicted spread of agriculture and how this impacts the spatial pattern of these refuges.

In this study, we combined landcover and elephant movement information within a statistical framework to model the likely prevalence of human-elephant conflict in the Trans Mara, and explored the implications of different land-use change scenarios on elephant crop raiding. Specifically, we aimed to: i) map the increase of agriculture in the Trans Mara between 2000 and 2015, ii) develop a logistic regression model to identify the factors that best predict its spread, iii) predict the future distribution of agricultural land under four habitat loss scenarios and; iv) estimate how this will change the area of land that will be susceptible to elephant crop raiding. To inform action on the ground, we conducted our analysis at a fine spatial scale and only considered local conditions. This is in contrast to national and global models of land-use and landcover change, which provide important broad-scale insights but make a set of assumptions that are generally less relevant at the fine-scale (Alexander et al., 2017; Prestele et al., 2016). Our approach contributes to future land-use planning and highlights the impacts of a growing agricultural frontier on elephant populations within the Greater Mara ecosystem.

2.3. Methods

2.3.1. Study area

The Trans Mara District is situated in South-West Kenya and forms part of Narok County. It had a human population of 274,500 in 2009, an increase of 63% since 1999, and human densities are higher in the west and south of the region (KNBS, 2010). Most of the people living in the Trans Mara are Maasai, who traditionally relied on pastoralism but have increasingly turned to farming because of changes in land ownership and the area's high rainfall and fertile soils (Sitati, 2003). The Trans Mara is highly biodiverse and contains the Nyekweri forest, an important patch of indigenous forest that is used by elephants and other wildlife for food and shelter. Natural pathways link the Trans Mara and the National Reserve through a steep escarpment, which the elephants use during their seasonal migration between the two areas (Sitati, 2003).

2.3.2. Modelling agricultural expansion

2.3.2.1. Mapping landcover

To understand agricultural expansion in the Trans Mara, we needed to determine how landcover has changed and identify the causal factors. We extracted data on forest, grassland and cropland cover from a landcover map produced in 2000 from 25 m resolution Landsat Thematic Mapper imagery. We then produced a landcover map showing the distribution of cropland, grassland and forest by on-screen digitising 2015 5 m CNES/Astrium, satellite imagery in QGIS (QGIS Development Team, 2015) using the OpenLayers plugin. The 2015 map was groundtruthed by consulting with local experts and comparing results with known patches of the three landcover types.

2.3.2.2. Producing the agricultural expansion probability model

We created an agricultural change map in QGIS by overlaying the 2000 and 2015 landcover maps to identify land that had been converted from forest or grassland to cropland. We then used the Create Random Points tool in ArcMap 10.3 (ESRI, 2015) to select 150 random sample points at least 2 km apart inside areas that were cleared for cropland since 2000, and 150 random sample points from land that remained natural (grassland or forest). We used a total of 300 points to ensure that the whole study area was covered and that there was enough distance (i.e. 2 km) between each of the points to reduce the effects of spatial autocorrelation. For the analysis, we then produced the following GIS layers to use as potential explanatory factors in the model: elevation, slope, distance to nearest village centre in 2000, distance to nearest farmland in 2000 and distance to roads in 2000. More details on how we produced the GIS data are given in the Supplementary Materials (Table S2.1).

To identify predictors of agricultural spread, we first undertook exploratory analysis and produced correlation matrices to perform pair plot analysis for each variable. We used a cut-off value of $r = 0.7$ to test for collinearity (Dormann et al., 2013), rescaled the variables to have a mean of 0 and standard deviation of 0.5 (Gelman et al., 2008), and applied a square root transformation to all of the distance variables to meet the assumptions of the test. We used a square root transformation for the distance variables as it was the optimal transformation compared to the alternatives (log, cube root). Using square root transformation enabled us to correct for the right skew in the data, whereas the other transformations induced a left skew to the distribution. We used the lme4 package (Bates et al., 2016) within the R statistical software package (R Development Core Team, 2016) to perform a logistic regression analysis using a binomial error family. We used this to identify the variables that were important for determining which sample points had been cleared for agriculture and which remained as natural vegetation. We used MuMIn (Barton, 2016) to evaluate all candidate models to examine the averaged parameter estimates (β), standard errors and confidence intervals of the predictor variables. MuMIn also allowed us to compare models using the Small Sample Aikake Information Criteria (AICc) and restricted changes in model AIC to less than four (ΔAICc < 4), to remove implausible models. Model averaging was not needed as our restricted model set resulted in only one model at ΔAICc < 4. We tested for the presence of spatial autocorrelation by calculating the Moran I statistic of the logistic regression residuals.

2.3.3. Future scenarios of agricultural expansion

We developed a spatially-explicit prediction model using the logistic model parameters to understand future patterns of agricultural expansion and its effects on forest cover and potential human-elephant conflict. For this, we needed to produce a risk map of agricultural expansion, estimates of annual forest loss and estimates of elephant crop raiding distances from forest to farm land. We produced the agricultural risk map using the parameters from the agricultural spread logistic regression model. This involved producing 25 m resolution raster layers for each of the important variables, and in the case of distance to farmland, we based this layer on the 2015 farmland map. We combined these raster layers in the ArcMap Raster Calculator to produce a surface showing the probability of each pixel being cleared for agricultural, and then used the Overlay function to show only those pixels that were forest in 2015.

As the annual forest loss between 2000 and 2015 was calculated as 2.8% per annum, we decided to model four scenarios based on future loss rates of 1%, 3%, 5% and 10%. The 1% value was selected to illustrate a “best case” scenario where deforestation rates were severely reduced. The 5% and 10% scenarios were selected to model the potentially large increases in deforestation that may occur in the future when land is sub-divided and landowners are given title deeds and can legally clear their land for agriculture. Land ownership in the Trans Mara has historically fallen under two categories (Sitati, 2003): (1) communal land/group ranches, where land was owned communally but had fixed and legally recognised boundaries (Swift and Lane, 1988); and (2) private land. Group ranches covered 82% in 2003 but this has rapidly declined over the last fifteen years with title deeds of individual plots of land being issued to group ranch members. Thus, there will be an increase in land being cleared or sold once title deeds have been officially given (Okello, 2005).

For each of the four scenarios, we then calculated the amount of forest that would be lost by 2025 based on the area in 2015 and the annual deforestation rates, and then produced new forest cover maps by removing the corresponding number of forested pixels with the highest probabilities of being cleared for agriculture.

We estimated the distance that elephants travel from forest patches to farmland using 1999-2000 crop raiding data collected as part of a previous study (Sitati et al., 2003). Given that forest cover has changed since that study, we also compared this result with 2015/2016 GPS collar data from an elephant that was known to have been involved in crop raiding during this time. From the 1999-2000 data, we used the Generate Near Table function in ArcMap10.3 to calculate the distance of 329 crop raiding incidents to the nearest forest patch in the 2000 landcover map. We then calculated the median distance, which was 0.66 km, and the maximum distance, which was 2.81 km. We used the GPS collared data that showed the location of the elephant at hourly intervals from April 2015 to April 2016, to determine an additional distance to use in our scenario modelling. We used the spatial join option in ArcMap to determine the landcover type found at each location and developed a Python script to identify a number of elephant "journeys", where the elephant moved from a patch of forest into farmland. In each case, the script identified the furthest distance the elephant moved into the farmland before returning to the same or a different forest patch. This produced data for 18 journeys from which we calculated the median and maximum journey length, giving a median value of 2.28 km and maximum of 7.05 km.

Given the disparity of the results from the two time periods, we decided to model results based on three crop raiding distance values: (1) the "low" value, which equalled the median 1999-2000 result; (2) the "medium" value, which equalled the maximum 1999-2000 result (and was similar to the median 2015/2016 result), and; (3) the "high" value, which is the maximum 2015/2016 result. For each forest loss scenario, we then calculated the area of farmland in 2025 that was within the low, medium and high crop raiding distances. Finally, we calculated how these three crop raiding vulnerability zones for each scenario compared to those based on forest cover in 2015.

2.4. Results

2.4.1. Modelling agricultural expansion

2.4.1.2. Mapping landcover

Landcover in the Trans Mara has changed markedly in the last 15 years. In 2000, there was 348.1 km² of forest, but forest cover declined by 38.8% leaving 213.3 km² of forest in 2015. Grassland also decreased, with 1029.5 km² remaining in 2015 compared to 1296.8 km² in 2000, a reduction of 20.6%. Crop land correspondingly increased by 42.5% in the last 15 years from 945.7 km² in 2000 to 1347.8 km² in 2015, an average 2.83% increase per annum over the study period.

2.4.1.3. Agricultural expansion probability model

The spread of agriculture was best predicted by the square root distance to existing farmland and longitude and latitude (Figure 2.1). Land was more likely to be cleared for agriculture when it was closer to current farmland (β = -0.0367, 95% confidence intervals = -1.583, -0.492), in the north (β = 0.0000564, 95% confidence intervals = 0.860, 1.978) and west (β = -0.000017, 95% confidence intervals = -1.040, -0.039). The model had a receiver operating characteristic (ROC) value of 0.756, indicating a good model fit (Swets, 1988) and was not affected by spatial autocorrelation (Moran's I = -0.046, Z = -1.447, p = 0.148).

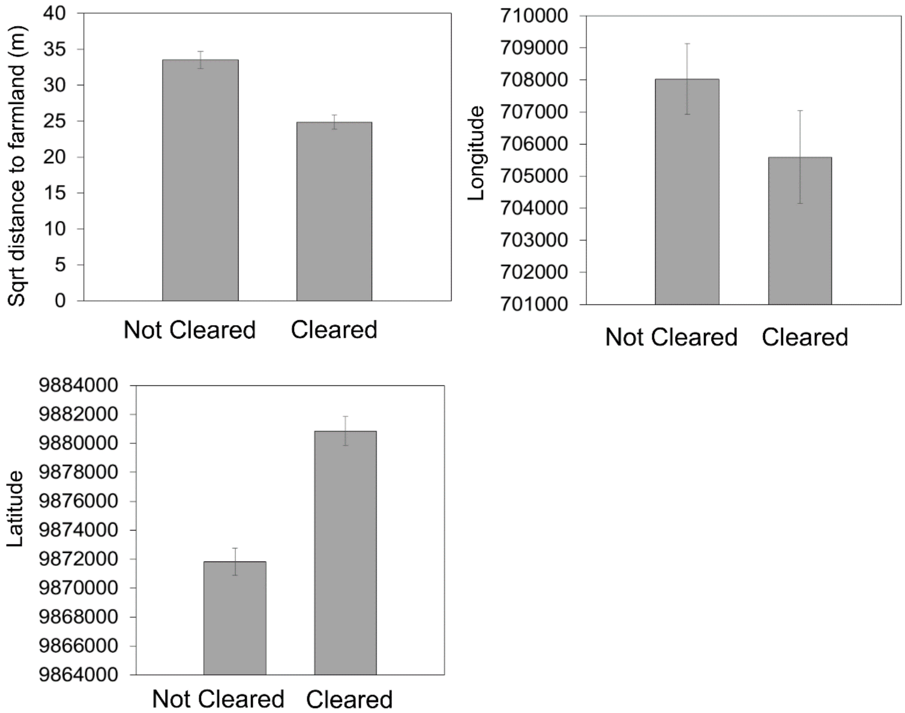

Figure 2.1. Mean values of distance to farmland, longitude and latitude of not cleared and cleared sampling points between 2000 and 2015. Longitude and latitude are measured in metres, based on the UTM36S reference system.

2.4.2. Future scenarios of agricultural expansion

2.4.2.1. Risk map of agricultural expansion

The agricultural risk model predicted that the small patches of forest furthest away from the Masai Mara National Reserve, in the north and north-east of the Trans Mara were most at risk of being cleared for agriculture (Figure 2.2). Forest in the centre of the Trans Mara was less at risk, especially in the middle of larger forest patches.

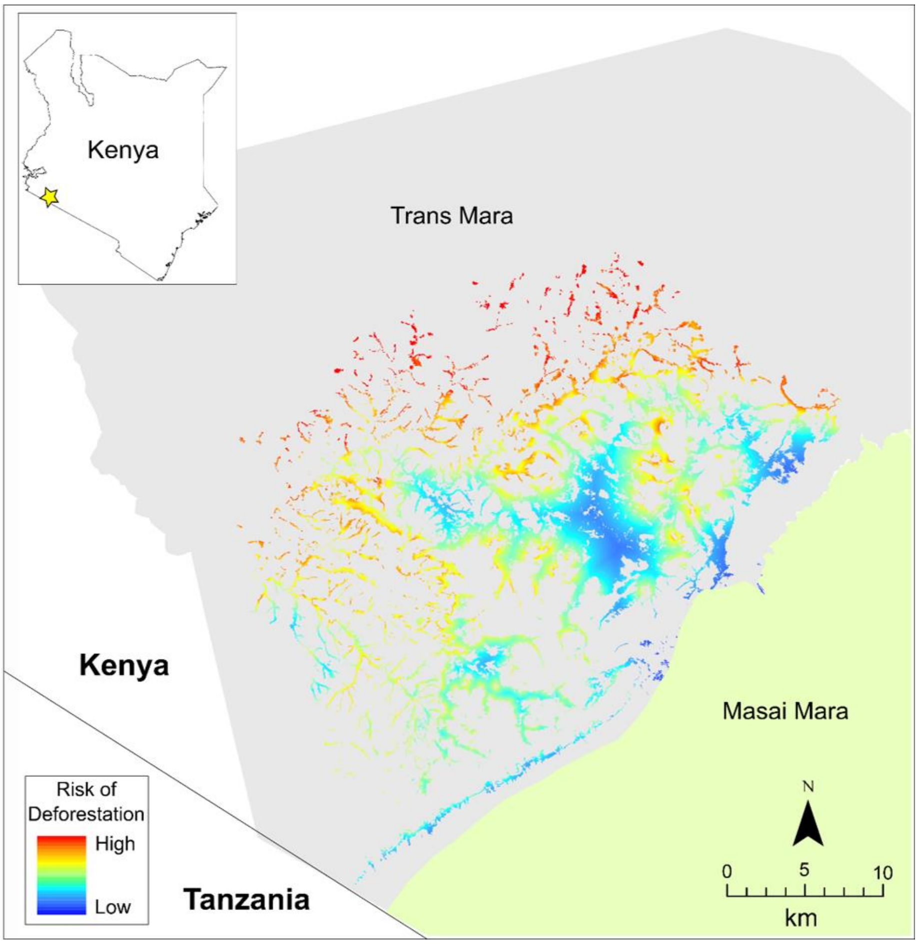

Figure 2.2. Predicted risk of forest loss in the Trans Mara District based on distance to existing agriculture and longitude and latitude

2.4.2.2. Modelling future changes in extent of forest cover and crop raiding

The four scenarios, based on annual forest declines of 1%, 3%, 5% and 10% respectively, showed the central part of the forest in the Trans Mara is likely to remain intact even with a high rate of forest loss (Figure 2.3). In addition, the results showed that the scenarios with higher deforestation rates led to fewer, smaller forest patches. Based on the three crop raiding distance values, we then calculated the total area at risk of future crop raiding based on the current forest cover and the four scenarios. For the current forest cover, 985.3 km^2 of farmland was within the low crop raiding incident distance, 1292.5 km^2 within the medium crop raiding incident distance and 1657.0 km^2 was within the high crop raiding distance. Based on the four scenarios, the area of farmland vulnerable to crop raiding reduced as deforestation increased. However, the relationship was not a linear one so, for example, Scenario 4 predicted a 65% reduction in forest cover but a 67% reduction in the area of farmland within the low crop raiding distance, a 45% reduction within the medium crop raiding distance and a 33% reduction within the high crop raiding distance (Table 2.1).

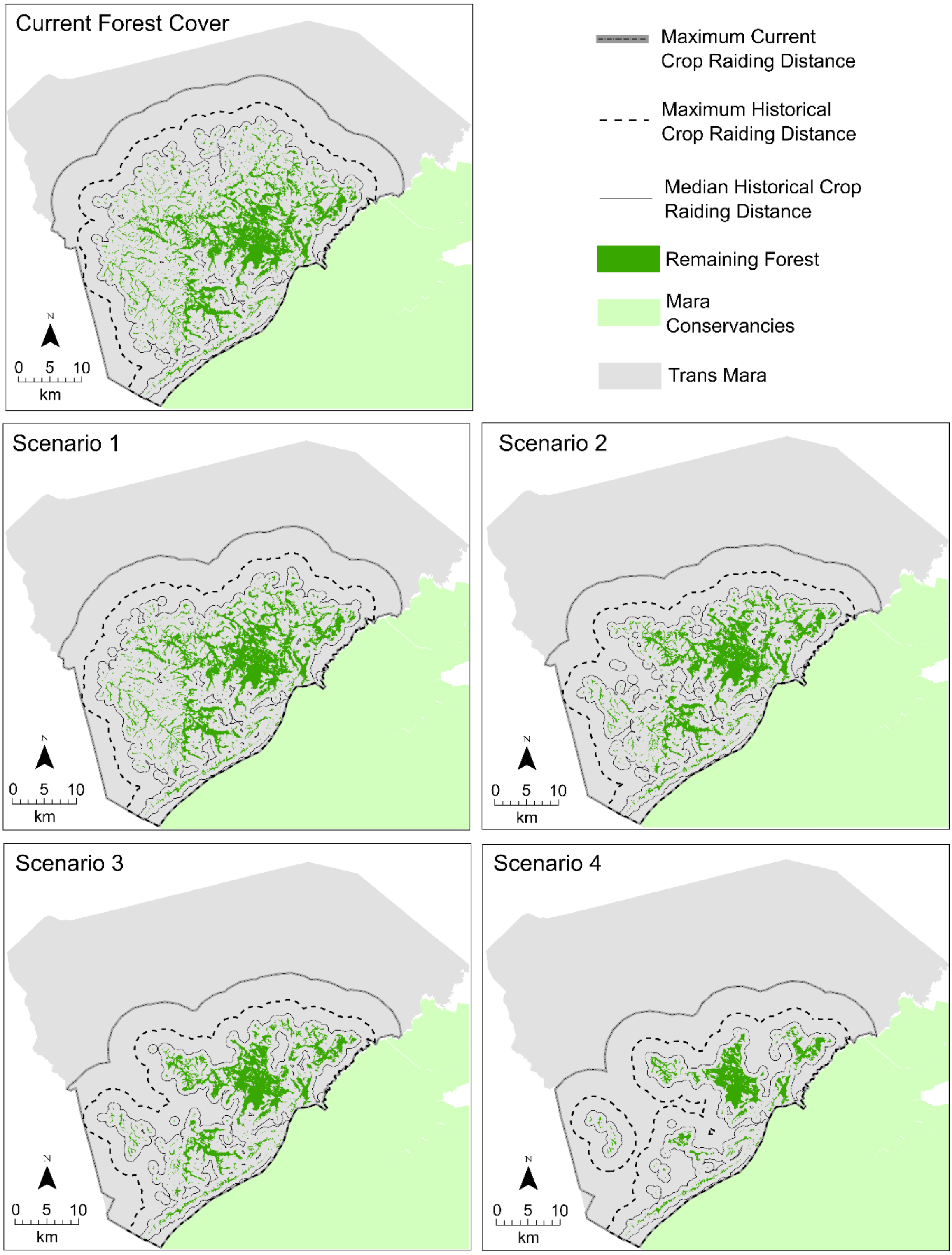

Figure 2.3. Current forest cover and the four different forest loss scenarios showing where elephants could crop raid in the Trans Mara District based on model of predicted agricultural expansion. The different scenarios are: Scenario 1 = 1%, Scenario 2 = 3%, Scenario 3 = 5%, and Scenario 4 = 10% annual forest loss over 10 years.

Table 2.1. Characteristics of current and future forest cover and farmland at risk of elephant crop raiding. Four scenarios predict forest cover in 2025 based on annual deforestation rates of 1%, 3%, 5% and 10%. Percentage decrease in crop raiding risk area is based on changes from the predicted area in 2015; all crop raiding risk maps assume that farmland that is within the low (0.66 km) and medium (2.81 km) and high (7.05 km) distances from forest are vulnerable to elephant crop raiding. The low and medium values are based on the median and maximum distance of recorded crop raiding incidents from forest based on 1999-2000 data; the high value is based on 2015-2016 data from a GPS-collared elephant.

Scenario	Forest area (ha)	No of forest patches	Median patch size (ha)	Total forest loss (%)	% decrease in crop raiding risk area – low	% decrease in crop raiding risk area – medium	% decrease in crop raiding risk area – high
2015	21330	1541	1.4	-	-	-	-
1% yr^{-1}	19270	2230	1.2	10.2	18	16.2	14.5
3% yr^{-1}	15720	1636	0.3	26.7	33.7	25.8	23.1
5% yr^{-1}	12780	1189	0.2	40.4	47.1	33.1	26.8
10% yr^{-1}	7430	725	0.2	65.3	67.1	44.7	33.1

2.5. Discussion

Agricultural expansion is one of the biggest threats to biodiversity (Green, 2005; Laurance et al., 2014; Maxwell et al., 2016; Tscharntke et al., 2012) and human-wildlife conflict is an increasing problem for people and other species sharing these same landscapes and resources (Balmford et al., 2001; Woodroffe et al., 2005). However, there is little research on how landcover change could impact human-wildlife conflict, so our research sought to fill that gap by mapping and modelling patterns of agricultural spread in an area of western Kenya, producing a risk map of future agricultural expansion, and combining this with data on elephant ranging patterns to model elephant crop raiding under different land-use change scenarios.

2.5.1. Drivers of agricultural expansion

Our study revealed that landcover has changed markedly in the Trans Mara since 2000, with a 43% increase in agriculture and a corresponding fall in forest cover and grassland. This produced an average rate of annual forest loss of 2.8%, which is comparable to deforestation rates of 3.5% in central Brazil (Bianchi and Haig, 2012) and 1.1% to 5.9% in Sumatra (Achard et al., 2002; Linkie et al., 2004). Such high rates of agricultural expansion have been documented elsewhere in the Masai Mara (Homewood et al., 2001;

Norton-Griffiths, 1996; Norton-Griffiths, 2006; Serneels et al., 2001; Serneels and Lambin, 2001), partly because this ecosystem makes up some of Kenya's highest quality arable land (Omondi, 2004). It also reflects global agricultural trends, especially across the tropics (Laurance et al., 2014), where farmland area increased by an average of 48,000 km² per year between 1999 and 2008 (Phalan et al., 2013).

Landcover change is often caused by multiple interactions that vary in time and space but there are often consistent patterns (Geist and Lambin, 2002). In the Trans Mara, we found the factors that best predicted patterns of agricultural expansion were distance to farmland and longitude and latitude, so that land in the north-west that neighboured existing farmland was most at risk of being cleared for agriculture. Other studies also revealed that distance to farmland is a good predictor of agricultural spread (Maeda et al., 2010; Smith et al., 2008), probably because it is generally easier for existing farmers to clear neighbouring land, and for new farmers to cultivate land where there is already a network of other farms and associated roads and markets (Homewood et al., 2001; Serneels and Lambin., 2001). Latitude and longitude were probably important for two reasons. First, census data show that human densities are higher in the West, which is close to the Tanzanian border, and in the North, which is closer to the main road network and further from the Masai Mara National Reserve (Homewood et al., 2001; Serneels and Lambin, 2001). Most people in the area are farmers, so human population density is likely to be a driving factor. However, the available census data were recorded at too coarse a spatial resolution to be usefully included in our model. Second, latitude and longitude could account for the observed pattern of spatial dependency, where neighbouring land patches have similar risks of being cleared. This is supported by the finding that including these two factors in the analysis produced models that were not affected by spatial autocorrelation (Dormann et al., 2007; Koenig, 1999).

Our analysis also found that a number of factors that predict landcover change patterns in other studies were not important in the Trans Mara. This was probably partly due to the local conditions as, for example, the terrain is relatively flat and so slope and elevation were not important (in contrast to: de las Heras et al., 2012; Green et al., 2013; Patarasuk and Fik, 2013; Pfeifer et al., 2012). More surprising was that distance to villages was not important, as found in a previous study from the Mara ecosystem (Serneels and Lambin, 2001). This could have been because our study focused on a smaller area, where the distance of each land parcel to a village varied less, which would explain why distance to roads was also not important, despite playing an important role elsewhere (Chomitz and Gray, 1996; Mann et al., 2010; Patarasuk and Fik, 2013; Pfeifer et al., 2012). It might also have been because distance to farmland and latitude and longitude better captured the relationship at this finer scale.

2.5.2. Future scenarios of agricultural expansion

Agricultural risk mapping is important for conservation planning as it can help identify areas in a landscape that are most at risk and in need of protection (Smith et al., 2008). In the Trans Mara, there is particularly concern about forest cover, as the remaining forest patches contain high levels of biodiversity, provide ecosystem services and often hold significant cultural value (Foley et al., 2005). Our risk map suggests that forest on the edges further from the central forest core will most likely be cleared for agriculture, but the extent of this loss will depend on future rates of agricultural expansion. This is why we developed four scenarios based on a range of agricultural expansion rates. Scenario 1 assumed a rate of 1% per annum, much lower than the average historical rate of 2.8%, which would result in ten percent forest loss over by 2025. Scenario 2 used a 3% annual rate, as this close to the current rate, and this would result in a more than a quarter of the forest being lost. Scenarios 3 and 4 were based on annual deforestation rates of 5% and 10% respectively, which were much higher than has been recorded but still provide useful insights, especially on potential forest cover after 2025. These predicted between 40% and 65% drops in forest cover, above the 30% decline which was identified as a threshold for increasing HEC in Assam, India (Chartier et al., 2011).

This suggests HEC will continue to be an important issue within the Trans Mara, especially as our scenarios predicted that there will still be patches of forest left in the region, even as forest cover drops. Such patches are known to act as refuges for elephants to avoid contact with humans before and after crop raiding in Assam (Wilson et al., 2013), and research from Laikipia, Kenya, found that distance to daytime refuge was a significant predictor of crop raiding spatial patterns (Graham et al., 2010). There is anecdotal evidence that the same occurs in the Trans Mara (Sitati, 2003), and although all our scenarios predicted a drop in the number of patches, there are two reasons why we expect HEC to remain prevalent. First, our scenarios predict that the reduction in forest patch number will mostly come from the loss of the small patches. Our modelling showed that despite size reductions of the larger patches, these would still be big enough to act as refuges for elephant groups. Second, our scenario modelling showed there would still be a considerable amount of farmland within travelling distance of these forest patches, which could be at risk of HEC.

We used three values when predicting how much farmland would be within crop raiding distance from forest patches, based on two different types of dataset. The estimates based on the 1999-2000 crop raiding incident data were much lower than that from the 2015-2016 GPS collar data from the known crop raiding elephant, so the maximum value from the former was close to the median value of the latter. This could be because forest cover was higher in the earlier period, so that more farms had nearby forest patches and elephants did not have to travel as far to crop raid. Alternatively, it could be that the method we used to analyse the 2015-2016 data were less accurate, incorrectly assuming that when the elephant was recorded in a farm that it was crop raiding. It is impossible to know without collecting more data, although results from another site in Kenya showed that the distances crop raiding elephants travelled from a refuge were similar to the higher values we calculated from the GPS collar data, i.e. most crop raiding incidents occurred within 2 km of an elephant refuge and the furthest distance recorded was 10 km (Graham et al., 2010). Either way, not all the farmland within these ranging distances will be affected by crop raiding, especially when farmers deploy mitigation strategies (Sitati and Walpole, 2006), or if levels of elephant poaching or retribution killings increase. However, our scenario modelling suggests much of the Trans Mara will remain vulnerable to HEC, even when more than half the forest is lost.

2.5.3. Conservation implications

Since 2000, agriculture has transformed the Trans Mara, with obvious negative impacts on the biodiversity of the region through loss of grassland and forest habitats. Just as importantly, it has disrupted ecological processes and impacted wide ranging species, such as elephants, which have core populations within the Masai Mara National Reserve but rely on land outside the protected area (Woodroffe and Ginsberg, 1998; Blanc et al., 2007; Perfecto and Vandermeer, 2010). This could lead to population declines and extirpations as wildlife will be restricted to protected areas, reducing movement and genetic flow. It has also had negative impacts on the people living in the region, as they have lost important ecosystem services provided by the remaining forest patches, such as water provision, food for livestock and medicines. Moreover, our study suggests this loss of forest habitat will not seriously reduce elephant crop raiding. Therefore, change is needed to promote co-existence between people and wildlife in the Trans Mara.

One solution to try to reduce human-elephant conflict in the Trans Mara is to focus specific deforestation projects in areas which have been highlighted in this study that are vulnerable to clearing and that have the minimum habitat requirements for elephants. These projects could include habitat restoration programmes and patrols within the forest to prevent illegal charcoal burning and clearing. Another solution to address the underlying causes of landcover change is to provide a viable source of income for local people that is not dependent on clearing more land for agriculture. This should be possible, as the Mara ecosystem is globally famous and attracts large numbers of tourists a year. A number of conservancies, which are owned and managed by local communities, have been set up elsewhere in the Mara ecosystem and throughout Kenya, showing that this approach could work within the Trans Mara. For example, the forest in the Trans Mara could be developed into a community conservancy or a carbon credit scheme could be set up where communities would benefit from their land. Finally, our analysis has shown that it is possible to model different scenarios of landcover change and these could be used to guide land-use decision making to balance the requirements of people and wildlife.

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2.7. Supporting information

Table S2.1. Tools used in ArcMap 10.3 to extract GIS data (elevation, slope and distance data) for each sample point; 150 sample points inside areas that were cleared for agriculture since 2000, and 150 sample points from land that remained natural (grazing or forest).

GIS layer	Source	Tool used to extract data for each sample point
Elevation	Shuttle Radar Topography Mission (SRTM)	Extraction
Slope	Shuttle Radar Topography Mission (SRTM)	Extraction
Distance to nearest village centre in 2000	Sitati, 2003	Generate Near Table
Distance to nearest farmland in 2000	Sitati, 2003	Generate Near Table
Distance to roads in 2000	Sitati, 2003	Generate Near Table

3. An uncertain future: changing seasonal, temporal and spatial crop raiding trends in a human-elephant conflict hotspot

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3.1. Abstract

Human-elephant conflict is a complex problem and is escalating due to rapid habitat loss and fragmentation. Reducing such conflict requires understanding its drivers and trends over time in order to develop and adapt effective management strategies. In this study, we investigated seasonal, temporal and spatial trends of human-elephant conflict in the Trans Mara, Kenya in 2014-2015 and compared these results with historical data from 1999-2000. We developed a new method for investigating the complexity of spatial trends at a fine scale, using Generalised Additive Models (GAMs). We found that crop raiding characteristics have changed over time, including a 49% increase in the number of incidents between 1999-2000 and 2014-2015; a decline in the amount of damage to farms from a mean of 1.17 ± 0.0096 ha in 1999-2000 to 0.20 ± 0.014 ha in 2014-2015; and year-round crop raiding damaging crops at all growth stages in 2014-2015 compared to 1999-2000 when there was seasonal crop raiding of mature crops. We also found a new elephant group type involved in crop raiding, comprising family + bull groups. Results from our GAM models show that increases in farmland area led to increases in crop raiding until a threshold of 0.4 km^2. The models also showed that farms 1 km from the forest boundary, 5 km from the protected area boundary and >2 km from village centres were most at risk of crop raiding. This study demonstrates the value of using a standardised conflict monitoring system to document human-elephant conflict trends over time in order to inform conflict mitigation. Management of human-elephant conflict should involve local communities to help build tolerance towards elephants, especially in the light of changing patterns of crop raiding, observed in the Trans Mara.

3.2. Introduction

One of the most complex issues in conservation is managing competition for space and resources between people and wildlife (Balmford et al., 2001; Woodroffe et al., 2005). This human-wildlife conflict is exacerbated by habitat loss and fragmentation (Foley et al., 2005; Newbold et al., 2015), and growing human populations around protected area boundaries (Wittemyer et al., 2008). Human-wildlife conflict is increasing and involves a large number of species, particularly large mammals (Nyhus, 2016). African elephants (*Loxodonta africana*) are particularly prone to conflict with people as they spend much of their time outside protected areas (Blanc et al., 2007). Local communities can incur substantial costs from crop raiding elephants, which damage crops and property and sometimes cause human injury or loss of life (Naughton-Treves, 1997). These costs can lead to retributive killing of elephants (Choudhury, 2004; Linkie et al., 2007; Mariki et al., 2015) and strongly undermine conservation efforts directed at managing this conflict (Dickman, 2010; Nyhus, 2016; Pooley et al., 2017). In this context, understanding seasonal, temporal and spatial trends of elephant crop raiding are integral to developing effective mitigation strategies (Naughton-Treves, 1998), as they can identify human-elephant conflict hotspots, and thus help target mitigation programmes.

To understand seasonal patterns, researchers have described elephant behaviour in terms 'optimal foraging theory', where individuals seek to gain the most energy for the lowest cost (Stephens and Krebs, 1986). This is why human-elephant conflict in savanna systems has often been related to rainfall patterns, as the quality of natural forage declines during the dry season at the same time that crops ripen (Chiyo et al., 2005; Goswami et al., 2015; Gubbi, 2012; Osborn, 2004; Webber et al., 2011). Temporal patterns are generally thought to be more driven by risk-avoidance behaviour, as elephants typically crop raid at night when they are less likely to be detected by farmers (Graham et al., 2009, 2010). This risk-avoidance has also been linked to the type of elephant group involved in crop raiding, although this is often site-specific. For example, in some locations bull elephants are largely responsible for crop raiding (Sukumar and Gadgil, 1988; Chiyo and Cochrane, 2005; Von Gerhardt et al., 2014), whereas in others female-led family groups are equally involved (Graham et al., 2010; Sitati et al., 2003; Wilson et al., 2013) or the most responsible (Smith and Kasiki, 2000). Thus, crop raiding behaviour can vary across sites, by elephant group type and over time, depending on the landscape and the behaviour of people towards elephants.

This risk taking behaviour is also thought to predict the spatial distribution and intensity of crop raiding. Once again, this is often context specific but there are some general trends that relate to elephants avoiding areas where they are most likely to be detected by farmers. For example, crop raiding tends to occur more frequently closer to forest edges and protected areas, further from roads and in areas of low human density (Barnes et al., 2005; Chen et al., 2016; Goswami et al., 2015; Graham et al., 2010; Guerbois et al., 2012; Sitati et al., 2003; Wilson et al., 2013). However, these relationships are complicated by multiple factors relating to food availability, such as farm location, farmer mitigation effort, number and types of crops and availability of food and water. In addition, understanding the factors that determine crop raiding depends on analysing the data at an appropriate scale. Previous analyses often used coarse-scale approaches, mostly to avoid the problems of spatial autocorrelation that occur when studying this type of spatially clustered data. However, these coarse scales may not be enough to explain the complexity of spatial drivers of crop raiding (Songhurst and Coulson, 2014).

In addition all previous studies have only analysed these seasonal, temporal and spatial patterns during one time period. This makes it difficult to determine the long-term significance of different factors, which is an important limitation given the rapidly changing land-use patterns and climate throughout most of Africa (Pozo et al., 2017). Thus, understanding patterns from a longitudinal point of view is a fundamental step in finding solutions to tackle human-elephant. To fill this gap, we repeated a previous study from 1999-2000 (Sitati et al., 2003) by analysing seasonal, temporal and spatial patterns of elephant crop raiding in 2014-2015 in the Trans Mara District in Kenya, a region of high human-elephant conflict that neighbours the Masai Mara National Reserve. We do this by: i) assessing crop raiding characteristics in terms of frequency, amount of damage and elephant group type; ii) determining temporal and seasonal trends of number of crop raiding incidents; iii) mapping and modelling the spatial drivers of crop raiding, using a finer-scale approach based on General Additive Modelling. This model incorporates complexities that can not be modelled using conventional linear statistical techniques.

3.3. Methods

3.3.1. Study area

The Trans Mara District is situated in South-West Kenya and borders the western portion of the Masai Mara National Reserve. The district forms part of Narok County and covers an area of 2,900 km^2, 76% of which is unprotected. The region is an important dispersal area for elephants and has traditionally been home to a resident population of 200-300 individuals (Sitati et al., 2003). There is also a portion of the Masai Mara National Reserve elephant population which migrates in and out of the Trans Mara (Sitati et al., 2003). Historically, the people living in this region were pastoralists but this has changed in recent decades, especially because the high rainfall and rich fertile soils in the Trans Mara make it highly suitable for farming (Sitati et al., 2003). The region's human population increased by 63% between 1999 and 2009 and this has led to high levels of land transformation (Chapter 2). So this landscape now consists of farmland interspersed with a mosaic of afro-montane, semi deciduous and dry-deciduous forests and Acacia savanna woodlands (Chapter 2). The region is recognised as a human-elephant conflict hotspot within Kenya, due to the high number of incidents each year (Litoroh et al., 2012).

3.3.2. Data collection

We collected data on elephant crop raiding between June 2014 and November 2015 following the methods developed by Sitati et al., (2003). Ten enumerators (community scouts) were trained to use an adapted version of IUCN's training package for enumerators of elephant damage (Hoare, 1999a), which is a widely used standardised human-elephant conflict monitoring system (Graham et al., 2010; Pittiglio et al., 2014; Songhurst and Coulson, 2014; Wilson et al., 2013). Enumerators were selected from the same 10 locations as Sitati et al., (2003), which covered the entire elephant range in the Trans Mara. Any crop raiding incident that occurred within an enumerator's assigned area was visited to verify the incident and to record the location using a Garmin Etrek30 Global Positioning System (GPS). Each incident, even if it occurred on the same farm, was classified as a unique event and we recorded the crop type damaged, the amount of damage, the time of the incident (to the nearest half hour), the number of elephants involved and their sex. Elephant group type was assessed by the enumerators based on the size and frequency of elephant dung and footprints (Balasubramanian et al., 1995; Chiyo and Cochrane, 2005).

3.3.3. Data analysis

3.3.3.1. Characteristics of elephant crop raiding

To assess and compare crop raiding characteristics over time we used the data from Sitati et al., (2003) that was collected in 1999-2000 and compared it to the 2014-2015 data described above. We classified the data based on elephant group type involved as: family group; bull group; family + bull group or `Unknown'. We then calculated the number of crop raiding incidents, the median percent of damage per farm, the mean amount of damage per incident and the median elephant group size involved in crop raiding.

3.3.3.2. Temporal and seasonal patterns of crop raiding

To investigate whether temporal and seasonal patterns of crop raiding had changed since 1999-2000, we calculated the start, end and duration of each 2014-2015 crop raiding incident by elephant group type. We also measured the monthly patterns of crop raiding in terms of crop age, based on four categories: (1) young; (2) middle; (3) old; (4) mature as defined in Sitati, (2003). We compared the seasonal patterns to mean monthly rainfall data, which were based on daily readings from weather stations across the Trans Mara.

3.3.3.3. Spatial patterns of crop raiding

Producing the spatial data

To investigate the spatial distribution of crop raiding across the Trans Mara, we used the same eight predictor variables adopted by Sitati et al., (2003): distance to rivers; distance to roads; distance to villages; distance to forest edge; area under forest; area under cultivation; elevation; and population density. We mapped forest and farm cover, roads, rivers and villages by on-screen digitising 5m CNES/Astrium satellite imagery from 2015, using QGIS (QGIS Development Team, 2015). The elevation and slope data were derived from 30 m resolution Shuttle Radar Topography Mission (SRTM) files, and the population density data were calculated as the mean value within each division of the Trans Mara (there are five administrative divisions in the Trans Mara), based on the 2009 census. Using the Euclidian Distance tool in ArcMap10.4, we created 25 m resolution layers showing distance to roads, rivers, villages and forest. We restricted all the analyses to the known elephant range, which we based on data from an ongoing project that uses GPS collared elephant individuals (Mara Elephant Project, 2017).

Univariate group type analysis

For each crop raiding incident, we calculated its distance to rivers, distance to roads, distance to villages, distance to forest edge and distance to protected area using the Generate Near Table function in ArcMap10.4. We also calculated the elevation of each crop raiding incident using the Extraction Tool in ArcMap10.4. We then determined whether these spatial characteristics of crop raiding incidents differed between group types using Kruskal-Wallis tests and carried out Mann-Whitney U tests to further explore these relationships.

Logistic regression analysis

To understand how the drivers of human-elephant conflict have changed over time, we replicated the analysis of Sitati et al., (2003) by using logistic regression analysis to determine the factors that best predict the presence of crop raiding in a series of grid squares. Sitati et al., (2003) used 5 km by 5 km grid squares because conducting a finer scale analysis, based on 1 km^2 grid squares, produced models that were influenced by spatial autocorrelation. Our exploratory analysis found similar problems when using 1 km^2 grid squares, so we also used 25 km^2 grid squares, allowing a direct comparison between the 1999-2000 and 2014-2015 datasets. This involved undertaking three separate analyses based on the three group types. We first identified which grid squares had experienced crop raiding in 2014-2015 by the three group types using a spatial join in ArcGIS. We then calculated the area of forest and farmland in each grid square by using the Tabulate Area function. We used the 25 m distance maps that we created to calculate the mean values of the distance variables (distance to roads, rivers, villages and forest) of each grid square by using the Zonal Statistics Tool. We used this tool to also calculate the mean elevation and slope of each grid square from the 25 m elevation and slope maps. The available human density data were mapped at the division level (the Trans Mara consists of 5 divisions). Only three of these divisions covered the study area. We therefore determined the mean human population density per division and then calculated the population density per grid square based on the proportion of each division that fell within each square. Using Pearson correlation coefficients and Variance Inflation Factors (VIF), we found no evidence of serious collinearity between our predictor variables ($r < 0.7$; VIF < 5; Dormann et al., 2013). All predictor variables were rescaled to have a mean of zero and a standard deviation of 0.5. Rescaling improves the interpretation of the model outputs as it puts the predictors on a common scale (Gelman et al., 2008).

To find which factors predicted crop raiding presence we used R (R Development Core Team, 2013) and the lme4 package (Bates et al., 2016) to carry out a logistic regression analysis, using a binomial error structure and logit link function. We used the package MuMIn (Barton, 2016) to evaluate all candidate models and examine the averaged parameter estimates (Beta), standard errors and confidence intervals of the predictor variables. MuMIn also allowed us to compare models using the Akaike Information Criteria (AICc), restricting the models to ΔAICc < 4 to remove implausible models.

Generalised additive model (GAM)

Analysing crop raiding data as a binary variable at a relatively coarse spatial resolution meant losing a lot of potentially important information. Thus, we also analysed the data on the number of incidents at a 1 km^2 resolution. For each elephant group type, we divided the elephant range into 1299 1 km x 1 km grid squares and calculated the number of crop raiding incidents that occurred within each square. We then assessed the influence of six predictor variables on the frequency of crop raiding (distance to rivers, distance to villages, distance to forest edge, area under cultivation, elevation and distance to protected area). Exploratory modelling identified persistent over-dispersion due to zero-inflation and non-linear relationships between the response and predictor variables. Furthermore, model residuals demonstrated increasing variance as a function of distance, indicating spatial autocorrelation. To overcome this problem, we modelled non-zero observations only using Generalized Addictive Models (GAM) that applied a smoothing term for non-linear data (Wood, 2006). We incorporated distance-weighted covariates into the modelling framework using the autocov_dist function in the R package "spdep". We used the package mgcv to fit GAMs for family groups and family + bull groups using a Poisson error and negative binomial structure respectively and log link functions. We were unable to use this approach for the bull groups because there were insufficient data points for the model to run, following removal of zero observations. For the final GAM models, we carried out model validation to confirm the absence of heteroscedasticity in model residuals and influential data points with high leverage (Cook's Distance > 1.0).

3.4. Results

3.4.1. Characteristics of elephant crop raiding

Elephant crop raiding in the Trans Mara has changed markedly in the last 15 years. Historically, crop raiding was carried out by two different elephant group types: (1) family groups and (2) bull groups, including lone bulls. However, we recorded an additional group type involved in crop raiding, which is a combination of a family group and bulls. These family + bull groups were involved in the most incidents and caused the highest amount of damage per incident (Table 3.1).

Crop raiding went from 263 incidents per annum in 1999-2000 to 392 incidents per annum in 2014-2015 in the Trans Mara, an increase of 49%, (Table 3.1). Despite the increase in the number of incidents, there was a decline in the area of damage per incident, as mean damage of all incidents (including by unknown group types) in 1999-2000 was 1.17 ± 0.0096 ha compared to 0.20 ± 0.014 ha in 2014-2015. The percentage of each field damaged in 2014-2015 was generally low: 67% of incidents involved damage of <10% of the total cultivated area being damaged, 5% of incidents led to >50% of cultivated area being damaged, 2% of incidents led to the entire cultivated area being damaged. As in

1999-2000, the main crop eaten in 2014-2015 was maize, but the total number of crops eaten increased from 18 in 1999-2000 to 26 in 2014-2015.

Table 3.1. Elephant crop raiding characteristics in 1999-2000 and 2014-2015.

Crop raiding Characteristics	**1999-2000** (329 incidents in 15 months)		**2014-2015** (588 incidents in 18 months)			
	Family	Bull	Family	Bull	Family + bull	Unknown
Number of incidents	64%	32%	24%	11%	28%	37%
Median percent of crop damage (ha) per farm area	30	25	5.2	1.7	6.0	5.5
Mean amount of damage (ha) + SE	1.18 ± 0.122	0.60 ± 0.060	0.20 ± 0.025	0.10 ± 0.020	0.22 ± 0.032	0.20 ± 0.023
Median elephant group size	8	3	6	3	10	-
Elephant group size range	3-40	1-9	3-50	1-6	4-65	-
Median incident duration (minutes)	180	90	90	60	90	60

3.4.2. Temporal and seasonal patterns of crop raiding

Seasonal and temporal crop raiding patterns also changed between the two study periods. The time range during which crop raiding occurred increased from 19:00-05:00 in 1999-2000 to 18:00-09:00 in 2014-2015, although incidents recorded after 06:00 were still rare (Figure 3.1). The amount of time each group spent crop raiding declined between 1999-2000 and 2014-2015, with the median time for family groups dropping from 180 minutes to 90 minutes and the median time for bull groups dropping from 90 minutes to 60 minutes (Table 3.1). The crop raiding incident duration in 2014-2015 for family + bull groups was the same as that for family groups.

In 2014-2015, crop raiding occurred every month for the 18 month monitoring period and affected crops at every growth stage. There was a decline in crop raiding incidents in February 2015, September 2015 and October 2015 which is related to the period after maize harvesting. In 1999-2000 there were clear peaks in crop raiding, with 2 months experiencing no crop raiding, and the majority of crops damaged were mainly mature or old crops (Figure 3.1).

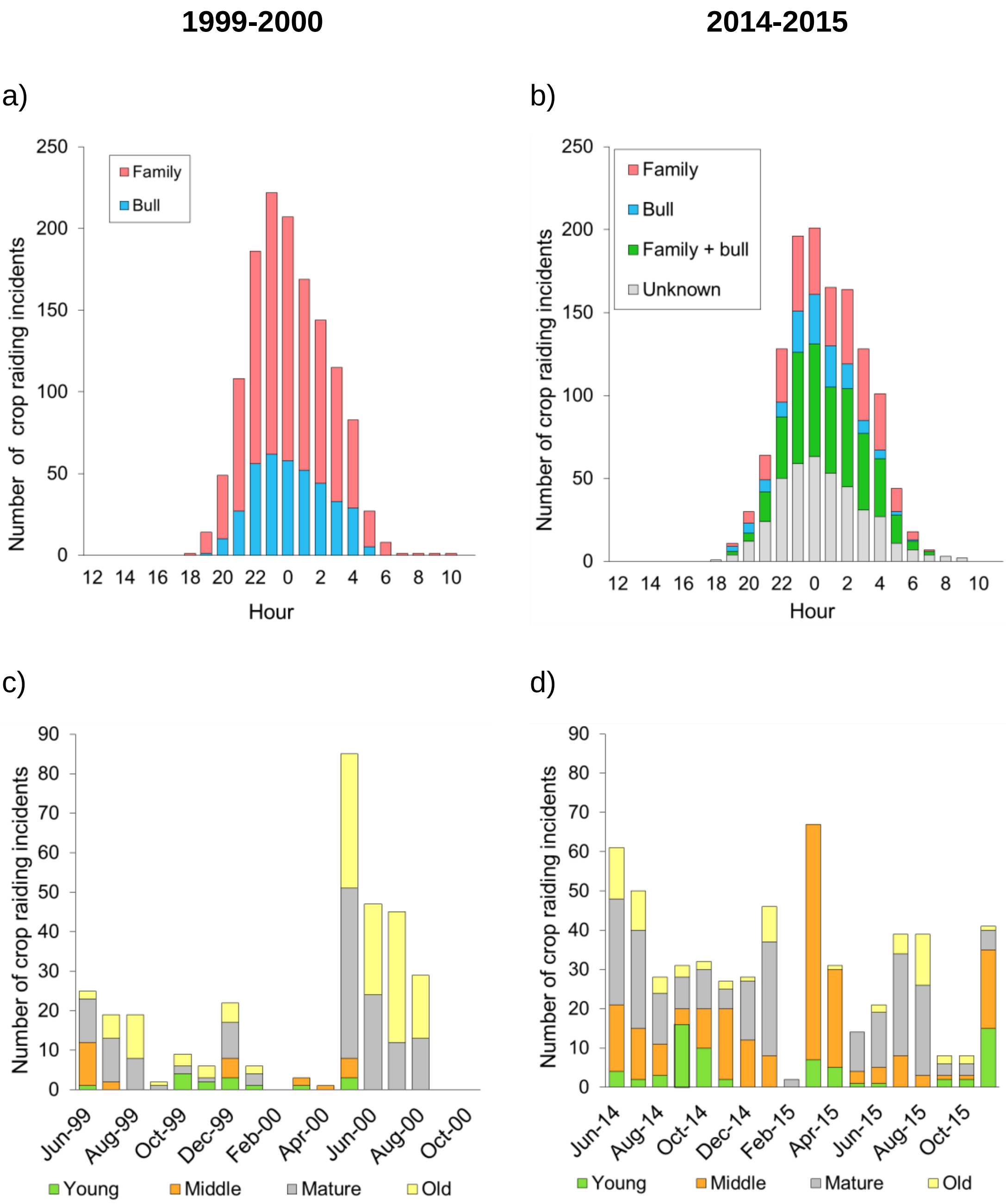

Figure 3.1. Elephant crop raiding (a) temporal patterns in 1999-2000, (b) temporal patterns in 2014-2015, (c) seasonal patterns in 1999-2000 and (d) seasonal patterns in 2014-2015. The temporal patterns show the number of groups recorded in hourly blocks and the seasonal patterns show the number of groups per month. The seasonal pattern graphs also show the crop age damaged per month.

3.4.3. Spatial patterns of crop raiding

Crop raiding incidents were spatially clustered in both 1999-2000 and 2014-2015 but their locations partly changed (Figure 3.2). In 1999-2000, more incidents occurred in the northwest of the Trans Mara, whereas crop raiding during 2014-2015 occurred along the edge of the protected areas and close to the forest. The cluster of crop raiding incidents in the east of the region was the same for both time periods.

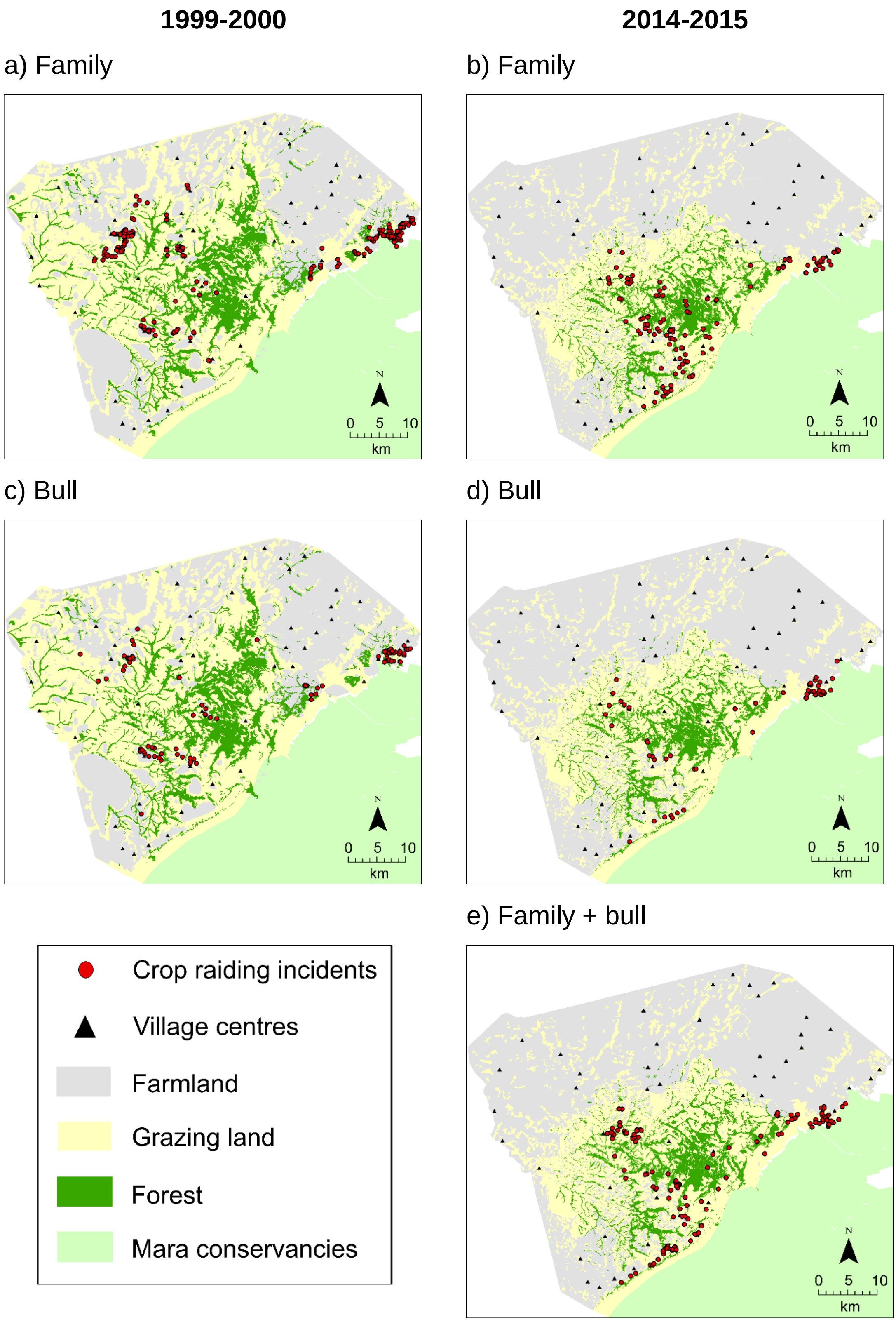

Figure 3.2. Spatial locations of crop raiding incidents of the different elephant group types and changes in landcover in the Trans Mara District in 1999- 2000 and 2014-2015.

3.4.3.1. Group Type Analysis

The spatial patterns of crop raiding varied by group type and there were differences between the distances that groups crop raided to the forest (n = 373, x^2 = 12.393, df = 2, p = 0.002, Figure 3.3), with family groups raiding closest to the forest, followed by family + bull groups and then bull groups. See Table S3.1 for Mann-Whitney U results highlighting the specific differences between each group . The opposite pattern was shown for distance to protected areas, with family groups raiding furthest from the protected areas (n = 373, x^2 = 12.315, df = 2, p = 0.002, Figure 3.3).

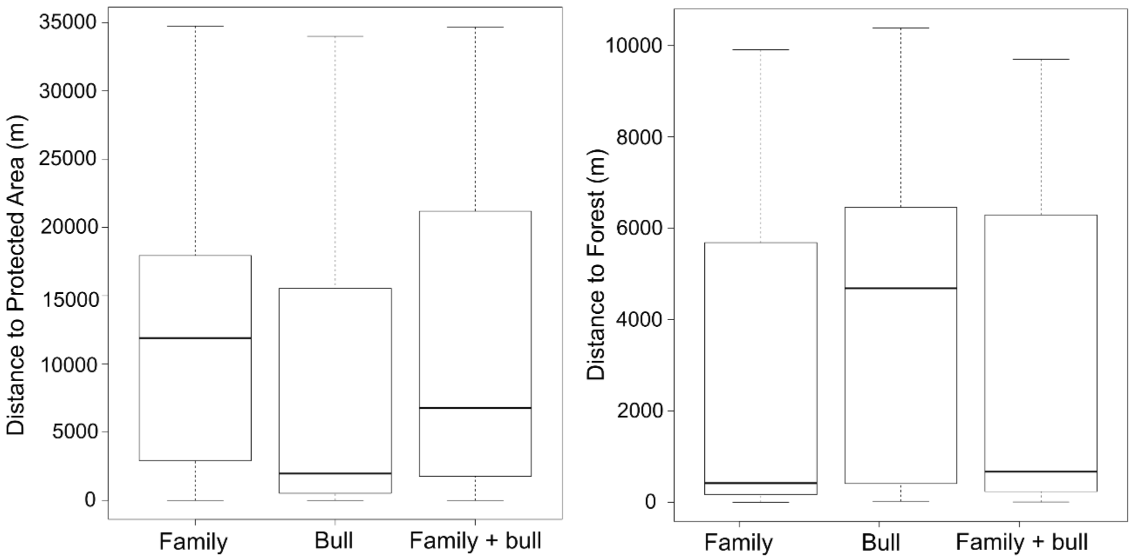

Figure 3.3. Distance to forest and distance to protected area for crop raiding incidents per elephant group type.

3.4.2.2. Logistic regression analysis

Of the eight potential predictor variables used in the logistic regression analysis, only area under cultivation predicted the spatial pattern of crop raiding for family groups (β = -6.68, 95% confidence intervals = -12.01, -1.36) and family + bull groups (β =-3.80, 95% confidence intervals = -6.68,-0.91, -1.36). In both cases the probability of crop raiding was higher in the 25 km^2 grid squares with low area under cultivation. For model selection results see (Table S3.1 and Table S3.2). None of the variables we tested predicted the probability of crop raiding by bull groups.

3.4.2.3. Generalised addictive model (GAM)

The GAM models we produced had low (<1) dispersion values, low AIC values and were not affected by spatial autocorrelation, although there was insufficient data to analyse the bull group spatial pattern. Area under cultivation was important for predicting crop raiding by both family and family + bull groups (Table 3.2). This relationship also showed a similar pattern for both group types: increases in farmland area led to increases in crop raiding until a threshold of 0.4 km^2, over which it declined (Figure 3.4c & d). Distance to forest edge was also important for both group types, with more crop raiding closer to the forest edge, until a threshold of 1.5 km after which it declined (Figure 3.4a & b). However, for family + bull groups, this decline was followed by another increase 4 km from the forest, followed by a final increase after 7 km, although confidence levels at these high distances were much lower (Figure 3.4b). Distance to villages was another important factor for predicting crop raiding by family + bull groups, with increases in distance from village centres leading to increases in crop raiding (Figure 3.4f). Finally, distance to protected area also predicted crop raiding by family groups but with a fluctuating pattern, as most crop raiding occurred closest to the protected area, although a few incidents occurred at 8 km and 15 km from the protected area (Figure 3.4f).

Table 3.2. GAM model outputs for the family group and the family + bull group analyses. GAM models provide a technique that fit a smooth relationship between the explanatory variables and the response variable. The higher the value of the estimated degrees of freedom (edf), the more the model had to smooth the data.

Elephant group type	Model	Significance	Distance to villages	Distance to protected area	Distance to forest edge	Area under cultivation
Family	GAM (poisson)	edf	< 0.001	6.795	2.235	1.944
		p value	p = 0.459	p < 0.001	p = 0.063	p = 0.035
		f statistic	0.000	26.453	4.893	5.636
Family + bull	GAM (negative binomial)	edf	1.023	< 0.001	4.394	1.691
		p value	0.029	0.358	p < 0.001	p = 0.043
		f statistic	0.457	0.000	4.075	0.546

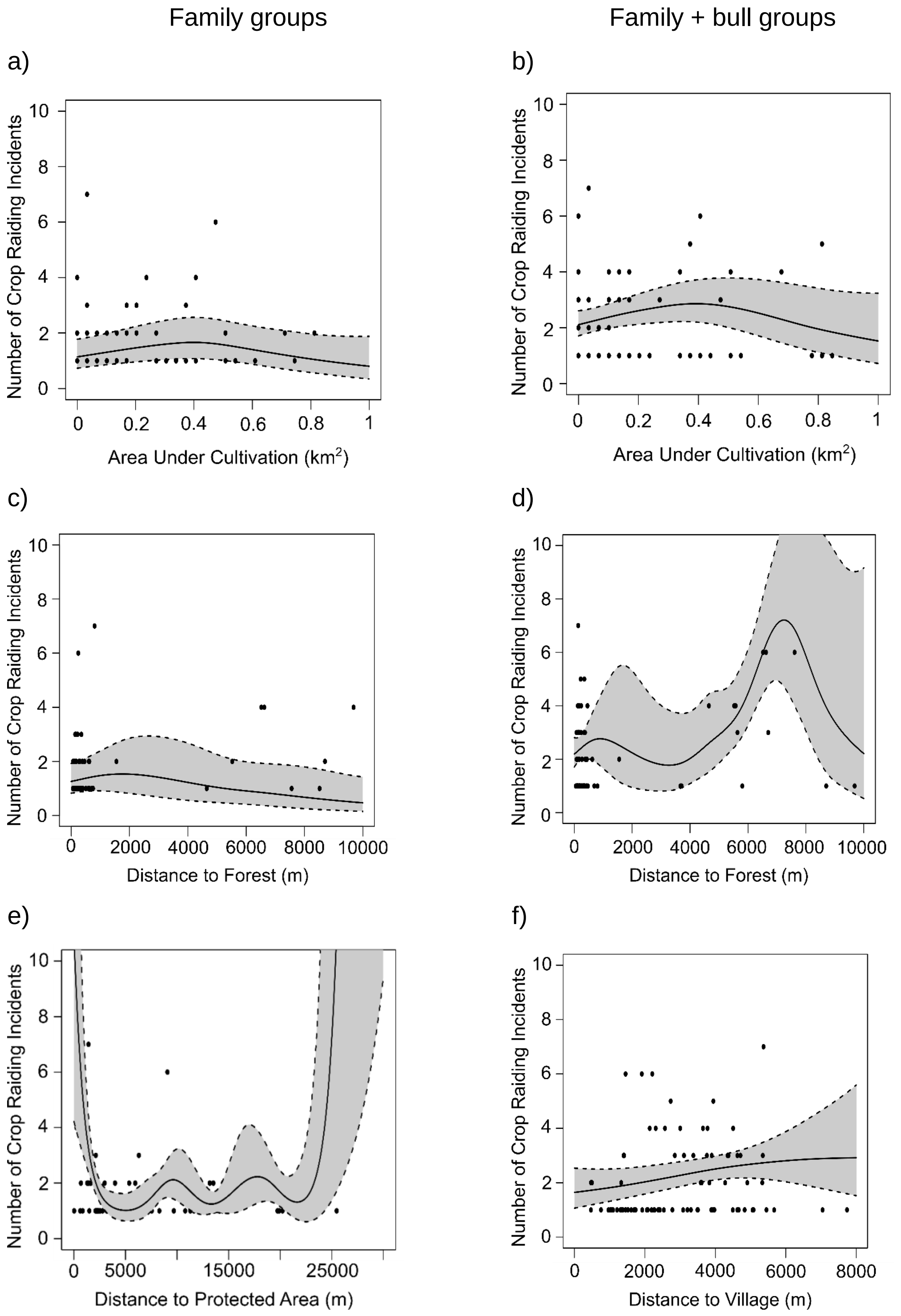

Figure 3.4. Predicted human-elephant conflict as a function of: (a & b) distance to forest, (c & d) area under cultivation, (e) distance to protected area and (f) distance to village. The dotted lines show the upper and lower confidence intervals and the points represent the 1 km^2 grid cells in which the data were analysed.

3.5. Discussion

3.5.1. Characteristics of elephant crop raiding

Elephant crop raiding has changed markedly in the Trans Mara since 1999-2000, with incidents per annum increasing by 49%. This is most likely due, in part, to agricultural expansion in the region, as farmland has increased by 42.5% (Chapter 2), and landcover change is a fundamental driver of conservation conflicts (Laurance et al., 2014). Maize was the main crop damaged, which has implications for farmers as they rely on maize as a cash crop and for subsistence. However, despite the increase in the number of crop raiding incidents, the actual amount of damage per farm in 2014-2015 was much lower than in 1999-2000. The mean damage per incident was 1.17 ha in 1999-2000, compared to 0.20 ha in 2014-2015, and so the total amount of damage per annum dropped from 308 ha to 78 ha. One reason for this could be that farmers have become more effective at guarding their fields. Previous studies have shown that the methods they use (guarding their fields throughout the night and using deterrents, such as fences, fire and fireworks) are the most effective (Sitati et al., 2005; Sitati and Walpole, 2006). Another reason for the decline in crop damage could be that there are less elephants crop raiding, either because risks are higher and/or, the elephant population in the Trans Mara has declined since 1999-2000. However, there are no current population estimates to clarify the latter hypothesis, which also highlights the need for a new population survey to be conducted.

This reduction in total crop loss is positive news but might not reduce human-elephant conflict. This is because the number of farmers affected has increased and previous studies have shown that people often perceive the amount of crop damage to be higher than the actual figure (Gillingham and Lee, 1999; Naughton-Treves, 1997). Such perceptions of higher threats could reduce farmers' tolerance towards elephants. In addition, if this reduction in the severity of each raid is due to more mitigation effort, then farmers could be experiencing higher direct and indirect costs from guarding and investment in deterrents such as fence material and fireworks (Thirgood et al., 2005; Barua et al., 2013). Thus, farmers living alongside elephants may still feel at a disadvantage, eliciting fear and anger and leading to retributive killing (Choudhury, 2004; Linkie et al., 2007). One limitation of this study is that we only analysed crop raiding trends. However, there are other impacts caused by elephants in the Trans Mara, such as fence and property damage, which may be higher than the actual costs of crop damage.

These other types of elephant damage could negatively impact tolerance and intensify conflict.

We also found that the types of elephant group involved in crop raiding has changed, as there was an additional group type of family + bulls which has previously only been observed in Asia (Wilson et al., 2013). Family groups have traditionally been the most responsible for crop raiding in the Trans Mara (Sitati et al., 2003) which is in contrast to studies from other parts of Africa where raiding is mostly by bull groups (Chiyo and Cochrane, 2005; Hoare, 1999b). Assuming that such behaviour is linked to optimal foraging theory and risk avoidance, there are three possibilities that could explain this: (1) family groups in the Trans Mara are less risk averse; (2) food quality is lower in the Trans Mara and so family groups have to adopt more risky behaviour to meet their nutritional requirements; (3) risks are lower, possibly because the long boundary between farmland and elephant refuges makes it easier to remain undetected. Thus, the formation of family + bull groups could be because these risks have further reduced, allowing bigger groups to successfully avoid detection. Alternatively, it could be because risks have increased and so family groups prefer to crop raid with bulls, as bulls may have more experience and knowledge of how to avoid detection during crop raiding. Also, it may be safer to crop raid in larger groups (Songhurst et al., 2015), which is reflected in the larger elephant group size that we recorded in 2014-2015 compared to 1999-2000. The fact that we found that incidents were shorter and caused less damage supports the second hypothesis, but further research is needed to understand this possible change and its implications for mitigation management.

3.5.2. Seasonal and temporal patterns of crop raiding

Temporal patterns have not changed significantly since 1999-2000, as elephants in 2014-2015 also crop raided at night, which is a commonly observed risk avoidance strategy (Graham et al., 2010, 2009). Seasonal trends in the Trans Mara, however, have changed. Many studies across sites in Asia and Africa show that crop raiding is strongly seasonal and correlated with rainfall patterns and cultivation cycles (Chiyo et al., 2005; Goswami et al., 2015; Wilson et al., 2013), and previous results in the Trans Mara were no different (Sitati, 2003). However, our results found that crop raiding occurred throughout the year and occurred at all stages of crop growth, which was not observed in 1999-2000, and contrasts with previous studies showing elephants prefer mature crops (Chen et al., 2016;

Chiyo et al., 2005; Gubbi, 2012; Webber et al., 2011). Our results suggest that crop raiding is being driven by trade-offs between risk and food quality, with elephants possibly raiding the less mature crops because they are less likely to be guarded by farmers. Similarly, elephants may be crop raiding throughout the whole year because the availability and quality of grass in parts of the Masai Mara have declined in recent years due to the increasing number of livestock, human settlement and farmland (Ogutu et al., 2011, 2016). Unfortunately, this new lack of climate-related predictability has serious implications for the livelihoods and well-being of farmers, as it forces them to spend more time guarding their crops.

3.5.3. Spatial patterns of crop raiding

Crop raiding incidents in the Trans Mara were highly clustered, which has been observed elsewhere in Africa (Graham et al., 2010; Songhurst and Coulson, 2014). However, the locations of crop raiding have partly changed, as more incidents occurred in the northwest in 1999-2000, compared to more incidents along the edge of the protected areas and close to large forest patches in 2014-2015. Landcover data suggest this shift is due to the spread of agricultural land since 1999-2000 (Chapter 2), as the northwest of the region is now largely transformed, with few forest patches in which elephants can seek refuge before or after crop raiding (Graham et al., 2009; Wilson et al., 2013). We also found there were differences between elephant group types, as family groups crop raided closest to the forest, followed by family + bulls and then bull groups. In this case, bull groups could be greater risk takers than family groups as they travel further from the forest to crop raid. The opposite pattern was shown for distance to protected areas, with bull groups crop raiding closest to the protected area, although in general incidents were much further from the protected area than from forest patches suggesting that the Masai Mara National Reserve was in general not acting as a staging post for crop raiding.

To look at spatial predictors of crop raiding, we first investigated changes since 1999-2000 by repeating the analysis by Sitati et al., (2003), which was based on 25 km^2 sampling units to avoid spatial autocorrelation. Like Sitati et al., (2003), we found that area under cultivation was a predictor of crop raiding but, in our case, the relationship was the inverse, with more crop raiding in units with the least farmland cover. A possible explanation is that during the Sitati et al., (2003) study many of the 25 km^2 units were completely forested, so it was easier for elephants to reach farms undetected, and they preferred units with the most farmland. In contrast, in 2014-2015, deforestation meant the sampling units with the most farmland tended to be much further from the forest patches that act as elephant refuges. Instead, the sampling units that were raided tended to include forest patches and so had lower farmland cover (Sitati et al., 2003; Graham et al., 2010; Wilson et al., 2013; Goswami et al., 2015). Thus, in effect both the 1999-2000 and 2014-2105 models predicted that elephant crop raiding depended on the presence of elephants and crops, although the factors that correlated with this overlap varied with time. This intuitive result provides little information to help understand elephant crop raiding behaviour, which is why we also analysed the 2014-2015 data using finer-scale Generalised Additive Models (GAMs) that accounted for spatial autocorrelation.

There was insufficient data to analyse the spatial pattern of bull group crop raiding using GAMs, presumably because many bulls had joined family + bull groups. For the other groups, our results suggest that crop raiding was driven by the availability of crops and the location of farmland in relation to distance to forest, protected area and village centres. For both family and family + bull groups, crop raiding declined when less than 40% of the 1 km^2 sample unit consisted of farmland. At this point, the risk of human retaliation may have been too high because refuges were too far away (Graham et al., 2009), providing more evidence that deforestation has driven the observed change in crop raiding spatial patterns. Our analysis also showed that farms 1 km from the forest boundary, 5 km from the protected area boundary and >2 km from village centres were most at risk of crop raiding. These findings are consistent with other studies from Africa and Asia showing that more crop raiding occurs within 6 km of the forest or protected area (Graham et al., 2010; Gubbi, 2012; Guerbois et al., 2012), and in areas with lower densities of people (Chen et al., 2016; Graham et al., 2010). Therefore, targeting mitigation in these ‘hotspots’ could be effective. A few crop raiding incidents occurred more than 10 km from the forest and protected area edge, supporting anecdotal evidence that two different elephant populations involved, one resident in the National Reserve and one in the Trans Mara (Sitati, 2003). It might also be because some elephant groups are willing to risk travelling greater distances from the protected area and forest. This ties in with a study from Laikipia, Kenya, where the furthest distance recorded of crop raiding from elephant refuges to farmland was 10 km (Graham et al., 2010).

3.5.4. The future co-existence of humans and elephants

This study shows the value of using a standardised conflict monitoring system to document human-elephant conflict trends over time. A fundamental step in finding solutions to human-wildlife conflict is to gain an understanding of seasonal, temporal and spatial trends, and how these have changed. This study found that crop raiding trends have changed significantly over time. Thus, this understanding will enable us to apply appropriate interventions and inform relevant policy. For example, the findings from this study can directly inform local management options as to where to direct mitigation as we have identified specific crop raiding hotspots and elephant crop raiding behaviour. In addition, this study shows the value of using fine-scale data to model the spatial distribution of crop raiding, as coarse spatial scale models were not enough to explain the complexity of spatial drivers of crop raiding. The methods used in this study can also be easily applied to other circumstances in order to identify human-wildlife conflict hotspots and fine-scale drivers of conflict. Analysing these data from the Trans Mara was particularly important, as they show that seasonal, temporal and spatial patterns of crop raiding are changing, probably because of human population growth, agricultural expansion and climate change. These analyses also suggest that current mitigation techniques are working, but better evaluation is needed to ensure that local communities are equipped with appropriate methods and means for mitigating crop depredation. Such mitigation management must engage and involve local communities to help build tolerance towards elephants, especially in the light of changing patterns of crop raiding. Without such engagement, the future of elephants in the Trans Mara is uncertain, as habitat loss and retributive killing of elephants are likely to become a more serious problem than poaching.

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3.7 Supporting information

Table S3.1. Results from Mann-Whitney U tests to look at differences in elephant group type of spatial patterns of crop raiding.

	Elephant Group Type	W	Significance
Distance to Forest (m)	Family + bull vs Bull	6401.5	p = 0.055
	Family vs Bull	5988.5	p < 0.001
	Family vs Family + bull	10088	p = 0.048
Distance to Protected Area (m)	Family + bull vs Bull	4280	p < 0.001
	Family vs Bull	3296.5	p <0.001
	Family vs Family + bull	12455	p = 0.2711

Table S3.2. Model selection results for factors predicting crop raiding by family groups in the Trans Mara District. AICc= Akaike's information criterion adjusted for small sample size; ΔAICc difference in AICc between each model and the best one; and logLik= log-Likelihood. 1= area under cultivation, 2= distance to villages, 3= elevation, 4= distance to forest.

Elephant Group	Model	logLik	AICc	ΔAICc	AICc Weight
	123	-16.78	42.55	0.00	0.39
	1234	-15.99	43.48	0.93	0.25
Family	13	-18.84	44.25	1.70	0.17
	12	-19.21	45.00	2.46	0.11
	134	-18.38	45.74	3.19	0.08

Table S3.3. Model selection results for factors predicting crop raiding by family + bull groups in the Trans Mara District. AICc= Akaike's information criterion adjusted for small sample size; ΔAICc difference in AICc between each model and the best one; and logLik= log-Likelihood. 1= area under cultivation, 2= distance to forest, 3= elevation, 4= distance to village, 5= slope.

Elephant Group	Model	logLik	AICc	ΔAICc	AICc Weight
	1345	-20.16	51.81	0.00	0.18
	134	-21.55	52.08	0.27	0.16
	14	-22.88	52.34	0.53	0.14
	135	-22.01	53.00	1.18	0.10
	13	-23.38	53.33	1.52	0.09
Family +	12345	-19.65	53.44	1.63	0.08
bull	145	-22.26	53.50	1.68	0.08
	1234	-21.49	54.48	2.66	0.05
	124	-22.86	54.69	2.88	0.04
	1235	-21.66	54.81	3.00	0.04
	123	-23.31	55.59	3.78	0.03

4. Elephant pathway movement in a human-dominated landscape

Planned for submission to Animal Conservation:

Tiller, L.N., Humle, T., Amin, R., Humphries, A., Seaman, D., Sitati, N., Smith, R.J.

Elephant pathway movement in a human-dominated landscape

4.1. Abstract

In human-dominated landscapes, pathways can play an important role in connecting elephants to resources. Pathways can act as least-effort routes to food resources, suggesting that elephants use them to optimise foraging strategies to gain the most energy for the lowest cost. They can also be a significant spatial driver of human-elephant conflict by enabling access into agricultural areas. Therefore, monitoring elephant movement and understanding pathway use may offer key insights into habitat requirements of elephants in fragmented landscapes. This study investigated the fine-scale movement of elephants migrating between the Masai Mara National Reserve and the Trans Mara, in southwest Kenya. We mapped elephant pathways and used camera trapping and elephant sign surveys over a one year period to understand seasonal and temporal patterns of pathway use. We used a Generalised Linear Model to determine factors driving high frequency of pathway use by elephants. We found strong seasonal trends in elephant pathway use, with peaks coinciding with the dry season. However, we found no correlation between rainfall and pathway use. Temporal patterns of pathway use indicate that elephants use risk avoidance strategies by moving between the Masai Mara National Reserve and Trans Mara in times of low human disturbance. Spatial analysis revealed that the most frequently used pathways were closer to farms, saltlicks and forest in the Trans Mara and those that had a higher percentage of forest cover. Our models also showed a positive relationship between pathway use and number of human-elephant conflict incidents. This study provides an in-depth investigation of temporal and spatial patterns of pathway use and their role in human-elephant conflict. As habitat loss continues, pathways may become more important for linking resources. However, they are also likely to facilitate an increase in human-elephant conflict. Thus, these results can help inform land-use planning by determing important wildlife dispersal areas and by facilitating the designation of targeted human-elephant mitigation. Land-use planning is a key strategy to reduce conflict and protect crucial resources for elephants and wider biodiversity.

4.2. Introduction

Wide-ranging mammal species often develop pathways by repeatedly following the same routes when travelling between favoured habitat patches. One well known example is the African elephant (*Loxodonta africana*), which uses these pathways to move between water, saltlicks and special fruiting trees (Blake and Inkamba-nkulu, 2004; Shannon et al., 2009; Vanleeuwe and Gautier-Hion, 1998; Von Gerhardt et al., 2014). Thus, pathways can act as least-effort routes to food resources (Blake and Inkamba-Nkulu, 2004), suggesting they use them to optimise their foraging strategy and gain the most energy for the lowest cost (Stephens and Krebs, 1986). Moreover, these pathways play a particularly important role in human-dominated landscapes, where important habitat patches are increasingly isolated by the spread of agriculture, especially because elephants have large ranges that commonly go beyond the existing network of protected areas (Blanc et al., 2007). Thus, maintaining these pathways is vital for the long-term viability of elephant populations.

In human-dominated landscapes, these pathways can also play a large role in determining the likelihood of elephants encountering people. This is especially the case in areas where cropland borders protected areas and other elephant refuges, as the pathways can determine whether and where elephants enter fields and consume and trample crops (Naughton-Treves, 1997; Thirgood et al., 2005). This human-elephant conflict has negative impacts on both species as it can severely affect people's livelihoods and lead to retaliatory killing of elephants (Choudhury, 2004; Linkie et al., 2007; Mariki et al., 2015). Therefore, there is a need to better understand the role of these pathways in agricultural landscapes and how they influence patterns of human elephant conflict, which is, in turn, important for land-use planning and human-elephant conflict mitigation (Adams et al., 2017; Smit et al., 2017; Songhurst et al., 2015; Von Gerhardt et al., 2014). To address these issues, in this study we investigated temporal and seasonal patterns of pathway use in a crop raiding hotspot next to the Masai Mara National Reserve in South-West Kenya.

The Masai Mara has high levels of human-wildlife conflict because of rapid land-use change and the spread of agriculture (Homewood et al., 2001; Maitima et al., 2009; Nyariki et al., 2009; Ogutu et al., 2011). To the west of the Masai Mara National Reserve are a series of natural pathways which connect elephants to a wildlife dispersal area called the Trans Mara. Elephants may be migrating into this area as their movement is driven by the need to access resources such as food, water and minerals (Chamaille-Jammes et al., 2007; Harris et al., 2008; Murwira and Skidmore, 2005; Wittemyer et al., 2008), which can be affected by seasonally driven rainfall (Birkett et al., 2012; Bohrer et al., 2014a; Cushman et al., 2005; Loarie et al., 2009b; Young et al., 2009), social factors (Wittemyer et al., 2007) and human presence (Loarie et al., 2009a). In areas of high human densities, elephants may alter their behaviour and adopt risk avoidance strategies such as travelling at night and moving faster in these areas (Cushman et al., 2005; Douglas-Hamilton et al., 2005; Graham et al., 2009).

Monitoring elephant movement and understanding pathway use may offer key insights into habitat requirements of elephants in fragmented landscapes. Thus, in this study, we used a combination of methods, such as elephant sign surveys and camera trapping to understand the fine scale movement of elephants migrating into the Trans Mara. Specifically, we aimed to: i) identify elephant pathways which connect the Masai Mara and Trans Mara; ii) understand the temporal patterns of elephants travelling up and down pathways; iii) understand seasonal patterns of pathway use and whether these patterns are correlated with rainfall; iv) determine elephant group types using the pathways; v) understand the spatial factors driving pathway use; vi) determine if high pathway use predicts high human-elephant conflict.

4.3. Methods

4.3.1. Study site

The Trans Mara District has an area of 2,900 km^2 and is situated in South-West Kenya, forming part of Narok County. Agriculture is the dominant landcover type (Chapter 2), interspersed by a mosaic of afro-montane, semi deciduous and dry-deciduous forests and Acacia savanna woodlands. The Trans Mara lies next to the world famous Masai Mara National Reserve, which is part of the Serengeti-Mara ecosystem that sees the annual migration of >1.2 million wildebeest (Sinclair and Norton-Griffiths, 1979). The Masai Mara ecosystem is approximately 6,000 km^2, of which c.25% represents the Masai Mara National Reserve and 75% is unprotected privately and communally owned land (Walpole et al., 2003). A steep escarpment divides the Trans Mara and the Masai Mara National Reserve, but there are a series of natural pathways along the escarpment that allow wildlife to move between them (Figure 4.1). Wildlife migrate into the Trans Mara because it contains the Nyakweri Forest, an important area for food, water and saltlicks. However, the forest is declining due to land being cleared for charcoal and agriculture (Liyama et al., 2017).

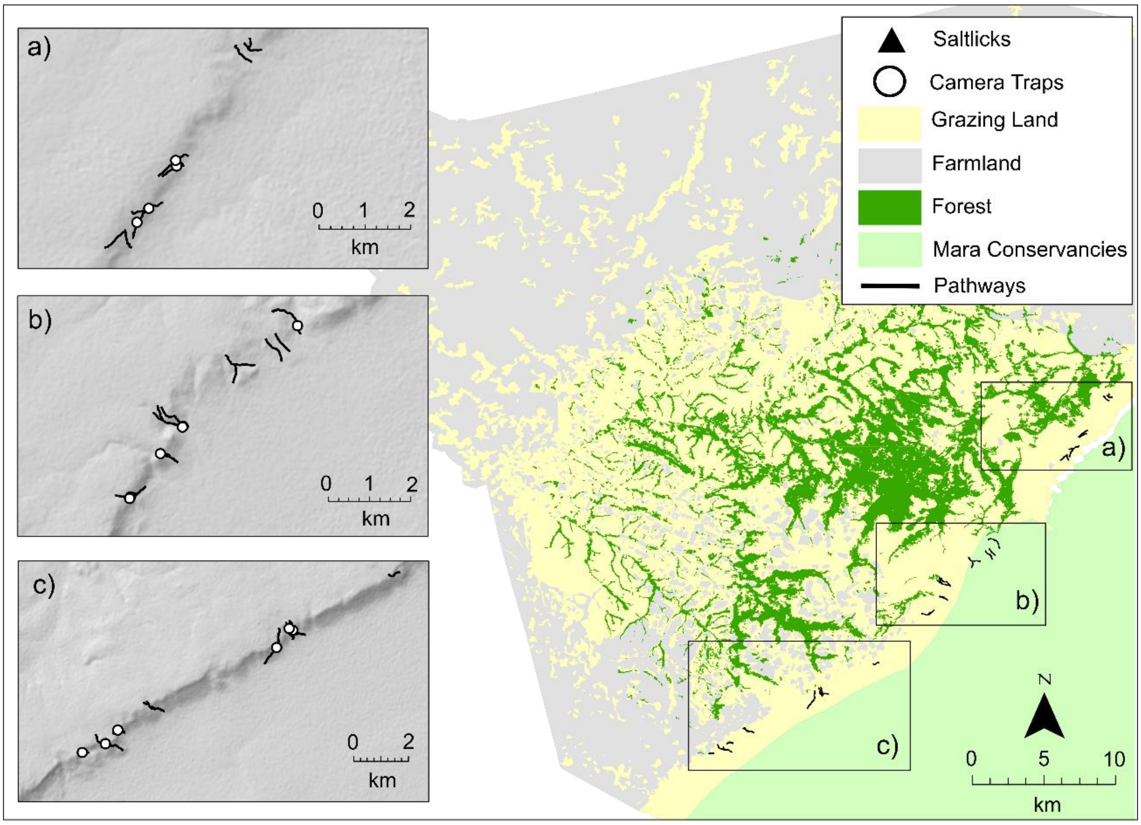
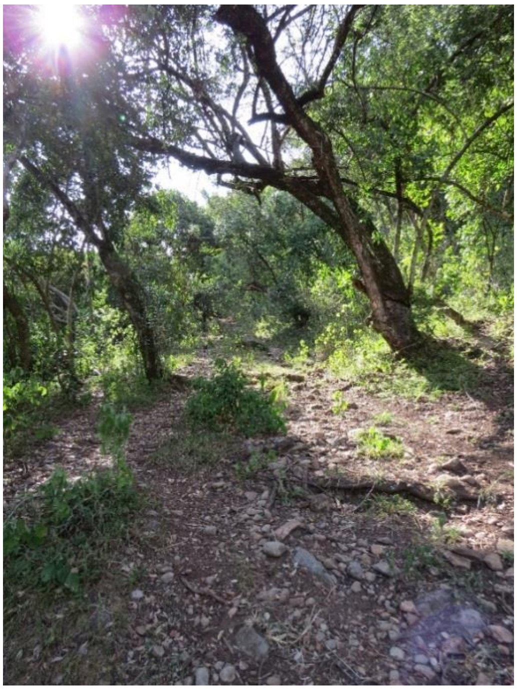


Figure 4.1. Location of the 22 elephant pathways along the escarpment connecting the Masai Mara to the Trans Mara District. Pathways are shown at a finer scale on inserts a), b) and c) which also show the location of the camera traps on 14 of the pathways. Each circle represents 2 camera traps, 1 camera trap facing up the escarpment and 1 camera trap facing down the escarpment to capture the direction of movement of the elephants.

4.3.2. Data collection

We identified active pathways along the escarpment with the assistance of local rangers and farmers (Figure 4.2). We assumed pathways were in use if the path was devoid of vegetation (Blake and Inkamba-Nkulu, 2004), were marked with elephant dung or footprints and showed signs of elephant browsing on the bordering vegetation (Von Gerhardt et al., 2014). Pathways that did not show any of these signs were not used in this study. We then mapped each pathway using a Garmin Etrek30 Global Positioning System (GPS). The GPS track was taken from the bottom of the escarpment on the border of the Masai Mara to the top of the escarpment. The end of the pathway was determined by the point at which the pathway widened and became open habitat. Habitat type was also recorded on each pathway using a classification system from Kindt et al., (2011). As each pathway went through a number of different habitats, we used a GPS to record the co-ordinate at which there was a change in habitat type. To determine annual pathway use, we conducted bi-weekly elephant dung surveys on each pathway from September 2014 to August 2015. During these surveys, we counted dung piles along two predefined transects, one going down the pathway and the other going up the pathway. Dung was removed after each count to avoid recounting.

a)



b)

c)

d)

Figure 4.2. Four (a, b, c, d) of the 22 elephant (*Loxodonta africana*) pathways along the escarpment connecting the Masai Mara to the Trans Mara District. We placed 32 camera traps on 14 of the pathways. At least one camera on each pathway pointed up the escarpment (c) and at least one camera pointed down the escarpment (d) to determine the direction of movement of elephant groups into and out of the Masai Mara.

To determine temporal patterns of pathway use and elephant group type using the pathways, we placed 32 heat and motion camera traps (Bushnell Trophy Cam HD 2013) on 14 pathways during two sampling periods: September 2014 – October 2014 and February 2015 – August 2015 (Figure 4.2). We were unable to place cameras on all the pathways due to limited camera availability and the unsuitability of some pathways for camera trap placement; i.e there were some pathways with limited trees/bushes to attach the cameras to and some pathways were too wide. To ensure elephants were captured on the 14 chosen pathways, we placed cameras on the narrowest part of the pathway or sections where we knew elephants would cross (e.g. by small water bodies). To obtain suitable photographs of elephants for group type identification, the camera traps were mounted on trees or erected posts at varying heights between 1 – 3 metres depending on the pathway slope. The height of the camera > 1 metre was to ensure the best capture of the head, pinnae, and tusks of elephants (Smit et al., 2017). Each pathway had at least one camera facing up the escarpment to capture elephants travelling down into the Masai Mara, and one camera facing down the escarpment to capture elephants travelling up into the Trans Mara. If pathways split, two cameras were placed on each sub-pathway to ensure elephants were captured. Cameras were set to take three colour photos per trigger with a five second interval between pictures within a trigger event. We downloaded the images from memory cards and changed the camera batteries every three weeks.

We then created a database of the camera trap images and recorded the site (pathway name), the position of the camera trap (up or down), the type of photo (e.g. wildlife, people or false trigger), the wildlife species in the photo and the data and time the image was taken. Specifically, for the elephant images, we recorded additional information including: (1) the direction in which the elephant was travelling; (2) the number of elephants in the image and; (3) the group type. Group type was determined by sexing elephants based on their genitalia (if visible), body size, shape of their head and length and configuration of tusk size (Moss, 1996). During the period in which an elephant group crossed a camera, depending on the size of the group, many images were taken. Thus, to avoid double counting elephant groups, we developed a Python script to select images from our database that were taken more than 15 minutes apart. This time marker was determined after reviewing all the images and calculating the average time between each independent group. Group type was then determined by reviewing the series of images within the 15 minute time frame.

To understand the relationship between pathway use and human-elephant conflict, we monitored HEC occurrence from September 2014 to September 2015. Please see Chapter 3 for the detailed methodology on HEC monitoring.

4.3.3. Data analysis

4.3.3.1. Temporal and seasonal patterns of pathway usage

We carried out all the data analysis using the statistical software R (R Core Team, 2016). We assessed the seasonal patterns of pathway use by totalling the number of dung piles counted across all pathways for each month and averaging rainfall readings from weather stations across the Trans Mara and Masai Mara National Reserve. We then carried out a Spearman's Rank Correlation test with dung piles and rainfall. Due to the potentially delayed effects of rainfall on the ripening of crops and greening of vegetation, we also ran correlations between dung counts and rainfall from the previous month.

To look at the temporal patterns of elephant groups travelling up the pathways into the Trans Mara and down the pathways into the Masai Mara, we sorted the camera trap data into time and direction. Images were grouped into time stamps of 24 one-hour intervals so that we had a frequency distribution of each elephants travelling up and elephants travelling down the pathways.

4.3.3.2. Elephant group usage on pathways

We produced descriptive statistics to summarise the number of elephant detections on each pathway.

4.3.3.3. Factors determining high pathway use

To investigate the factors driving high elephant pathway use, we used four predictor variables: distance of pathway to nearest farm, forest and saltlicks and the percentage of forest cover on pathways. To measure the percentage of forest on each pathway, we calculated the length of the pathway and then used the GPS co-ordinates from the habitat survey to work out the proportion of the pathway that we had classified as forest. We mapped farmland and forest cover and locations of saltlicks by on-screen digitising of 5 m CNES/Astrium satellite imagery from 2015 using QGIS (QGIS Development Team, 2015). We then calculated the distance from the end of each pathway to the nearest farm, forest and saltlick and forest and farm using the Generate Near Table function in ArcMap10.4, where we defined the end of the pathway by the point at which the pathway widened and became open habitat.

We then carried out exploratory analysis including graphical inspection, correlation matrices and bivariate tests. Variance inflation factors (VIFs) were used to test for collinearity amongst the predictor variables and we found no evidence of collinearity between our predictor variables ($r < 0.7$; $VIF < 5$; Dormann et al., 2013). Exploratory modelling identified persistent over dispersion between the response and predictor variables. Thus, to overcome this problem, we fitted a GLM with a negative binomial error structure and all predictor variables were scaled to have a mean of zero and a standard deviation of 0.5 (Gelman, 2008). For model selection, we used a model averaging approach (Burnham and Anderson, 2002) using the MuMin package (Barton, 2016), which examines average parameter estimates, standard errors and confidence intervals of the predictor variables. The model set contained all possible combinations of main effects and combinations of explanatory variables. Prior to model averaging, models were restricted to $AICc<2$ (Akaike Information Criterion) to exclude potentially implausible models with low AIC weights (Burnham and Anderson, 2002). The relative importance (RI) of explanatory variables was then calculated by summing the Akaike weights across all models in which the variable was present, resulting in an estimate of probability that the variable of interest features in the best model. Finally, we applied a goodness of fit test to the model set to determine if the models fitted the data well.

4.3.3.4. Human-elephant conflict and pathway use

To determine whether high pathway activity predicted high human-elephant conflict, we used the number of HEC incidents per month as our response variable and the total number of dung piles across all pathways as our predictor variable. We then fitted a Linear Model (LM).

4.4. Results

We identified 22 active elephant pathways along the escarpment. The mean (±1SE) pathway length of was 878.5 m ± 62.59, the mean minimum slope was 4.12º ± 0.52 and mean maximum slope was 27.70º ± 1.80. Pathway forest cover ranged between 0 and 74.06% (mean 20.12% ± 5.57).

4.1.1. Temporal and seasonal patterns of pathway usage

Signs of elephant activity were highest in September 2014 and August 2015, with over 1000 dung piles recorded on the pathways (Figure 4.3). Signs were lowest in November 2014 and May 2015 and non-existent in June 2015 when no dung piles were recorded, suggesting that elephants did not use the pathways during this month. Rainfall fluctuated from 14.1 mm in January 2015 to 191.37 mm in April 2015 and there was no relationship between rainfall and pathway use (Spearman's Rank correlation: $r_s = -0.006$, $p = 0.991$).

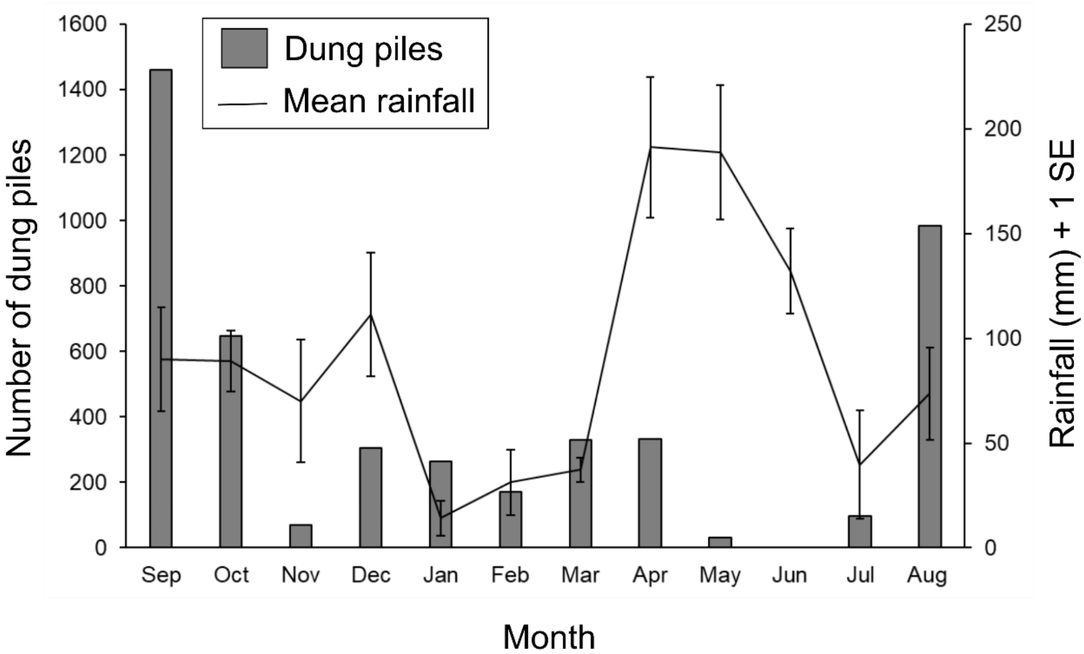


Figure 4.3. Seasonal patterns of elephant pathway use as measured by the total amount of dung piles recorded each month from September 2014 to August 2015.

There was a distinct pattern in the times when elephants travelled up and down the pathways (Figure 4.4). Elephants were photographed travelling up the pathways into the Trans Mara predominantly during 17:00 – 24:00 (median = 19:00) and back down the pathways into the Masai Mara National Reserve during 04:00 – 09:00 (median = 06:00).

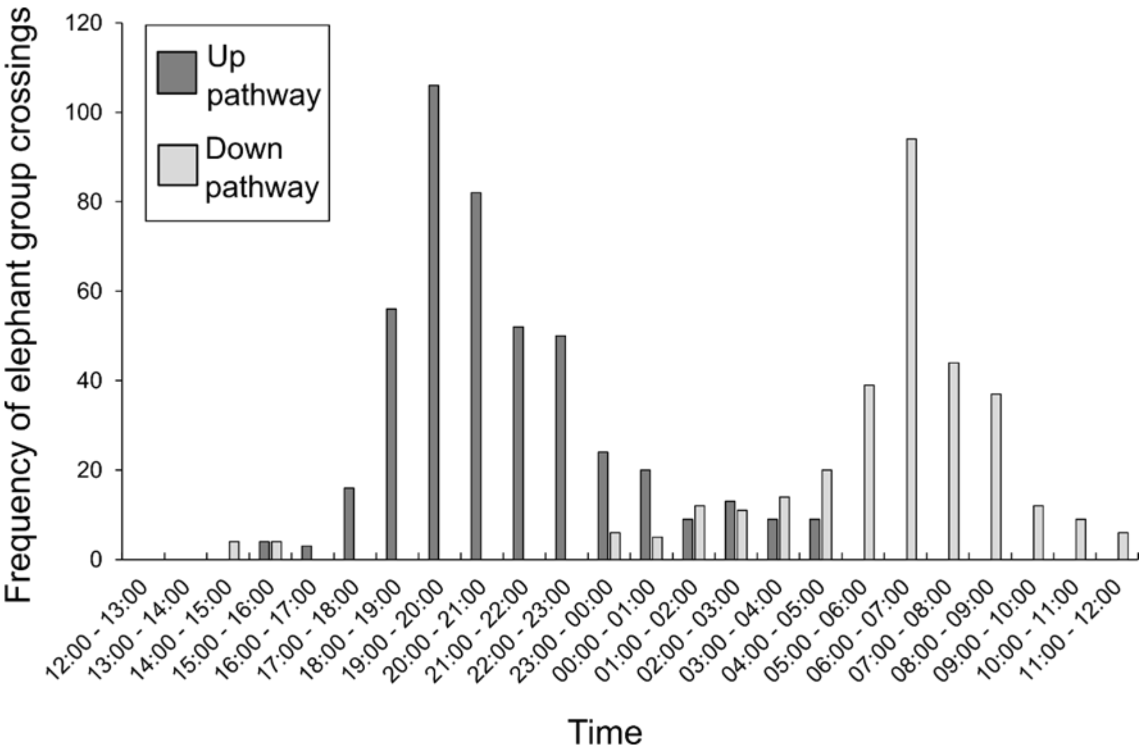


Figure 4.4. Temporal patterns of elephants travelling up the pathways into the Trans Mara District and down the pathways into the Masai Mara National Reserve, as determined through camera traps.

4.4.2. Elephant group types using pathways

During the nine months of camera trapping, we recorded three elephant group types (bull groups, female-led family groups and family + bull groups) using the pathways 825 times (341 moving down and 484 moving up). There was a mean of 72 ± 26.49 groups per pathway and the mean size of an elephant group was 4.25 ± 0.13. Pathways Enkiu and Mara West were used more frequently than other pathways (Figure 4.5).

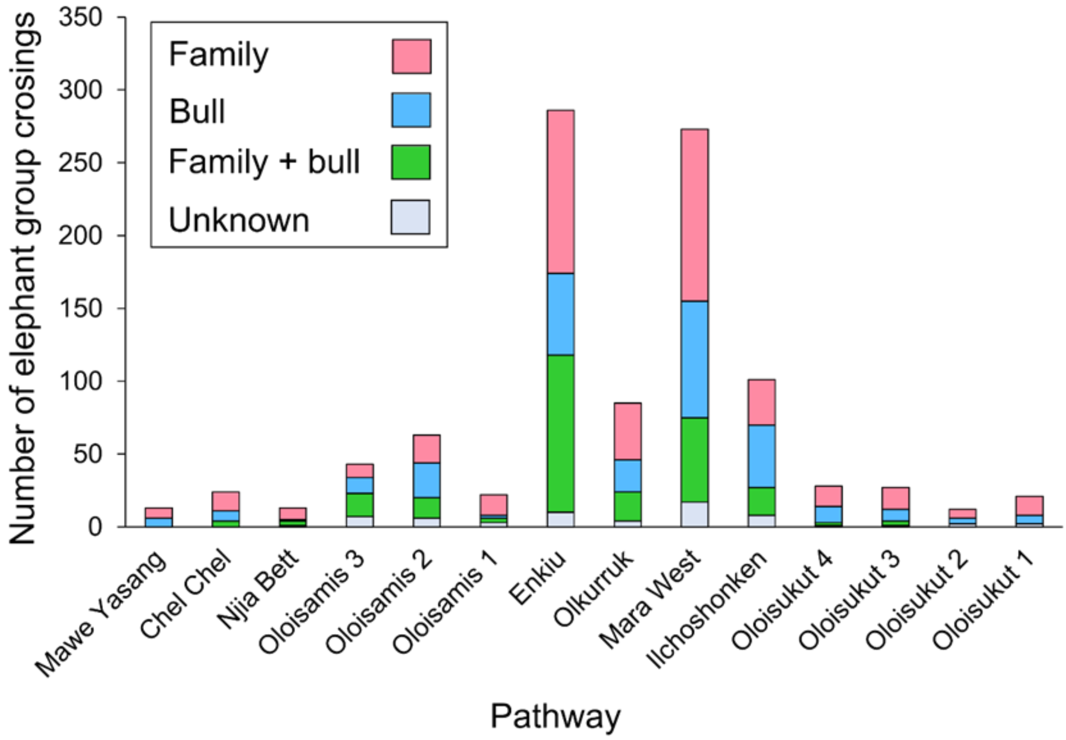


Figure 4.5. The number of elephant captures on camera trap pathways of each elephant group type.

4.4.3. Factors determining pathway use

The most frequently used pathways were closer to farms, saltlicks and forest in the Trans Mara and those that had a higher percentage of forest cover. Distance to farms was the strongest predictor as it appeared in all models prior to averaging (RI 1.0). Distance to saltlick and percentage of forest cover on pathways appeared in 70% (RI 0.70) of models, while distance to forest appeared in 30% (RI 0.3) of models prior to averaging (Table 4.1). For model selection results see (Table S4.1).

Table 4.1. Results of model averaged GLM fitted with negative binomial errors to investigate predictors of high pathway use by elephants from September 2014 – September 2015. Significant predictor variables from our averaged models where confidence intervals do not cross zero. Averaged parameter estimates (β), unconditional standards errors (SE) and relative variable importance factors (RI) are also reported. The Akaike Information Criterion correction (AICc) was used to rank models and any model that ranked ΔAICc <2 was averaged to obtain final estimates presented. Relative importance (RI) refers to the summed Akaike weights across all models in which the variables were present.

Predictor	***β***	***SE***	***LCI***	***UCI***	***RI***
(Intercept)	5.610	0.116	5.354	5.865	
Distance to farm	-0.418	0.135	-0.720	-0.115	1.0
Distance to saltlick	-0.677	0.145	-0.999	-0.354	0.70
Distance to forest	-0.438	0.138	-0.741	-0.135	0.30
Percent of forest cover on pathways	0.540	0.139	0.231	0.849	0.70

4.4.4. Human-elephant conflict and pathway use

The number of HEC incidents was significantly and positively associated with the number of dung piles on pathways ($\beta = 0.656$, $SE = 0.238$, $P < 0.05$) (Figure 4.6).

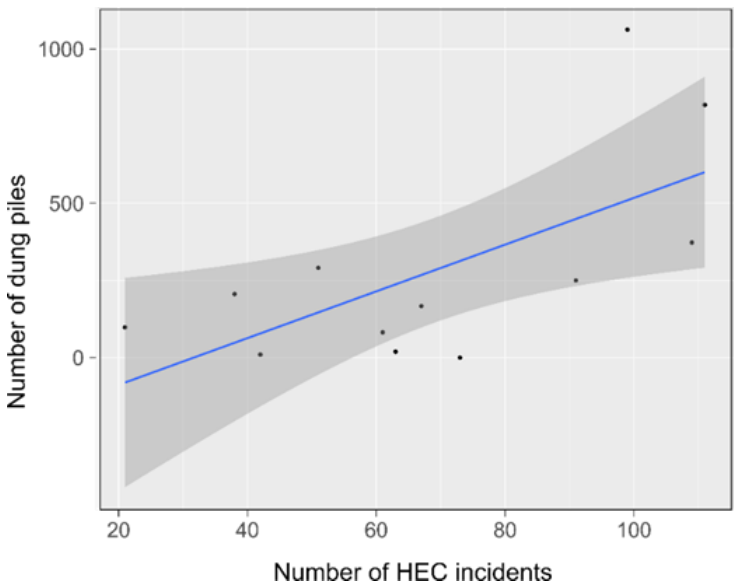


Figure 4.6. The positive relationship between the number of human-elephant conflict incidents and the number of dung piles recorded across the pathways each month. The blue line represents the regression line, the grey shading represents the 95% confidence intervals and the points represent the month in which the data were analysed.

4.5. Discussion

By mapping elephant pathways, conducting elephant sign surveys and carrying out camera trapping, we were able to understand fine-scale movements of an elephant population based in the Masai Mara National Reserve. Our study provides an in-depth investigation of the use of elephant pathways and their role in human-elephant conflict.

4.5.1. Temporal and seasonal patterns of pathway usage

There were strong seasonal trends in elephant pathway use, with two peaks in elephant activity in September 2014 and August 2015, with over 1000 dung piles recorded in each of these months. These peaks coincided with the dry season which is between June and October in the Masai Mara (Sitati, 2003). During the dry season, elephants are constrained by limited forage and water (Birkett et al., 2012; Bohrer et al., 2014) and may need to use the pathways to access different resources in the Trans Mara. The increase in pathway use during September 2014 and August 2015 also coincided with the peak movement of the wildebeest migration from the Serengeti ecosystem in Tanzania to the Masai Mara (Boone et al., 2006). Anecdotal evidence suggests that, during this time, elephants seek refuge in the Trans Mara to avoid the large numbers of wildebeest who compete for grass (Sitati, 2003). Despite these seasonal patterns, we found no relationship between pathway use and rainfall. This was unexpected as previous studies found a relationship between high periods of rainfall and elephant movement (Bohrer et al., 2014b; Cushman et al., 2005; Loarie et al., 2009b). However, the absence of such a relationship in our study could be due to elephants seeking resources in the Trans Mara all year round, as the quality and quantity of grass in the Masai Mara National Reserve has become degraded due to overgrazing (Ogutu et al., 2011, 2016). Elephants may also favour crops in the Trans Mara as they provide high nutrition (Sukumar, 2003, 1990) and are available throughout the year at different stages of growth (Chapter 3).

There was a distinct pattern of elephant activity on the pathways, as elephants travelled up the pathways into the Trans Mara at night and travelled down the pathways into the Masai Mara in the early morning. These travel times are consistent with other studies (Smit et al., 2017; Von Gerhardt et al., 2014) and suggest risk aversion behaviour as human activity is low during these times, and darkness makes it easier for elephants to go undetected (Graham et al., 2010; Von Gerhardt et al., 2014). Travelling during these times also minimises time spent in dangerous areas, i.e. where there are high human densities (Douglas-Hamilton et al., 2005).

4.5.2. Elephant groups using pathways

Pathways were used by all elephant group types (bull groups, female-led family groups and family + bull groups) and there were no differences in pathway use by group type. Bull groups in other parts of Africa have been reported to use pathways more than female-led family groups, especially when pathways lead to farmland (Smit et al., 2017). In other studies, bulls have been reported to use specific pathways closer to human settlements, whereas female-led family groups have tended to avoid such pathways (Songhurst et al., 2015; Von Gerhardt et al., 2014). These studies suggest that bulls are more risk taking than females. However, in our study, we found that all groups used the pathways, which was also found in Botswana (Adams et al., 2017). This could be because female-led family groups in the Masai Mara are less risk averse than those in other parts of Africa, as they are also crop raiders (see Chapter 3). Also, the risk of travelling may be lower than in other areas as some of the pathways had high forest cover, enabling different elephant group types to travel without detection.

4.5.3. Factors determining pathway use

All 22 pathways were used by elephants but some pathways were used more than others. Our results show that high pathway use was driven by distance to farmland, distance to saltlicks, distance to forest and percentage of forest cover on pathways. The strongest predictor was distance to farmland, which suggests that pathway location strongly influences elephant movement (Songhurst et al., 2015) and that, in the Trans Mara, elephants are using the pathways to access farmland. Farmland is now the most dominant landcover type in the Trans Mara, covering 1348 km^2 of the region (see Chapter 2), and the average distance from the end of a pathway to farmland is 1.64 ± 0.25 km. Thus, farmland is easily accessible for elephants and the pathways play an important role in human-elephant conflict, as they make it easier to move into farmland. Other studies across Africa have reported similar findings (Guerbois et al., 2012; Smit et al., 2017; Songhurst et al., 2015; Von Gerhardt et al., 2014).

Our models also suggest that the distance to forest and saltlick are important predictors of pathway use, although they were not as strong a predictor as distance to farmland. The use of pathways to access resources, such as saltlicks and browse in the forest, suggests that the Trans Mara is an important dispersal area for elephants. Thus, the pathways are likely to play a crucial role in resource access, which has been reported in other parts of Africa, where pathways lead to favoured areas such as water, saltlicks and preferred trees (Blake and Inkamba-nkulu, 2004; Shannon et al., 2009; Vanleeuwe and Gautier-Hion, 1998; Von Gerhardt et al., 2014). Saltlicks provide an important source of sodium for elephants and it is suggested that elephants exhibit geophagy to substitute for a lack of sodium in their diet. Geophagy can be greater in female elephants compared to bulls, as females lose sodium when they lactate (Holdo et al., 2002).

Optimal foraging theory would suggest that elephants use pathways as least-effort routes between food resources (Blake and Inkamba-nkulu, 2004; Von Gerhardt et al., 2014). Another low energy foraging strategy is to avoid travelling on steep slopes (Wall et al., 2006). However, the pathways along the escarpment are steep, ranging between 4.1º and 27.7º, and so elephants used a high amount of energy climbing these pathways. Thus, our results suggest that there must be a high nutritional gain for elephants to travel into the Trans Mara that also compensates for the energy lost climbing the steep pathways. These benefits could be in the form of the resources in the forest, the saltlicks and crops. In particular, elephants could be targeting crops, as they are highly nutritious and more palatable compared to wild forage (Sukumar, 1990, 2003), and therefore offer a high reward for climbing the pathways.

Finally, percentage of forest cover on the pathways came out as an important predictor of pathway activity, which could be due to elephants using the forest as cover to avoid detection and/or feeding on the vegetation on the pathways (Wilson et al., 2013). The contribution of pathway vegetation to the diet of elephants needs to be explored further.

4.5.4. Human-elephant conflict and pathway use

Pathways play an important role in human-elephant conflict as our model showed a positive relationship between the total number of dung piles recorded on the pathways each month and the number of human-elephant conflict incidents in the Trans Mara. The temporal patterns of elephant pathway use also coincided with human-elephant conflict incidents, which occurred between the hours of 18:00 and 09:00 (Chapter 3). Our study also found that distance to farmland was the strongest predictor of pathway use, suggesting that pathways act as crop raiding staging posts. These findings are consistent with other studies in Africa, which found that pathways are key spatial drivers of crop raiding, and farms closest to pathways experience a higher frequency of crop raiding (Guerbois et al., 2012; Songhurst and Coulson, 2014).

Based on the results from this study, a number of strategies could be implemented in order to ensure connectivity for elephants between the Masai Mara and Trans Mara and to reduce human-elephant conflict in the region. Firstly, the key resource areas and pathways could be incorporated into land-use planning to provide protection for these areas, thus providing safe passage for elephants into these important dispersal areas. Secondly, for pathways leading directly to farms, mitigation could be specifically targeted along these pathways preventing access for elephants. Types of mitigation that could be used include fencing, such as chili rope fences and early warning detection systems. However, caution should be taken when implementing mitigation on pathways as this could potentially shift the problem elsewhere. Thus, further research is needed to understand the implications of mitigation focused on specific pathways.

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4.8. Supporting information

Table S4.1. Model selection results for factors predicting of pathway use by elephants in the Trans Mara District. AICc= Akaike's information criterion adjusted for small sample size; ∆AICc difference in AICc between each model and the best one; and logLik= log-Likelihood. 1= distance to farm, 2= distance to forest, 3= distance to saltlick, 4= Percent forest.

Model	logLik	AICc	∆AICc	AICc Weight
134	-84.395	186.3	0.00	0.368
12	-87.753	188.0	1.66	0.160
2	-90.531	189.5	3.17	0.075
34	-88.556	189.6	3.27	0.072
24	-89.175	190.8	4.50	0.039
13	-89.241	190.9	4.64	0.036
1	-91.319	191.0	4.75	0.034
124	-86.923	191.3	5.06	0.029
1234	-83.751	191.5	5.21	0.027
4	-91.561	191.5	5.23	0.027
3	-91.981	192.4	6.07	0.018
123	-87.458	192.4	6.13	0.017
23	-90.446	193.3	7.05	0.011
234	-88.111	193.7	7.43	0.009
14	-90.938	194.3	8.03	0.007

5. Discussion

The findings from this thesis have provided new insights into human-elephant conflict trends over time. These results will feed into key strategic objectives for the 'Kenya Wildlife Service Conservation and Management Strategy for the Elephant in Kenya 2012-2021' (Litorah et al., 2012). In particular, providing knowledge of more efficient methods to analyse crop raiding trends. Additionally, the results from this thesis have already fed into a number of regional reports and management strategy documents for the Masai Mara Ecosystem. For example, some of the findings were used in a document about elephant movement in the Masai Mara, which was prepared for the county government to help with their spatial planning process (Poole et al., 2016).

The main aim of this thesis was to improve understanding of human-elephant conflict in the Trans Mara and how it has been impacted by land-use change, thus informing conservation strategies and land-use planning to reduce conflict. Specifically, this thesis aimed to: (i) determine the implications of agricultural expansion on elephant crop raiding; (ii) understand the seasonal, temporal and spatial drivers of crop raiding and compare these to historical data and; (iii) investigate elephant pathway use and their role in human-elephant conflict. Each of these topics is covered in separate chapters, so here I discuss the broader implications and significance of this work. I do this by first describing the implications for managing human-elephant conflict and then suggest recommendations for the region and avenues for further research.

5.1. Implications for managing human-elephant conflict

5.1.1. General agriculture trends and the impacts on human-elephant conflict

The intensification of agriculture has had major impacts on the world's natural ecosystems (Maxwell et al., 2016; Tscharntke et al., 2012; Venter et al., 2016) and is one of the greatest threats that conservation is facing. This research provides further evidence of how land-use change is impacting wildlife populations. Chapter 2 documents high rates of agricultural expansion in the Trans Mara, reflecting increasing global trends, especially across the tropics (Laurance et al., 2014; Phalan et al., 2013). Ecosystems have been transformed into human-dominated landscapes where important remaining habitat patches are increasingly isolated by the continual spread of agriculture (Haddad et al., 2015). This is problematic for wildlife, such as elephants, which rely on land outside protected areas, as their movement can be restricted. This can reduce genetic flow and, more seriously, lead to population decline and extirpations (Blanc et al., 2007; Goswami et al., 2014; Woodroffe and Ginsberg, 1998).

A further impact of greater areas of farmland being next to protected areas and other elephant refuges is the increased likelihood of human-elephant conflict, especially when elephants enter fields and consume and trample crops (Chen et al., 2016; Goswami et al., 2015; Graham et al., 2010; Wilson et al., 2013). Chapter 3 identifies an increase in the number of crop raiding incidents over a 15-year time period. This is most likely due to agricultural expansion, as one of the main spatial drivers of crop raiding is the amount of land under cultivation. Chapter 2 predicts that, in the next 10 years, the area vulnerable to elephant crop raiding will not proportionally decline with forest loss caused by agricultural expansion.

The increase in agricultural land in the Masai Mara ecosystem also reflects shifting land-use practices from pastoralism to agriculture (Maitima et al., 2009; Nyariki et al., 2009). This is important as pastoralism can be a sustainable land-use practice that is compatible with wildlife co-existence (Maitima et al., 2009). However, the shift from pastoralism to agriculture, could lead to a continual increase in human-elephant conflict; and the people most likely to suffer from conflict are the newcomers to the area. Historically, people did not live directly on the borders of protected areas. However, over time, due to agricultural expansion and increasing human populations (Roberts, 2011; Wittemyer et al., 2008), newcomers to areas are acquiring land close to protected areas that were once unoccupied.

The analysis used in Chapter 2 and Chapter 3 are useful methods that can be applied in other circumstances to help inform policy and conservation management; they can be used to identify human-wildlife conflict hotspots and the fine scale drivers of land-use change. This can directly inform local management options for mitigating crop raiding by providing local agencies with an evidence base. This could inform options for assisting local people, managing elephant groups, directing future land use planning or a combination of these factors. Land-use change and scenario modelling can help identify areas in a landscape that are most at risk of deforestation and in need of protection (Smith et al., 2008) and Generalised Additive Models (GAMs) show spatial trends of elephant crop raiding at a fine scale. Previous studies of spatial trends of elephant crop raiding often use approaches which may not be sufficient to explain the complexity of spatial drivers of crop raiding (Songhurst and Coulson, 2014).

5.1.2. The complexity of human-elephant conflict trends

A fundamental step in finding solutions to human-wildlife conflict is understanding temporal trends, which requires having an efficient system to monitor incidents of conflict (Songhurst, 2017). A number of studies have found human-elephant conflict in savanna systems to be strongly seasonal and correlated with rainfall patterns and cultivation cycles (Chiyo et al., 2005; Goswami et al., 2015; Wilson et al., 2013). This was also previously documented in the Trans Mara (Sitati, 2003). However, this thesis found that elephants moved into the Trans Mara all year round using pathways to access resources, including crops. Thus, crop raiding occurred throughout the year and at all stages of crop growth. This could be due to two reasons. Firstly, the risks for elephants associated with crop raiding are lower. This is because the forest patches, which have been created through agricultural expansion, can act as refuges for elephants to avoid contact with humans before and after crop raiding (Graham et al., 2010; Wilson et al., 2013). Therefore, there are shorter boundaries between farmland and elephant refuges which could make it easier for elephants to remain undetected. Secondly, the availability and quality of grasses in parts of the Masai Mara have declined in recent years due to the increasing number of livestock, human settlements and farmland (Ogutu et al., 2011, 2016). Thus, elephants are being driven to find resources outside the reserve to meet their nutritional requirements and are able to do so through the pathways connecting the two areas.

For farmers, this new lack of climate-related predictability of crop raiding has serious implications for their livelihoods and well-being, as it forces them to spend more time guarding their crops (Barua et al., 2013), and mitigation can represent a substantial cost (Naughton-Treves and Treves, 2005). Thus, given these new unpredictable trends, farmers will have to be more flexible and adaptive with mitigation strategies. In the past, mitigation could be focused during particular crop raiding seasons. However, with climate change, crop raiding is occurring year-round. Farmers may have to rotate between different types of mitigation and be flexible in the use of new techniques. However, Chapter 3 highlights that even though the number of crop raiding incidents has increased, the amount of damage has actually decreased. Thus, further research is needed to determine if it is specific mitigation techniques that are better at deterring elephants or whether farmers themselves are getting better at deterring elephants.

Despite farmers experiencing less damage to their crops, there are more farmers being affected by crop raiding, especially those on the front line, i.e. living closest to the protected area and forest. For these farrmers, living next to protected areas may still feel at a disadvantage. This can elicit fear and anger, leading to retributive killing of elephants (Choudhury, 2004; Linkie et al., 2007). Another factor that could be influencing tolerance towards elephants is the high perception of threat. Threat may seem higher to farmers, as they are experiencing crop raiding all year round and, even though there is less crop damage per incident, there are more farmers being affected. Previous studies have shown that people often perceive the amount of crop damage to be higher than the actual amount (Gillingham and Lee, 1999; Naughton-Treves, 1997). Such perceptions of higher threats could reduce farmers' tolerance towards elephants and again lead to retributive killing of elephants. Thus, understanding local people's perceptions of threat and attitudes can help determine their responses to wildlife and the extent to which they may be able or willing to tolerate wildlife presence (Hill, 2018).

5.1.3. Understanding human-human conflict

Although human-wildlife conflict inevitably involves negative impacts to both humans and wildlife, at a deeper level it is argued that conflicts reflect a manifestation of underlying human-human conflicts between authorities and local communities, or between different cultures of people (Dickman, 2010; Dickman et al., 2013; Pooley et al., 2017; Redpath et al., 2014). This has been characterised as, "*two or more parties with strongly held opinions clash over conservation objectives and when one party is perceived to assert its interests at the expense of another"* (Redpath et al., 2013). Thus, it is important to distinguish between human-wildlife impacts and human-human conflicts as these need to be managed differently. Impacts can be reduced through technical solutions i.e mitigation methods. However, human-human conflicts are more challenging to resolve and require novel and comprehenisive approaches for long-term resolution (Dickman, 2010). In human-human conflict situations, wildlife is frequently not represented, as conflict resolution is focused on the interests of humans and seeks to find a win-win situation between the different human parties involved (Vucetich et al., 2018).

Thus, both human and wildlife-perspectives need to be considered when managing conservation conflicts.

This thesis has provided an in-depth understanding of the drivers and impacts of human-elephant conflict in the Trans Mara and, although not in the direct scope of the research objectives, it has highlighted a number of tensions between different stakeholders within the Trans Mara. It has thus highlighted another underlying but important driver of human-wildlife conflict that should be investigated further and also considered when implementing management strategies in the region. In the Trans Mara, the attempt of government agencies (Kenya Wildlife Service) to address conflict is often hampered by limited resources, and by the fact that crop raiding is hard to predict and is a widespread problem (Graham et al., 2010). Delayed responses to crop raids and problems identifying the individual/group of elephants involved leaves farmers feeling dissatisfied and frustrated with the response from the authorities, thus resulting in tension (Evans and Adams, 2016). Another source of tension is many farmers having been promised compensation for crop losses through the new 'Wildlife Management Act' (Wildlife Conservation and Management Act, 2013). Tension has arisen because, despite many farmers having submitted claims, most farmers have yet to receive any compensation. This creates a false expectation of what Kenya Widlife Service, as the wildlife authority, will deliver, and so when expectations are not met, further tension is created. Thus, in the Trans Mara, to fully understand and respond to crop raiding by elephants, there needs to be a focus on not just the quantity of crop loss or number of incidents of conflict, for instance, but a focus also on what local people think and feel about wildlife (Hill, 2018
Further investigation is important to understand the underlying tensions of the different stakeholders as, without a comprehensive understanding, any mitigation implemented may fail. Figure 5.1 is a conceptual framework diagram showing the interactions and feedbacks between the different aspects of human-elephant conflict and where this thesis has provided new insights into the literature. Figure 5.2 is a more detailed conceptual diagram of human-elephant conflict in the Trans Mara. The diagram also highlights key findings from this research and how these drives different aspects of conflict.

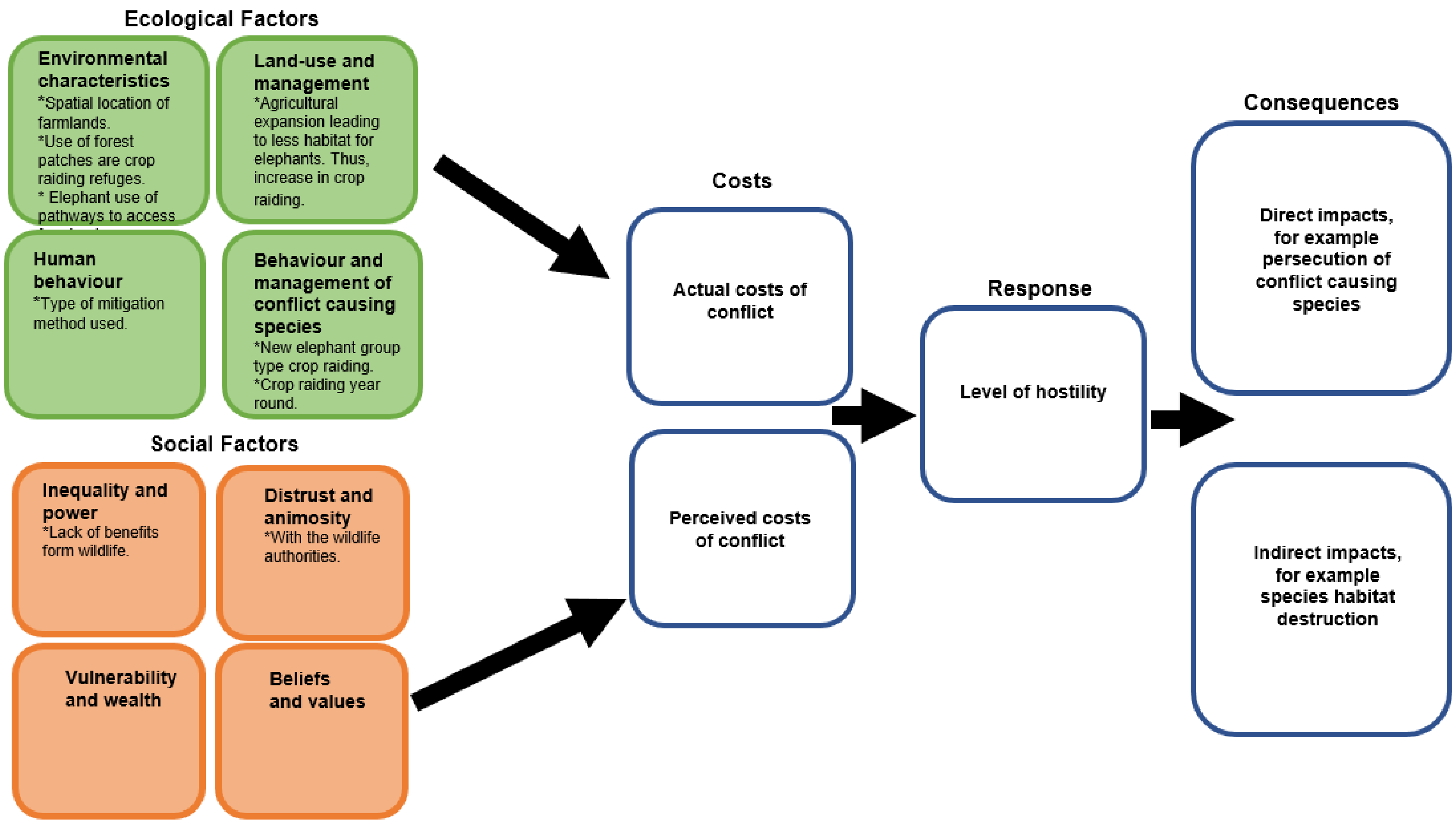

Figure 5.1. A conceptual framework diagram adapted from Dickman (2010), showing the interactions and feedbacks between the different aspects of human-elephant conflict. * Indicate where this thesis has provided new insights into the literature.

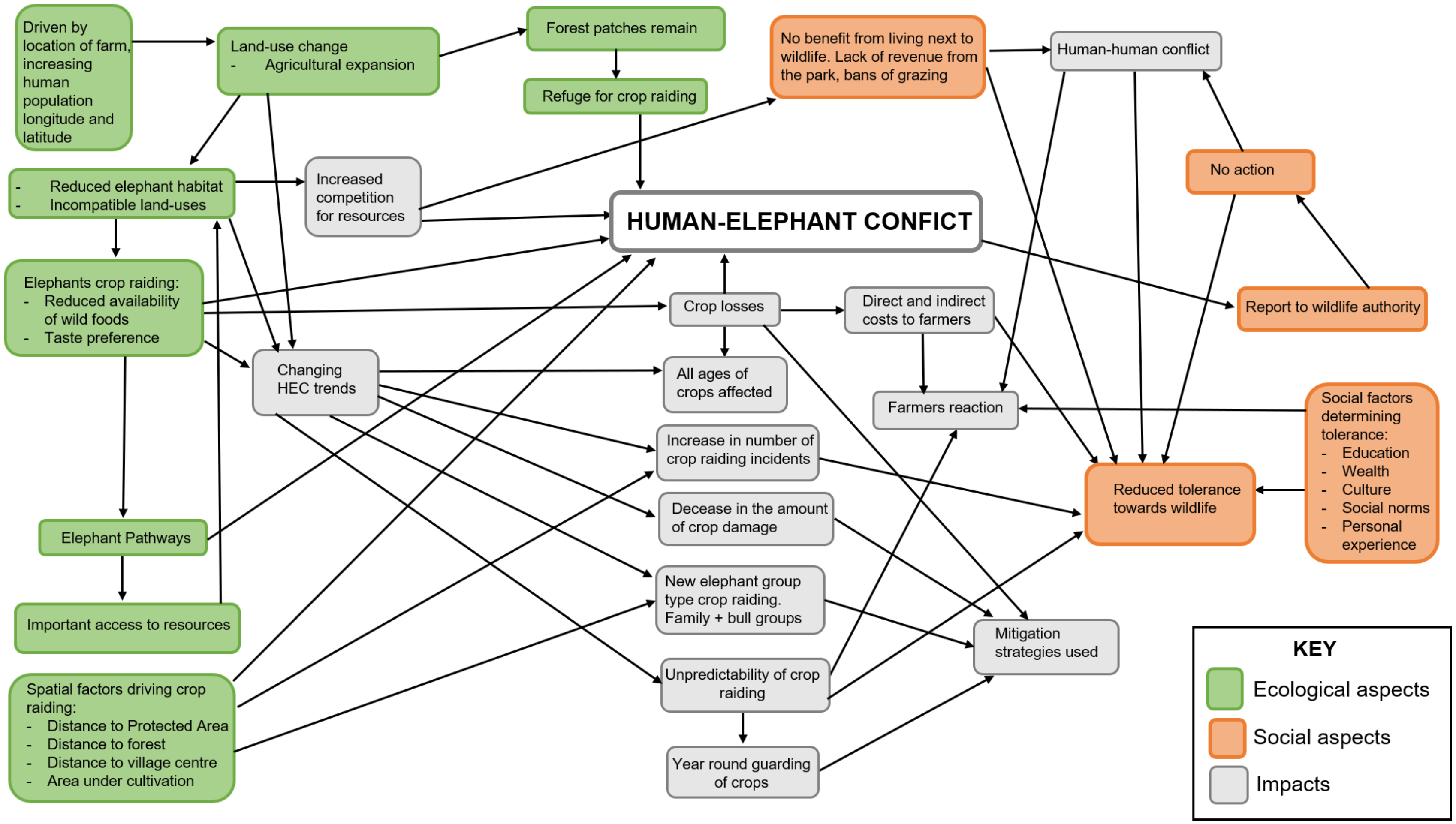

Figure 5.2. A conceptual framework diagram showing the interactions and feedbacks between the different aspects of human-elephant conflict in the Trans Mara.

5.1.4. Alleviating HEC through community engagement

If communities participate in, and benefit from, conservation and management of wildlife on their land, then this may help to increase tolerance towards wildlife and reduce tension between different stakeholders (Biggs et al., 2016; Cooney et al., 2016; MacKenzie et al., 2017). One option is to provide revenue to farmers from sources other than agriculture, such as tourism and ecosystem payments (Andam et al., 2010; Canavire-Bacarreza and Hanauer, 2013; Ferraro et al., 2015, 2011; Ferraro and Hanauer, 2014; Hanauer and Canavire-Bacarreza, 2015; Suich et al., 2015). For example, in Tsavo, Kenya community land owners receive carbon credit payments from a REDD+ project, which was set up on a wildlife corridor to protect land from charcoal burning and provide communities with benefits (Githiru et al., 2017). Tourism has reduced poverty for communities living next to protected areas in other countries (Andam et al., 2010; Canavire-Bacarreza and Hanauer, 2013) and protected wildlife dispersal areas from being cleared. For example, in the Maasai Steppe in Tanzania, direct payments from park fees to communities has resulted in large areas of community land being protected for wildlife (Sachedina and Nelson, 2010). This could be a viable option in the Trans Mara, as the Masai Mara National Reserve earns high revenues each year (KNBS, 2016). However, despite the new Wildlife and Conservation Act (Wildlife Conservation and Management Act, 2013) stating that 14 % of tourism revenues from the Masai Mara should be equally distributed to the surrounding communities, very few communities have benefitted. This is due to a few elites pocketing most revenue (Walpole and Thouless, 2005), and benefits being unevenly distributed between age, gender and education groups (DeLuca, 2004). Thus, unless these issues are resolved, then tourism will not be a feasible alternative to farming and farmers will continue to bear the costs of conflict, and will not appreciate the value of wildlife. Although out of the scope of this thesis, it is important to highlight that if elephant-related costs are not reduced, and tolerance towards elephants remains negative, then poaching may continue. Farmers may tolerate poaching as a means of eliminating their problem.

5.1.5. Alleviating HEC through mitigation measures

The amount of crop damage in the Trans Mara has declined since 1999-2000, suggesting that current techniques, such as fences and guarding, are working. These community-based techniques have also been successful in mitigating crop raiding in other areas (Davies et al., 2011; Gunaryadi et al., 2017). This is good news. However, better evaluation is still needed to ensure that farmers are equipped with appropriate methods and means for mitigating conflict in the light of the changing patterns and higher occurrence. Currently, mitigation is at the individual farmer level, but having landscape level protection could be more effective. For instance, this thesis shows that pathways are drivers of crop raiding, and the fine scale spatial analysis in this thesis found that farms 1 km from the forest boundary and 5 km from the protected area boundary are in conflict hotspots. Thus, mitigation could be specifically targeted at pathways and around the forest, preventing elephants from entering a whole village. Such mitigation could include a combination of techniques, such as early warning detection systems and fencing. However, even seemingly simple mitigation techniques, such as fences, can actually exacerbate conflicts (Evans and Adams, 2016), causing human-human conflict between local people and conservationists. This would be likely to negatively impact upon conservation outcomes (Pooley et al., 2017). Thus, caution is needed if implementing such measures on a large scale.

5.1.6. Alleviating HEC through long term solutions such as land-use planning

Despite short term solutions offering some relief to conflict, they tend to just treat the symptoms of conflict and not address the underlying cause (Barnes, 2002), which is land-use and land-use change. Protected areas in Kenya are not enough to protect wildlife. Instead, they need to be integrated with human-dominated areas into wider connectivity landscapes. This thesis highlights the importance of the Trans Mara as a dispersal area for wildlife and the results can directly feed into national policy such as the 'Securing Wildlife Migratory Routes and Corridors', which is a joint initiative between Kenya's Ministry of Environment and Natural Resources, Kenya Wildlife Service and numerous other institutions (Ojwang et al., 2017). This initiative recognises the need to protect key corridors and dispersal areas and one of these areas highlighted in the document is the Masai Mara.

Land use planning is crucial to conserve remaining natural habitats, biodiversity and ecosystem services. It should be holistic, including protected areas and human-use areas. The methods used in this thesis can help to guide land-use planning through scenario modelling, fine scale spatial analysis of crop raiding and the knowledge gained about pathway use. Thus, land-use planning options that incorporate our findings to define human-use areas and wildlife-dispersal areas could be effective in mitigating conflict, while conserving the long- term viability of elephants. Such approaches could include land-use zoning (Linnell et al., 2005) or creating conservancies. The creation of a conservancy should be possible within the Trans Mara, as the Mara ecosystem is globally famous and attracts large numbers of tourists each year, potentially providing a viable source of income for local people that is not dependent on clearing more land for agriculture. A number of conservancies, which are owned and managed by local communities, have been set up elsewhere in the Mara ecosystem and throughout Kenya, showing that this approach could work within the Trans Mara (Bedelian and Ogutu, 2017; Blackburn et al., 2016). The creation of a conservancy in the Trans Mara could reduce HEC. However, one major consideration is that land is mostly owned by the rich, and so the poor may be unable to invest in, or allocate land for, such schemes (Bedelian and Ogutu, 2017; Börner et al., 2010; Corbera et al., 2007).

5.2 Recommendations

There are a number of key recommendations that have resulted from this research which could be implemented in the Trans Mara:

1. Focus specific deforestation projects in areas vulnerable to clearing and areas which have the minimum requirements for elephants. These projects could include habitat restoration programmes and patrols within the forest to reduce charcoal burning. Althernatively, developing Nykweri forest into a community conservancy would be the most ideal situation as it would prevent further clearing of forest and provide communities with benefits at the same time. A carbon credit scheme could also be another consideration for the area ensuring that communities are benefitted from their land.

2. Continue monitoring human-wildlife conflict. During this study only 6 % of crop raiding incidents were reported to Kenya Wildlife Service. Thus, having a community-based monitoring system that also assists Kenya Wildlife Service officials would provide a feasible, local scale system that would be important to monitor changing human-wildlife conflict trends. Monitoring should also address broader issues beyond providing a record of damage incidents. For example, data on farmer attitudes associated with human-elephant conflict incidents. This could have a greater effect on management and help design more effective strategies (Songhurst, 2017).

2. Trial out a community led consolation scheme for human-wildlife conflict. In the Trans Mara, community members could buy in to such a scheme run by the community. This would reduce the total reliance on government compensation which is further intensifying conflicts.

3. Better structures to be put in place for better transparency of revenue sharing from Masai Mara National Reserve park fees so that all communities benefit and not just a few elites.

4. Conduct a social study across the Trans Mara looking at the atitudes and tolerances of local communities and feelings towards the different stakeholders.

5. More resources for the Kenya Wildlife Service to be able to deal with human-wildlife conflict incidents. This would also improve community relations.

6. Focus mitigation on specific pathways which lead directly to farms. For example, mitigation could be a combination of techniques, such as early warning detection systems and fencing However, caution should be taken when implementing mitigation on pathways as it is not known whether this would cause nutritional stress on the elephants by blocking their movement into farmlands. Currently, natural forage in the Masai Mara is declining due to illegal overgrazing of cattle. Thus, we do not know how much elephants are relying on cultivated food crops as part of their diet. So completely blocking them from farms could put a strain on elephants. Also, by blocking elephants from certain villages in the Trans Mara, could simply move the problem elsewhere.

5.3. Future research

There are many avenues for further research following the different issues covered in this thesis. The case study of the Trans Mara District provides an in-depth understanding of the implications of land-use change, trends in human-elephant conflict over time, elephant movement and the socio-economics of the communities living there. However, further studies are required to:

- **Determine the impacts of climate change on human-wildlife conflict**.
  Climate change is an important threat facing people and wildlife, and yet its impact on human-wildlife conflict is unclear (Nyhus, 2016). Chapter 3 highlights how the seasonal trends of human-elephant conflict have changed markedly over the last 15 years. Thus, determining how future patterns of human-wildlife conflict will be affected by climate change will be very important.

- **Understand the extent to which elephants rely on crops as part of their diet**.
  This thesis identifies elephant movement into the Trans Mara and crop raiding throughout the whole year, contrasting with previous research in which crop raiding occurred during two peaks of the year (Sitati, 2003). Thus, there is a need to understand how much elephants rely on crops, especially in the light of natural resources, such as grasses, becoming degraded in parts of the Masai Mara National Reserve (Ogutu et al., 2016, 2011). More work is needed to understand how blocking access to farmlands would impact elephants' diet and energy requirements.

- **Understand why scientifically proven mitigation measures, such as chili fences, are often ignored or discontinued by communities**. This is an aspect of conflict mitigation that is currently under-researched (Pooley et al., 2017). The use of chili fences as a mitigation method has been proven successful in the Trans Mara (Sitati and Walpole, 2006), but such fences are currently not being used by farmers. It would be important to understand why these techniques have been ignored, as there may be underlying issues, such as scepticism, lack of capacity and social tensions that could explain this lack of uptake.

- **Determine elephant population estimates in the Trans Mara and other forest habitats in Kenya**. There is a need for accurate elephant population estimates for forest habitats in Kenya as they have been difficult to assess (Litoroh et al., 2012). In the Trans Mara, this information would be helpful, as population numbers, trends and densities of elephants can help inform more effective and appropriate conservation management (Songhurst et al., 2015).

- **Determine the impacts of the wildebeest migration on elephant movement**. Chapter 4 documented that many elephants moved into the Trans Mara during the months when the wildebeest were in the Masai Mara National Reserve. Currently, anecdotal evidence suggests that elephant movement and the high numbers of wildebeest are linked, but this has not been tested. Future management would gain from a better understanding of why this happens and the measurement of the extent that this impacts elephants in terms of pressures on food resources and water. Also, it would be important to determine whether this is happening in other dispersal areas in the Masai Mara.

5.4. Conclusion

Human-wildlife conflict is increasing due to shrinking and fragmenting habitats. It is a "wicked problem" (Game et al., 2014) and one of the greatest challenges facing conservationists today. This thesis provides an in-depth understanding of the effects of land-use change on human-elephant conflict in the Trans Mara District, which is a typical example of what is occurring throughout Sub-Saharan Africa. The results from this study highlight the value of long-term monitoring of human-elephant conflict, as the nature of conflict has changed over time, with an increase in frequency but a decrease in intensity. Trends are becoming less predictable and conflict will continue to be a problem, even with high amounts of forest loss. This is because elephants will continue to use pathways to access resources, including crops, in the Trans Mara. There are a range of people who are affected by conflict and to help alleviate conflict, especially in the light of its changing patterns, land-use planning is crucial to balance the needs of humans and wildlife. The integration of knowledge gained in this thesis, such as the areas vulnerable to conflict, the drivers of crop raiding, the nature of elephant movement in human-dominated landscapes and the socio-economic context of the Maasai communities in the Trans Mara will help underpin management strategies. For such strategies to be successful, tolerance towards wildlife must be established, with local communities reaping the benefits of wildlife. Without such engagement, the future of wildlife is uncertain, as habitat loss and retributive killing are likely to become a more serious problem.

5.5. References

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