Poaching and Human-elephant Conflict: A Destructive Duo

How Poaching May Alter Male Elephant Society and Indirectly Influence Human-elephant Conflict

by

Amy Cocksedge

Supervised by

Dr. Greg Thiemann

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Foreword

My major research paper (MRP) acts as a case study in which I explore all the major themes set out in my POS. In general, I set out to study the dynamics of wildlife conservation. I specifically was interested in exploring animal behaviour, wildlife biology, the wildlife trade, human-wildlife conflict, and wildlife management. My MRP is an in-depth look at the role of the ivory trade in elephant society and human-elephant conflict.

This MRP research allowed me to look critically at all the specific elements of my POS. I took a major focus examining male elephant behaviour and society, thus examining animal behaviour. This also allowed me to branch into the study of wildlife biology in general, examining broader theories on habitat use, the role of hormones, and society. The wildlife trade component of my POS was explored through the case study of the ivory trade, a major focus of my MRP. Human-wildlife conflict was explored through human-elephant conflict, while wildlife management was explored both specifically in the ability of people to cope with human-elephant conflict and generally in terms of the role that the ivory trade and elephant behaviour might play.

As such, my MRP exploring the potential impact that the removal of male elephants for the ivory trade might have on elephant behaviour and thus human-elephant conflict acts as a case study exploring all major elements of my POS.

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Abstract

The uncertain future of African elephants (*Loxodonta africana*) is currently a popular issue in conservation circles, largely due to the ongoing poaching crisis. Compounding the threat of illegal offtake are the added pressures of habitat loss and human-elephant conflict (HEC). HEC specifically is a complex challenge to conservation and a major threat to elephants across their entire range, leading not only to retaliation killings but the erosion of local support for conservation. While the issues of poaching and human-elephant conflict have been considered separate issues, an examination of elephant behaviour and HEC under a political ecology framework highlights the possibility that these processes are becoming increasingly interconnected. Elephant bull society, specifically the influence of mature males, aids not only in proper social development of adolescents but controls musth in younger males. As older males have the largest and thus most desirable tusks, the ivory trade presents a unique challenge to bull society by removing the positive influence of older conspecifics. This stifles the ability of young males to learn proper foraging and leads to early musth. As pre-musth males must forage heavily, and foraging behaviour is learnt by association with older males, the ivory trade may lead to heavy crop raiding by young males and thus exacerbate HEC. When we consider that the social and economic situations that are thought to drive poaching activity are the same as those that both put people at higher risk of HEC and drive retaliation killings, it is likely that poaching influences levels of HEC.

Introduction

African elephants (*Loxodonta africana*) currently face a myriad of challenges. Their largest threat by far is offtake for the illegal ivory trade. Scientists warn that the current rate of poaching exceeds the species' intrinsic growth rate (Wittemeyer, 2014, p. 13,118), thus threatening the survival of the species. Compounding the threat of illegal offtake are the added pressures of habitat loss and conflict with humans (Archie & Chiyo, 2014; Nelson, Bidwell, & Sillero-Zubiri, 2003). Human-elephant conflict (HEC) specifically is a complex challenge to conservation and a major threat to elephants across the entirety of their range (Fernando et al., 2005; Webber, Sereivathana, Maltby, & Lee 2011, p. 243). Conflict with people not only leads to retaliation killings, but is particularly challenging for conservation, as local support is seen as key to the success of protected areas (Naughton, Rose, & Treves, 1999; Nelson et al., 2003). While the issues of poaching and human-elephant conflict have been considered separate issues, examination under a political ecology framework, with a focus on elephant behaviour, highlights the possibility that these are becoming increasingly interconnected. As older males have the largest and thus most desirable tusks, the ivory trade presents a unique challenge to bull society by removing the positive influence of older conspecifics. This stifles the ability of young males to learn about proper foraging and leads to early musth. As pre-musth males must forage heavily, and foraging is learnt by association with older males, the ivory trade may lead to heavy crop raiding by young males and thus exacerbate HEC. When we consider that the social and economic situations that are thought to drive poaching activity are the same as those that both put people at higher risk of HEC and drive retaliation killings, it is likely that poaching influences levels of HEC.

This paper seeks to examine the role that the ivory trade plays in HEC, specifically crop raiding. It will begin by briefly overviewing the ivory trade in order to establish a basis of understanding of what drives the desire to poach. It will then turn to the importance of elephant male society for the development of adolescent males as well as the control of musth. Further examination of the dynamics of HEC will then highlight the ways in which elephant behaviour can help identify patterns of crop raiding and assess risk. It will tie these elements together to examine the possibility that the removal of older males alters bull society in a way that fosters crop raiding behaviour in pre-musth bulls.

In addition to incorporating individual theories on animal behaviour, this analysis will be situated within a political ecology framework to understand the relationship between poaching, animal behaviour, and human-wildlife conflict. Political ecology is an approach that considers political economies and cultural studies while branching into the relationships between society and the natural world (Keil, Bell, Penz, & Fawcett, 1998). It is a broad theory that examines the ‘winners and losers’ in regards to nature (Robbins, 2012). According to Michael Watts, the goal of political ecology is to explain environmental conflict in terms of struggles over “knowledge, power and practice”, and “politics, justice and governance” (Watts, 2012, p. 257). The ivory trade and human-elephant conflict are issues that span across the social and natural sciences. As this paper aims to encapsulate the role of animal behaviour in connecting these issues, a political ecology framework will allow considerations not only of both disciplines, but their connections and applications for real-world action.

The Ivory Trade

The trading of mammal ivory in general is considered to be one of man’s oldest trades, with evidence suggesting it dates back to Aurignacian times, between 38,000 BCE and 29,000 BCE (Parker, 1979). Between the 17th and 19th centuries, the demand for ivory expanded greatly (Larson, 2013). A significant surge in game hunting by wealthy Westerners in the early 1900s led to mass production of ivory items. Conveying a status of wealth, its use as a social-status symbol led to detrimental drops in elephant populations. From early 1900 to 1980, elephant numbers in Africa fell from an estimated 10 million to below 1 million. While western consumers realized the consequences of the trade, Asian demand grew (Larson, 2013). As a result, the first ivory crisis arose in the 1970s and 80s (Orenstein, 2013, p. 47). Coupled with widespread poverty, lawlessness, and political instability, poaching thrived (Orenstein, 2013, p. 47). By 1989, elephant numbers had fallen to approximately 600,000 individuals. This prompted the CITES ban on commercial ivory trading (Larson, 2013). CITES (the Convention on International Trade of Endangered Species of Wild Fauna and Flora) is responsible for overseeing the legal trade of endangered species. While the ivory ban temporarily contained the trade in the early 1990’s (Orenstein, 2013, p. 177), the trade has since resurged. From 2010 through 2012 alone, an average of 33,630 elephants were illegally killed per year. This represents ~6.8% of the total estimated population – a level of offtake exceeding the species' intrinsic growth rate (Wittemeyer, 2014, p. 13,118). Today, the trade continues to decimate the elephant population, and scientists warn that with the current unsustainable levels of offtake, African elephants are at risk for both local extirpation and global extinction.

The ivory trade poses a specific threat to older male elephants (Milner-Gulland & Mace, 1991). While females also have tusks and can be targeted, older males have larger tusks and correspondingly larger financial rewards. Indeed we observe selective harvesting of large tuskers by poachers due to the higher monetary return per individual killed (Chiyo, Obanda, & Korir, 2015, p. 5217; Usman & Ahmad 2015, p. 127).

Figure 1. IDENTIFIED POACHING HOTSPOTS. Countries are: Gabon, Republic of the Congo, Cameroon, Equatorial Guinea, the Central African Republic, Chad, Democratic Republic of the Congo, South Sudan, Kenya, Tanzania, and Mozambique (Christy, 2015).

As a market, the ivory trade is supported by the three pillars of supply, demand, and distribution - all of which are highly dependent on the economic and political situations of countries involved. Here, we will consider what drives and perpetuates the supply of ivory in order to situate the act of poaching in the political ecology framework.

Illegal ivory is primarily sourced from African elephants. Throughout the continent, “hot spots” have been identified from which the vast majority of illegal ivory originates (Wasser et al., 2008, p. 1,066) - see Figure 1. The desire for individuals to participate in supplying ivory (i.e. poaching and local transport) is seen as a consequence of the political and economic situations of supply countries. These situations also facilitate the perpetuation of the trade itself due to the inability to properly police and patrol poaching. Low economic status combined with high returns on ivory sales and high levels of corruption combine to fuel the supply trade. Indeed, studies have found a positive relationship between levels of both corruption and poverty with estimated PIKE[1] levels. These found that poverty, governance, and demand explained nearly two thirds of the variation observed in PIKE levels across African sites examined – poverty and governance explaining a spatial pattern and demand accounting for the temporal trends - see Figure 2 (Blanc et al., 2013).

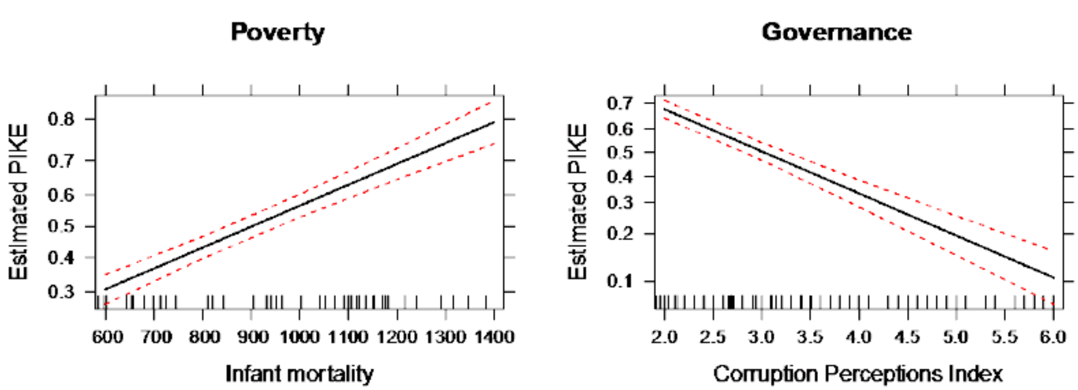

Figure 2. POSITIVE RELATIONSHIP BETWEEN PIKE, POVERTY, AND GOVERNANCE. Dotted lines represent confidence bands (Blanc et al., 2013, p. 8)

All identified hot spot countries are ranked ‘lower-middle’ or below in a GDP

[1] PIKE is an acronym for the CITES-run ‘Percentage of Illegally Killed Elephants’ program, which calculates the percentage of all elephant carcasses that are believed to have been killed illegally.

classification – with the exception of Gabon ranked ‘upper-middle’ (see Appendix A). With prices for poachers reaching between USD $66 and $496 a pound (Christy, 2015), the economic incentives for individuals to participate in the trade are self-evident. In addition to poor economies, there is a significant history of corruption and political turmoil in many of the countries identified as hot spots. According to Transparency International’s Corruption Perceptions Index, all of the states hosting an ivory hot spot were ranked 101 or higher in 2016 (“Corruptions Perceptions Index”, 2017) - see Appendix B. A complication of economic incentives to poach is that when authority is fragmented and motivations to engage in illegal activity lie at the local level, it becomes increasingly complicated to control (Le Billon, Macrae, Leader, & East, 2000, p.10). Indeed, a ‘weak’ state is seen as a facilitator for the benefits that individuals gain from business deals with criminal networks, which reach into world markets (Ballentine & Nitzschke, 2005, p. 2). People driven into the supply trade by local issues thus have the opportunity to capitalize on globalization and disorderly states (Le Billon, 2001, p. 576), elevating the trade into a global network.

Understanding the dynamics of the ivory trade - what tusks are most desired, where ivory is supplied from, and the political and economic drivers of supply - we can now move into examining elephant behaviour and human-elephant conflict. In doing so, we will begin to tie together the ways in which the removal of males by the ivory trade can have detrimental effects on bull society and how the political and economic situations that drive poaching are similar to those that sponsor low tolerance and high retaliation against ‘problem’ elephants.

Elephants: Bull Society and Natural History

Elephant behaviour is affected by both real and perceived threats from humans, including poaching pressures, human settlements, and human activity in elephant ranges. These activities have been seen to alter ranging and activity patterns, as well as influence human-avoidance behaviours (Gunn et al., 2013, p. 130). To analyze how the ivory trade affects elephant behaviour, a comprehensive understanding of social organization, sexual patterns, and behavioural dynamics under 'normal' circumstances is needed.

Social Organization & Male Adolescence

The family unit is the centre of social organization for the African elephant (Poole, Kasman, Ramsay, & Lasley, 1984; Poole, 1989a). Elephants live in 'fission-fusion' societies, wherein composition of social groupings is fluid, changing over time (Poole & Moss, 1989). Within large herds, elephants live in defined family units comprised of adult females and juvenile males and females (Desai & Riddle, 2015). Adult males live independently of these groups, occasionally joining them for mating and periods of travel (Moss & Poole, 1983; Poole and Moss, 1989). Accordingly, male and female elephants demonstrate different social dynamics. While females remain with their natal herd upon reaching sexual maturity, males will either leave or be forcibly ejected after reaching puberty (between the ages of 14 and 17) (Poole, 1989; Poole et al., 1984; Baskaran, Balasubramanian, Swaminathan, & Desai, 1995). Upon leaving, males no longer show strong bonds with their natal herds (Baskaran et al., 1995), instead joining older males - 'bulls' - to form all-male groups in established 'bull areas', away from breeding herds (Druce, Pretorius, Druce, & Slotow, 2006, p. 133).

While adult bulls are primarily solitary (Baskaran et al., 1995), adolescent males undergo a unique phase of socialization by associating with older bulls. A recent study by Evans and Harris revealed adolescents to be the most social age group in males, demonstrating preferences for larger social groupings (Evans & Harris, 2008). They believe this preference is resultant from the educational opportunities provided by older bulls, suggesting that much as matriarchs are repositories of social and ecological knowledge within natal herds, mature bulls are equivalent repositories for bull societies (Evans & Harris, 2008).

Adolescence is a vital stage of development for male elephants. Though few mammals undergo such a period, it is believed to be influential in the development of behavioural characteristics (Evans & Harris, 2008, p.779). ‘Adolescence’ is considered the interval between puberty and effective reproduction (Pereira & Altmann, 1985), occurring in elephants between the ages of 10 and 20 (Moss & Poole, 1983). It is a dynamic period of changing sexual states, ranks, associations, and behaviours wherein individuals experience growth spurts, the development of secondary sexual characteristics, and the attainment of sexual maturation (Poole, 1987; Poole, 1989b). It is during this time that individuals acquire skills and develop relationships that have both immediate and long-term benefits to their survival and reproductive success (Evans & Harris, 2008). This period is demonstrative of the importance of what is known as ‘cultural transmission’ of knowledge - a form of learning wherein information is transferred from individual to individual through social learning (Dugatkin, 2009, p.159). This type of learning allows individuals to gain knowledge on habitat selection, mating, familial relationships, and even aggression (Dugatkin, 2009, p. 158). For adolescent males, older bulls act as ‘models’, wherein the observer copies the actions of the model in order to learn new behaviours. This is a particularly important periods as when young males leave natal herds, they enter into a new social system and must learn how to survive independently for the first time (Hall-Martin, 1987, p. 616). Three particularly important elements of elephant sociality that are observed during this period are the establishment of dominance hierarchies, understanding home ranges and habitat selection, and foraging.

Social hierarchies are vital to animal sociality, as where an individual places in a dominance hierarchy has both proximate and ultimate implications (Dugatkin, 2009, p. 458). Individuals at the top of hierarchies have better access to food, enhanced mating opportunities, and safer territories than those at the bottom (Dugatkin, 2009, p. 459). For elephants, interactions with other males, specifically sparring, determine these dominance hierarchies (Evans & Harris, 2008, p. 783). Sparring most often occurs between males of similar age to not only establish, but reinforce the hierarchies that govern male societies (Miller & Byers, 1998). Sparring decreases with age, indicative of an early establishment of social hierarchies and ritualistic male-male competition (Evans & Harris, 2008).

Following adolescence, mature bulls occupy specific home ranges to which they show great fidelity. These ranges determine much of their movement and access to resources (Desai & Riddle, 2015, p. 10). The spatiotemporal use of home ranges across occupiable habitat is based on both resource availability and dominance hierarchies (Desai & Riddle, 2015, p. 10). In undisturbed habitats, home ranges are significantly affected by both access to water and an avoidance of human settlements (Desai & Riddle, 2015, p. 10). The establishment of home ranges is based on the hierarchal dominance order among bulls in a particular range (Hall-Martin, 1987, p. 616). As such, the hierarchies established during adolescence through interactions within bull society have important implications on the future home ranges of adolescent males. Cultural transmission also plays an important role in habitat selection. Social learning allows animals to identify territory boundaries, the identities and personalities of ‘neighbors’, and the nature and value of resources in a given area - all of which allow for profitable habitat selection (Dugatkin, 2009).

Adolescence is also the time when males learn to foraging independently. Socializing with older bulls allows them to learn the locations of profitable foraging areas, thus reducing the time they spend gathering information - energy much better used for growth and socializing (Stamps, 1987). Indeed, cultural transmission is an important tool in many species ability to learn about foraging, as information can be transmitted when individuals observe others to understand how they find food and what foods they eat (Dugatkin, 2009, p. 356). For adolescent elephants, cultural transmission plays a vital role in social development.

Musth

In male elephants, sexual maturity is reached long before mating begins. From an evolutionary perspective, such a delay presumably confers some adaptive adavantage. In primates, it has been suggested that a prereproductive yet sexually mature adolescent period may enable males to learn about their physical and social environments, prior to reproductive attempts (Bogin, 1999; Poirier & Smith, 1974). This period also increases opportunities to learn a variety of skills, and may even enable longer periods of brain growth so that association areas in the cerebral cortex can mature. As such, this learning process during adolescence may benefit reproductive success as an adult, justifying the delay in reproduction despite physical maturity (Walters, 1987). Male African elephants have one of the longest such delay periods. Puberty occurs between ages 9 and 15 (Hanks & McIntosh, 1973; Lee, 1986; Short, Mann, & Hay, 1967) and sexual maturity is reached at age 17 (Laws, 1969; Poole, 1994). Yet, males rarely mate until they are in their 30s (Poole, 1994). As older, larger males get the most mating opportunities (Poole, 1987; Poole, 1994), it is believed that mating success is directly related to musth (Poole & Moss, 1981) - a sexual phenomenon that may have significance to human-elephant conflict. Understanding the phenomenon of musth is vital in analyzing elephant behaviour as well as understanding the influence of poaching on bull society.

Musth: What Is It & What Physiological Changes Are Seen

Musth is a periodic physiological and behavioural condition experienced by male elephants, wherein individuals experience elevated testosterone levels as well as heightened levels of aggression and sexual activity (Druce et al., 2006, p. 134; Hollister-Smith et al., 2007, p. 287; Poole, 1987; Poole et al., 1984; Poole & Moss, 1981, p. 830; Slotow, van Dyk, Poole, Page, & Klocke, 2000). Musth is characterized by several observable signs, including increased aggression, swollen and weeping temporal glands, strongly-scented urine dribbling, green-penis syndrome, distinctive posture, trunk and ear movements and other minor displays, and extensive movement over an enlarged home range (Kahl & Armstrong, 2002, p. 161; Poole, 1987; Hall-Martin, 1987, p. 617).

Age in Years	Length in Days
16 - 25	2
26-35	13
36-40	52
41-45	69
46-50	81
51 +	54

Figure 3. OBSERVED MEDIAN LENGHTS OF MUSTH. Adapted from Poole, Lee, & Moss, 2011.

Males typically begin to experience musth around the age of 29 (Poole, 1987). These younger males will experience comparatively shorter bouts of musth, generally lasting a few days or weeks. With age, musth lasts for longer periods of time - however begins to decline once males pass the age of 51 (Hollister-Smith et al., 2007, p. 287). Observed median times of musth are demonstrated in Figure 3. In addition to length, the regularity of musth changes with age. Younger males will experience musth at irregular intervals, while older males will have musth periods that have stabilized to a generally annual occurrence (Poole, 1987, 1989a; Pool, 1989b).

However, there is no synchronicity amongst older males - musth is observed throughout the year, however, relatively few males within a population appear to experience it simultaneously (Poole, 1987; Poole, 1989a).

Physiologically, musth is a costly state. Bulls in musth lose weight, with their overall physical condition visibly deteriorating as musth progresses (Poole, 1989a). Changes in behaviour may contribute to this, as during musth bulls spend significantly less time feeding and more time walking (Poole, 1989a, p. 146) - a behaviour believed to result from an increased focus on locating females and subsequent devaluing of feeding during this time. However, weight loss may also be related to the increased metabolic rate that is associated with high androgen levels experienced during musth (Poole, 1989a, p. 146). Due to their increased movement and decline in foraging activities during musth, pre-musth males focus on feeding and improving their body condition (Sukumar, 1989). Significantly, it has been observed that prior to musth, males engage in risky behaviours. One such behaviour is crop-raiding, which has seen to be elevated before wet seasons, when most females come into oestrus (Webber et al., 2011, p. 249).

In addition to physiological deterioration, bulls in musth also experience significant behavioural changes. The most obvious behavioural change is heightened aggression (Hollister-Smith et al., 2007). Musth bulls experience dramatic surges in circulating testosterone (Kahl & Armstrong, 2002, p. 159; Slotow et al., 2000, p. 425). Heightened levels of androgenic steroid hormones are known to mediate aggressive behaviour in mammalian species (Hall-Martin, 1987, p. 616). Specifically, aggressive behaviour during musth is associated with elevated levels of serum testosterone and dihydrotestosterone (Hall-Martin, 1987, p. 616). Indeed, the heightened levels of aggression associated with elevated testosterone levels indicates that this state is a physically competitive strategy (Ganswindt, Rasmussen, Heistermann, & Hodges, 2005, p. 89).

Musth: Role in Mating & Relationships With Females

It is believed that musth forms an important part of elephants reproductive strategy, elevating the ability of bulls to gain access to females in oestrous. As females represent a very scarce and highly mobile resource, male ability to locate and mate with them demonstrates intense intrasexual selection pressure (Hollister-Smith et al., 2007, p. 287). Indeed, studies of paternity success in musth males have revealed higher successes than expected. A study by Hollister-Smith et al. (2007) showed that 74% of calves in their study group were fathered by males known to be in musth, compared to 26% by males not known to be in musth (p. 292). This success is thought to be due to the fact that musth allows elephants to both locate females and signal sexual availability more successfully than under regular circumstances (Hall-Martin, 1987; Poole, 1989b). As males must locate oestrus females through an intensive searching effort (Poole & Moss, 1989), elevated wandering behaviour associated with musth heightens the chance that a male will encounter an oestrus female. As musth males urine-dribble and mark their scent as they travel, this may leave olfactory cues that alert others that they are close by. This may both attract prospective mates and deter potential competitors (Kahl & Armstrong, 2002, p. 169), thus contributing to the heightened reproductive success of musth males.

Significantly, both musth and reproductive success are positively related to age. Bull elephants represent the exception in mammalian reproductive success. Most mammals will reach their sexually reproductive peak at full body size, when physical condition and dominance rank are at their highest. As body condition deteriorates, they can no longer compete with younger males and their reproductive success declines. The consequence is that the breeding life span is a fraction of its full potential, due to competition with younger males. Elephants, however, show high mating and paternity success until late in life (Hollister-Smith et al., 2007, p. 293). Reproductive success of bulls increases with age due to the positive relationship between body size and dominance (Poole, 1989a, p. 151) and increased periods of musth (Hollister-Smith et al., 2007, p. 293). While non-musth, younger males can mate successfully, musth and age do have significant effects on paternity success – see Figure 4 (Hollister-Smith et al. 2007, p. 287). Additionally, female elephants also appear to prefer older, musth males. A study by Hollister-Smith et al (2007) found that females maintained close proximity to older males in musth whilst they were in oestrus. Musth thus increases bulls' ability to find oestrus females and signal sexual availability, an ability that increases with age due to the relationship between both dominance rank and musth length with age.

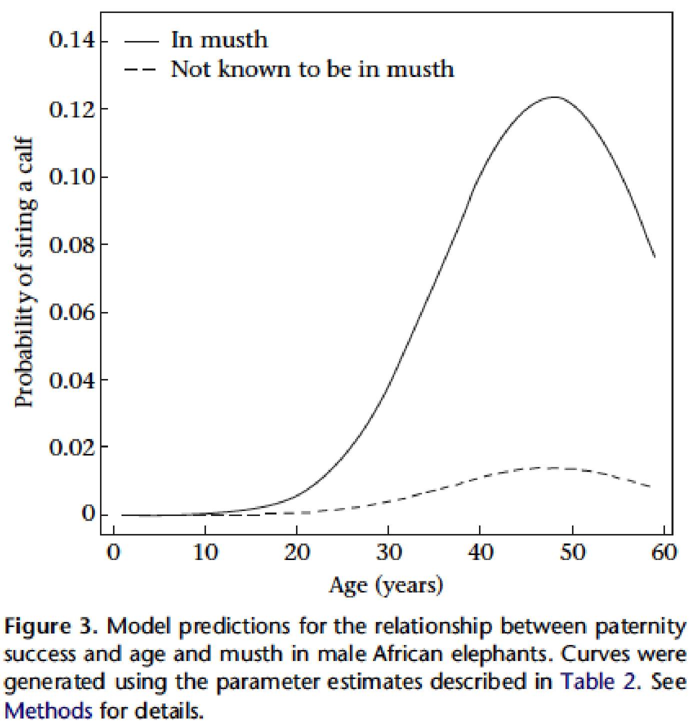

Figure 4.THE EFFECTS OF AGE AND MUSTH ON PATERNITY SUCCESS IN MALE AFRICAN ELEPHANTS. (Hollister-Smith et al., 2007, p. 293)

Musth: Impacts on Interactions With Other Males

To be advantageous in elevating an elephant's position within a hierarchy, musth must be communicable to others (Hall-Martin, 1987, p. 620). Urinary analyses have shown that males chemically signal musth, likely via the ketones 2-butanone, acetone and 2-pentanone, and 2-nonanone, which are considerably elevated during musth (Rasmussen & Wittemyer, 2002, p. 853). Musth is also communicated through behavioural changes, including musth rumbling, the musth walk, and temporal gland secretions (Rasmussen & Wittemyer, 2002, p. 858). These changes have two important effects on bull society, specifically temporary alterations to dominance hierarchies and the control of musth in young bulls.

If more than one bull seeks to mate with a female in oestrus, predetermined dominance hierarchies determine which bull will mate (Hall-Martin, 1987, p. 616). However, musth has the ability to alter these hierarchies by temporarily raising a bull's dominance status above those that would otherwise outrank him (Poole 1987; Poole 1989a). This ability reflects the 'resource value' placed on mating by each bull. Studies have demonstrated that the ability to correctly estimate one's relative role allows for violent conflict to be avoided (Poole, 1989a, p. 150). As musth is both chemically and behaviourally signaled, this allows bulls to assess their role in a potential conflict. As musth males are highly aggressive, it would be a poor adaptation for non-musth bulls to engage in conflicts as the risk (conflict) is higher than the potential gain (mating), particularly when they will themselves experience musth in the future. As such, small (and thus younger) musth males are able to dominate larger non-musth males when the time-specific value that is placed on winning the conflict by the musth male is large enough, and the value placed on winning by the larger male is small enough, to override the differences in their fighting ability. When this difference in value occurs, size-specific fighting ability is overridden by the high value placed on winning by the musth male, and the lower value placed on winning by the larger, non-musth male (Poole, 1989a, p. 150). Thus, the ability to signal musth can temporarily alter dominance hierarchies. However, musth does not nullify the hierarchy, as a young, musth male will still be unable to override the position of an older, musth male (Poole, 1987; Poole, 1989a).

Musth also has the apparent ability to allow older males to physically suppress musth in younger males (Hollister-Smith et al., 2007, p. 293; Poole 1989a; Slowtow et al., 2000). In the early 1990s, Pilanesberg National Park, South Africa, experienced issues when young male elephants entered musth and became extremely aggressive, killing over 40 rhinoceroses and becoming aggressive toward tourists. They entered musth at the age of 18 years old for periods of up to five months - periods that would be unusually long for males twice that age (Slotow et al., 2000, p. 425). These elephants were orphans from culling operations in Kruger National Park, who as a result has not grown up in association with older males (Slotow & van Dyk, 2001; Slotow et al., 2000). In an attempt to resolve the situation, six older bulls were introduced into the system. These males suppressed the musth behaviour in the younger males, and subsequently their violent behaviour (Slotow et al., 2000).

This situation is demonstrative of the idea that older bulls actually control musth in younger males. Field studies by Joyce Poole revealed that small males experienced musth more often in the absence of higher-ranking males, while smaller males were seen out of musth significantly more often in the presence of higher-ranking musth males (Poole, 1989a, p. 143). Further studies have shown that bulls can switch on urine dribbling (i.e., enter musth) within hours of finding an estrous female, and switch urine dribbling off (i.e., come out of musth) within just minutes of encountering a higher ranking musth bull (Ganswindt et al., 2005, p. 89; Poole, 1987; Slotow et al., 2000, p. 425). This reflect the principles of ‘assessment theory’, which predicts that natural selection should favour individuals that are able to assess both the costs and benefits of fighting and their probability of winning, and adjust their behaviour accordingly. As such, the 'control' of younger males is believed to be an adaptive strategy wherein by dropping out of musth in the presence of larger musth males, younger males can avoid the high costs of being in musth and reserve this period for when paternity success is higher; i.e. when no larger males are in musth (Poole, 1987a, p. 150). Indeed, lower-ranking males can increase the relative payoffs of musth by retracting their announcements of aggression in the vicinity of older musth males, who are more likely to win in an altercation, thus increasing immediate survival and therefore the long-term reproductive fitness of the younger male (Poole, 1987a, p. 150).

Human-elephant Conflict

Conflicts arise between species when they share a limited resource (Ngene & Omondi, 2008, p. 77). As a result of rapidly growing human populations, many species of wildlife are facing intense competition with people for space and resources, resulting in increasing levels of human-wildlife conflict (Pimm, Russell, Gittleman, & Brooks, 1995; Balmford et al., 2001). African elephants are no exception - elephants and humans conflict over water, space, and food (Ngene & Omondi, 2008, p. 77). Indeed, conflicts occur wherever elephants live, as their large ranges bring them into contact with an ever-expanding human population (Desai & Riddle, 2015). Here we examine human-elephant conflict (HEC) to identify its dynamics and drivers and potential connections to elephant behaviour and the ivory trade.

<u>What Is HEC & Why Is It A Problem</u>

What is Human-elephant Conflict?

Human-elephant conflict is defined by the Kenya Wildlife Service as: "any and all disagreements or contentions relating to destruction, loss of life or property, and interference with rights of individuals or groups that are attributable directly or indirectly to elephants," (1994). This can take many forms, including: when elephants feed on crops; destroy homes or farms; injure or kill people; kill livestock; disturb activities such as travel to work and school; and retaliatory human actions (Chartier, Zimmermann, & Ladle, 2011, p. 528; Sitati, Walpole, Smith, & Leader-Williams, 2003, p. 668). Crop raiding, however, is the main form of conflict between humans and elephants (Sitati et al., 2003, p. 668; Williams, Johnsingh, & Krausman, 2001, p. 1101), and will be the focus of our considerations.

Crop raiding is generally divided into two forms: opportunistic and habitual. Opportunistic crop raiding occurs where crop protection is either absent or minimal, and elephants with access to such crops will see them as a concentrated food source. This form is common throughout agricultural areas and is the easiest form of crop raiding to manage, with little to no impact on elephant well-being. Issues arise when elephants move from opportunistic to habitual crop raiding (Desai & Riddle, 2015). When opportunistic raiders become accustomed to ineffective or routine crop protection, they may become habitual raiders. These elephants have lost their fear of humans and usual crop protection methods, and have learned how to negotiate barriers. Elephants become persistent and problematic as raiding becomes habitual, or even obligatory - when elephants have inadequate resources in their home ranges, resulting in dependence on raiding for nutritional needs (Desai & Riddle, 2015). As habitats are continually degraded, fragmented, and even lost, elephants begin to raid of out necessity. As such, the degree and severity of crop raiding will often reflect the extent of habitat loss/degradation. In such circumstances, elephants become extremely difficult to contain and pose a major issue to elephant conservation (Desai & Riddle, 2015).

Why is Human-elephant Conflict a Problem?

HEC is considered one of the most serious threats to elephant conservation in Africa today (Sitienei, Jiwen, & Ngene, 2014, p. 323; Nelson et al., 2003, p. 1). Not only do retaliation killings pose a serious threat to the survival of elephant populations, but HEC creates negative attitudes toward elephants, thus adversely affecting conservation efforts and creating conflict between local farmers and wildlife authorities (Amwata & Mganga, 2014, p. 23; Woodroffe, Thirgood, & Rabinowitz 2005). Indeed, HEC has negative impacts on people, elephants, and conservation in general (Nelson et al., 2003, p. 1).

EFFECTS ON PEOPLE

Crop-raiding is considered the most detrimental form of HEC (Naughton-Treves, 1997), inflicting both direct and indirect costs upon people. Direct costs include the loss of crops, property damage, and physical injury or loss of life (Jadhav & Barua, 2012). Indirect costs include both the money and time taken to avoid and prevent damage to crops and homes, as well as the psycho-social well-being of communities constantly under threat by such conflicts (Graham, Notter, Adams, Lee, & Ochieng, 2010, p. 435; Jadhav & Barua, 2012).

The direct and high financial costs of crop raiding by elephants can be detrimental for individuals, particularly in countries where GDP is low and tightly connected to farming (Eba'a Ayi et al., 2008). For example, a study by Inogwabini et al. (2013) in the Democratic Republic of the Congo estimated that in the Malebo region, mean income losses from crop raiding totaled US $75,600 annually. This study considered 1,500 fields, of which ~15% had been raided. These losses are enormous losses for such communities (Inogwabini, Mbende, Bakanza, & Bokika, 2013, p. 62). With similar findings reported across other sites in Africa (Inogwabini et al., 2013, p. 62), the financial threat to small-scale farmers is wide reaching.

It has been found that farmers experiencing the highest risk for crop raiding reside at the edges of protected areas (Naughton et al., 1999). Significantly, it is these farmers who are most likely to retaliate and kill elephants (Naughton et al., 1999). Figure 5 outlines various socioeconomic and ecological factors that play a role in determining the tolerance or intolerance of crop raiding. It demonstrates that self-sustaining farmers with scarce lands, little opportunity for alternative incomes or protection measures, and who are facing high levels of crop damage are the least likely to tolerate problem animals and thus conduct retaliatory killings. This is due to the fact that an individual's capacity to cope with crop loss is affected by environmental, social, and technological factors. While wealthier individuals have heightened capabilities to manage losses, poorer individuals suffer 'compounding vulnerability'. These poorer farmers tend live in the riskiest areas for crop raiding and have fewer resources to cope with the resulting losses (Naughton et al., 1999). Where wealthier farmers can hire guards or build barriers to protect their crops (Naughton et al., 1999), poorer farmers with smaller landholdings cannot buffer themselves from wildlife conflict nor hire additional labour to protect their crops. As these farmers are also generally those who are in closest proximity to protected areas - as these lands are less costly and less desirable - their vulnerability compounds (Naughton et al., 2009).

Tolerance		Intolerance
	Socioeconomic Factors	
Abundant Land	**Land Availability**	Scare Land
God, Self, Community	**Ownership of Pest**	Government or Elite
Varied, Unregulated	**Coping Strategies**	Narrow, Highly Regulated
Community, Group	**Social Unit Absorbing Loss**	Individual, Household
Abundant, Inexpensive	**Labor Availability**	Rare, Expensive
High	**Game Value of Pest**	Low
Low	**Capital and Labor Investment in Crop**	High
Subsistence	**Type of Crop Damaged**	Cash or Famine Crop
Various	**Alternative Sources of Income**	None
	Ecological Factors	

Small, Non-threatening	**Size of Raiding Species**	Large, Dangerous
Early	**Timing Relative to Harvest**	Late
Solitary	**Pest Group Size**	Large
Cryptic	**Damage Pattern**	Obvious
Narrow, One Crop	**Crop Preference of Pest**	Any Crop
Leaves Only	**Crop Part Damaged**	Fruit, Tuber, Pith, Grain
Diurnal	**Circadian Timing of Raid**	Nocturnal
Self-limited	**Crop Damage in Each Raid**	Unlimited
Rare	**Frequency of Raiding**	Chronic

Figure 5. SOCIOECONOMIC AND ECOLOGICAL FACTORS RELATED TO THE TOLERANCE OR INTOLERANCE OF CROP RAIDING (Naughton et al., 1999, p. 20).

EFFECTS ON ELEPHANTS

While retaliation against HEC of all forms exist, retaliation killings resulting from crop raiding are a major source of elephant mortality. Although elephants are not the only 'pest' species in Africa, nor the most damaging overall, elephants inflict severe and localized damage within affected areas and have the ability to destroy entire fields of crops in a single raid (Barnes, Asika, & Asamoah-Boateng, 1995; Hillman-Smith, de Merode, Nicholas, Buls, & Ndey 1995; Lahm, 1996; Naughton-Treves, 1998). As such, their destructive abilities are often viewed as much worse than other pests. Their threat is amplified when we consider that as large, strong - and during musth, aggressive - animals, elephants pose a very real threat to the safety of people. As such, the responses we see to HEC are often much more aggressive and devastating for elephant populations than for other problem animals.

As HEC intensifies, tolerance wanes (Heffernan & Cuong, 2004). With high costs of HEC, responses such as injuring or killing 'problem' elephants become increasingly common (Chiyo, Moss, Archie, Hollister-Smith, & Alberts, 2011, p. 788). The result is that intensified HEC can lead to local extirpation of small elephant herds (Heffernan & Cuong, 2004). Unfortunately, compounding the threats of habitat loss and heavy poaching, human-elephant conflict is now recognized as a major threat to elephant conservation due to retaliation killings

(Sitati et al., 2003). Indeed, mortality from conflict is accelerating the demise of many wildlife populations that are already experiencing significant declines from other human-induced pressures (Andren et al., 2006). Conservationists have warned that HEC is second only to the ivory trade in terms of working against the conservation of elephants (Barnes, 1999), and as such represents a very real danger to elephants.

THREATS TO CONSERVATION

In addition to the risks posed directly to people and elephants, HEC has a negative effect on elephant conservation efforts overall due to the stifling of local support. Conflict between humans and wildlife in general is considered one of the highest ranking threats to conservation in Africa, alongside the loss of habitat and illegal hunting (Amwata & Mganga, 2014, p. 24). These conflicts present very real challenges to local, national, and even regional government and non-governmental conservation efforts (Treves & Karanth, 2003). HEC specifically has become a very important issue for conservationists in the past three decades (Sarker & Roskaft, 2010), and is now a major obstacle to community support for conservation, as the negative attitudes of local peoples can severely undermine conservation initiatives (de Boer & Baquete, 1998; Gillingham & Lee, 1999; Naughton-Treves 1997; Nchanji and Lawson, 1998; Newmark, Manyanza, Gamassa, & Sariko, 1994).

The dynamics of HEC and elephant management can have negative impacts on surrounding communities and thus degrade local support for conservation initiatives. For example, despite the disruption of farmlands and destruction of crops by elephants, people living adjacent to parks are denied access to the protected areas while being expected to tolerate the elephants housed there. This has been seen to incite anger and desperation amongst local communities who have to bear the costs associated with elephants while receiving little to no compensation for the damages they inflict (Amwata & Mganga, 2014, p. 24). Communities viewing elephants as a threat to their lives and livelihoods thus often resent both the animals and the protected areas that act as their refuges (Naughton et al., 1999). Due to the extreme damage that elephants can cause, many African communities both fear and detest elephants (Barnes et al., 1997). This is a common theme throughout the region, where many, if not most, local farmers would eliminate elephants from their environments if given the chance (Naughton et al., 1999). As such, HEC represents a myriad of threats to local people, African elephants, and conservation in general.

Drivers & Dynamics of HEC

Drivers

While no single factor nor condition explains any form of HEC (Naughton et al., 1990), the main, overarching driver of human-elephant conflict is habitat alteration, including fragmentation, degradation, and loss. As Nelson et al. (2003) argue, HEC is a direct outcome of the excessive changes in land-use patterns and the continued conversion of natural elephant habitat to human use. In recent decades, human-wildlife conflict in general has been increasing in Africa due to the increasing human population and expansion into natural areas (Akama, Lant, & Burnett, 1995; Siex & Strushsaker, 1999, p. 1009). Urbanization, agricultural growth, and encroachment upon elephant habitat all put humans in closer proximity to elephants (Gunn et al., 2013, p. 130) while simultaneously destroying habitat. All of these processes have resulted in competition between people and elephants for increasingly scarce land (Barnes, 1996; Gachago & Waithaka, 1995; Graham, 1973; Hill, 1997; Kiiru 1995; Tchamba, 1996; Thouless, 1994; Thouless & Sakwa, 1995), thus increasing incidences of HEC (Siex & Struhsaker, 1999, p. 1009). While not always directly the culprit, habitat loss, fragmentation, and degradation play a vital role in driving HEC as it pushes elephants and humans into closer proximity, removes and denies access to home ranges for elephants, and destroys access to natural food and water sources.

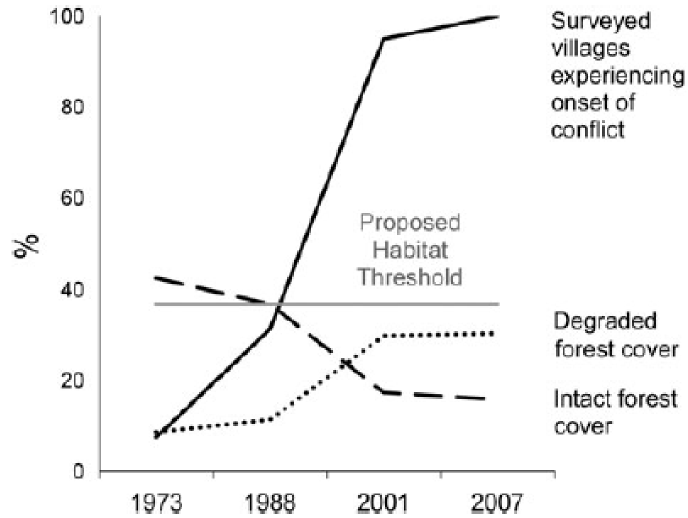

Fig. 4 Trends in habitat loss and human–elephant conflict. The percentage total intact forest cover, percentage total degraded forest cover and percentage total surveyed villages claiming to experience the onset of conflict in each of the years are shown. The proposed conflict threshold, in grey, is at c. 37% forest cover.

Figure 6. RELATIONSHIP BETWEEN PERCENTAGE OF TOTAL VILLAGES REPORTING CONFLICT AND PERCENTAGE OF TOTAL DEGRADED FOREST COVER (Chartier et al 531).

Habitat loss plays such a large role in wildlife conservation that researchers have identified thresholds, beyond which any small additional loss of habitat can have large effects on the extinction risk of a population (Chartier et al., 2011, p. 528). When examining thresholds between human and elephant densities, Hoare and du Toit (1999) found that where there were 15 people in a $1km^2$ area, representing a transformation of land use of 40-50% for human activity, elephants disappeared from the landscape. Further studies demonstrate that there is a highly significant, negative correlation between the percentage of total forest cover and the percentage of total survey villages reporting conflict with elephants (Chartier et al., 2011, p. 530). Chartier et al. (2011) found a highly significant correlation between the percentage of total villages reporting conflict and the percentage of total degraded forest cover - see Figure 6 (Chartier et al., 2011, p. 530). The results of this study suggest that a critical threshold for forest cover may exist between 30 and 40%, below which conflict expanded from a few villages to the majority of those surveyed (Chartier et al., 2011, p. 531). This 30-40% forest cover threshold is similar to those found in other studies (Chartier et al., 2011, p. 531).

The destruction and loss of habitat also influences elephants' needs for space in terms of social organization, ranging behaviours, and ecological needs (Desai & Riddle, 2015). Clans of elephants have well-defined home ranges, to which they show strong fidelity. Within these overarching ranges often exist seasonal ranges, for which elephants follow specific migratory routes. As such, elephants are fixed to their spatial surroundings and do not openly move across the landscape (Desai & Riddle, 2015). Unfortunately, even when there are clusters of protected areas, home ranges are not necessarily protected (Baskaran et al., 1999; Desai, 1991). Settlements thus not only contribute to the loss of habitat, but deny the use of significantly large and preferred areas (Desai & Riddle, 2015).

Perhaps the most detrimental outcome of habitat alteration is the removal of natural forage for elephants that leads to obligatory crop raiding. The change from nomadic pastoralism to crop farming specifically has resulted in higher incidences of crop raiding (Ngene & Omondi, 2009, p. 78). This change, in combination with a growing human population, has not only resulted in increasing proximity with elephants, but a need for elephants to rely on these crops (Gubbi, 2009). Elephants disperse from their home range when their range or social organization is severely disrupted (Desai & Riddle, 2015, p. 16). Such dispersals lead to issues of HEC as there is generally no suitable habitat outside the existing elephant range, thus leading elephants to become dependent on crops for survival (Desai & Riddle, 2015, p. 16). In areas with degraded habitat, crops may offer greater nutritional contents and palatability than wild forage (Sukumar

& Gadgil, 1988). Significantly, the majority of elephants raid of necessity, and not as a foraging strategy. This need to raid is a direct outcome of the loss or degradation of part or most of their home ranges, to a point where the resources available no longer support their dietary needs (Desai & Riddle, 2015, p. 15). Elephants that are not significantly affected by the loss or degradation of their home range do not usually raid crops (Desai & Riddle, 2015, p. 15).

In addition to habitat loss and degradation, habitat fragmentation also affects levels of HEC. Habitat fragmentation is the use of land by humans that breaks up large habitat patches into smaller fragments (Desai & Riddle, 2015). The danger lies in the fact that the true impact of fragmentation is not recognized due to the 'small' extent of habitat that appears to be lost (Desai & Riddle, 2015). However, where habitats are fragmented, rather than completely lost, access to critical resources (i.e. water) is often denied (Desai & Riddle, 2015). Fragmentation also divides elephant home ranges, both for clans and individuals. In these circumstances, elephants are unable to move across their home range without negatively affecting agriculture or human-use areas, thereby igniting HEC issues (Desai & Riddle, 2015). Additionally, people may place their homes or fields in areas along elephant migratory routes (Hoare, 1998; Hoare, 2000). Unfortunately, with the lack of any overarching mechanism that monitors and guides development, while taking elephants into account, most development has compounded the issues resultant from habitat loss and degradation with habitat fragmentation (Desai & Riddle, 2015).

The combined impacts of habitat alteration have intensified issues of HEC. With the natural habitat of elephants diminishing, pushing them into closer proximity with humans and forcing them to consume crops as a source of food, local tolerance erodes and leads to retribution killings (Webber et al., 2011, p. 250). This intensifies the pressure that habitat loss already puts on this endangered species, thus posing a major issue not only to HEC but elephant conservation in general.

Dynamics

While HEC occurs throughout the African elephant range (Sitati et al., 2003, p. 668), certain patterns exist. Research on crop raiding specifically has begun to identify these patterns in an attempt to assess risk and inform management. Identifying the spatial, temporal, and demographic dynamics of crop raiding allows us to understand the role that elephant behaviour plays in this issue, as well as the way that poaching may intensify it.

SPATIAL PATTERNS

Research on crop raiding has revealed specific spatial patterns of occurrence. One such pattern is that crop raiding occurs more often in close proximity to protected areas that act as elephant refuges (Barnes et al., 1995; Bhima, 1998; Parker & Osborne, 2001). In fact, conflict between people and wildlife in general more often occurs outside protected areas as the ranges of people and animals overlap (Siteinei et al., 2014, p. 323). For elephants, 70% of their range as of 2007 occurred outside of protected areas (Siteinei et al., 2014, p. 323). A study conducted by Graham et al. (2010) in Laikipia, Kenya found that crop-raiding intensity was significantly correlated with the distance to daytime elephant refuges, as well as human settlement density and percentage of cultivated land (p. 440). This study found that on average, incidents occurred within 1.54 km of areas of natural habitat, where elephants were able to hide during the day - ‘daytime elephant refuges’ (Graham et al., 2010, p. 435). This demonstrated that distance from such refuges was a significant predictor of crop raiding (Graham et al., 2010, p. 441). This same pattern was found in a study by Nelson et al in 2003. This is significant when we consider that those farmers living at the edge of reserves are those that are small-scale, subsistence farmers with little ability to withstand crop-raiding and are more likely to violently retaliate.

The size of the area under cultivation is also a significant determinant of crop-raiding risk. Graham et al found that small-scale farms at densities below 20 dwellings per km^2 were particularly vulnerable to crop-raiding. Above this threshold, raiding tended to decline (Graham et al., 2010, p. 435). This 'area under cultivation' predictor was also found to be significant by Sitati et al. (2003), who studied the ability to predict spatial patterns of HEC. Such a relationship between crop raiding and settlement density demonstrates the role of landscape structure in identifying levels of vulnerability to crop raiding in small-scale farmers (Graham et al., 2010, p. 440).

A final spatial determinant of HEC is the disruption of elephant migration routes and access to water. This is particularly important in light of ongoing habitat fragmentation. A study be Inogwabini et al. (2013) in the Malebo region of the Democratic Republic of Congo found that fields that were most damaged by elephants were located along permanent elephant trails leading to permanent water points (p. 62). This implied that elephants searching for water likely came across the fields containing nutrients they required and damaged them. While in this study water retreated to permanent water points during the dry season, other studies across Africa in different ecological locations have also found permanent water points to determine elephant movement (Tchamba, 1998; Vanleeuwe & Gauthier-Hion 1998). Further, elephant movement in general is influenced by factors such as searching for food, water, and minerals, in addition to being affected by levels of disturbance (Amwata & Mganga, 2014, p. 24). As this movement may be regular between wet and dry seasons (Amwata & Mganga, 2014, p. 24), identifying movement patterns in relation to human settlements is important in determining risk of crop-raiding or other forms of HEC.

TEMPORAL PATTERNS

Certain temporal patterns have been identified that allow us to understand when elephants may be most inclined to crop raid and thus aid in management of farms to avoid risk. These patterns relate to lunar cycles, migration patterns, and seasonal influences.

The hypothesis that elephants alter their behaviour to reduce the risk of encountering humans is important when we consider the temporal patterns of crop raiding. For animals in general, activity patterns through the 24h daily cycle are commonly related to season (Hill et al., 2003), food availability and access (Donati, Bollen, Borgognini-Tarli, & Ganzhorn, 2007), and predation risk (Lang, Kalko, Römer, Bockholdt, & Dechmann, 2006). Elephants are active both during the day and night, however they almost exclusively raid crops at night (Graham, Douglas-Hamilton, Adams, & Lee, 2009; Hillman-Smith et al., 1995; Sitati et al., 2003). This suggests that they avoid the risks associated with diurnal human activities (Gunn et al., 2013, p. 130). For example, Gunn et al (2013) studied the link between lunar phases and crop raiding. They found that elephants avoided crop raiding closer to the full moon, when visibility was highest. Similar results were found by Barnes et al. (2007), wherein nocturnal crop raiding decreased on brightly lit nights. Well lit nights give humans a visual advantage that elephants may not be willing to risk (Gunn et al., 2013, p. 130), thus weather and lunar cycles may affect vulnerability.

It has been found that seasonal patterns of crop raiding also exist, by influencing both the natural migration patterns of elephants and cultivation patterns of farmers. The natural foraging and migration movements of elephants allow identification of periods of risk for farmers. As elephants tend to shift their movement patterns in response to availability of water and forage (Amwata & Mganga, 20140, p. 24), seasonal changes have important influences on the likelihood of encountering crops and therefore crop raiding. For example, in Malebo (DRC), the most damaged fields were located along permanent elephant trails that led to permanent water points. This implies that elephants searching for water came across fields with valuable nutrients and raided them (Inogwabini et al., 2013, p. 62). Parker and Osborne (2001) also found that the majority of crop-raiding incidents occurred along major rivers, as elephants move to areas with sufficient water sources during the dry season. Further, seasonal crop raiding patterns have been found to be associated with the specific crop type (Sukumar 1989 and 1990 in Webber et al 244), elephants' attraction to high nutrient quality, (Sukumar 1989 and 1990, Chiyo et al 2005 in Webber et al 244), the high water retention of cultivated crops in comparison with wild vegetation (Sukumar 1989 and 1990, Chiyo et al 2005 in Webber et al 244), and seasonal reductions in wild grass availability and quality (Osborn 2004 in Webber et al 244).

The cultivation patterns of farmers combine with the behavioural effects of rainfall patterns to create a 'window' of crop-raiding elephants (Graham et al., 2010, p. 436). Two studies, one by Siteinei et al and another by Ngene and Osmondi, demonstrate the relationship between seasonal elephant movements and seasonal patterns of farmers. They both revealed that during the drier months, elephants moved into forested areas as the water supplies away from forests dessicate and the quality of browse and grazing decreases (Siteinei et al., 2014, p. 328). While crop raiding is not directly affected by rainfall, it is an indirect determinant due to its effects on elephant movement through food abundance and quality (Siteinei et al., 2014, p. 328). In both studies, this coincided with the time that maize and bean crops were maturing (Ngene & Osmondi, 2009, p. 84; Siteinei et al. 2014, p. 328). Indeed, Ngene and Osmondi found that the total number of farms raided by elephants was higher during the drier months (Ngene & Osmondi, 2009, p. 85).

DEMOGRAPHIC PATTERNS

In addition to spatial and temporal patterns, the demographics of raidings elephants reveal important characteristics and patterns significant to managing crop raiding.

Various researchers have noted the significance of a sexual composition to the elephants involved in HEC conflicts (Graham et al., 2010). In most polygynous species that have been studied, more males than females take crop raiding risks (Chiyo et al., 2011, p. 793). Such sex differences in crop raiding composition may result from the differences in the costs and benefits of such actions. Because males in polygynous social systems have greater variance in their reproductive success than females, sexual selection is expected to enhance behaviours that increase this reproductive success. In male elephants, this success is highly influenced by social dominance and the onset and duration of musth (Poole & Moss 1981; Poole, 1989b; Hollister-Smith et al., 2007). These, in turn, are dependent on age and nutritional state (Poole 1989b; Sukumar 2003). Sexual selection should therefore favour males that adopt foraging strategies that maximize nutrient gains that can be allocated for both growth and the maintenance of musth (Chiyo et al., 2011, p. 794). Indeed, it has been argued that males will adopt behavioural strategies of risk-taking to optimize nutrient intake and maximize reproductive success (Hoare, 1999; Sukumar & Gadgil, 1988). Conversely, females are more likely to incur higher risks from raiding than males, as they have dependent offspring, and as such the gains may not be enough to offset the risks (Chiyo et al., 2011, p. 794).

High-risk and high-gain foraging strategies are consistent with natural foraging behaviour in male sexually size-dimorphic mammals. Males are more likely to seek more abundance or high quality forage at the risk of predation, while females may sacrifice forage abundance to minimize predation risk when there is a positive correlation between the abundance of food and predation risk (Apollonio, Ciuti, & Luccarini, 2005; Bleich, Bowyer, & Wehausen, 1997; Hay, Cross, & Funston, 2008; Mac-Farlane & Coulson, 2007). A study by Chiyo et al. (2011) in Amboseli National Park highlighted the importance of sex in crop raiding behaviour. They found that raiding occurred around the park in spite of the fact that there were relatively large tracts of natural range available. They concluded that raiding behaviour in male elephants is a manifestation of natural high-risk, high-gain foraging strategies that are commonly observed in the males of many polygynous mammals (p. 794).

The same conclusions were reached by Hoare (1999), who suggested that in relation to their inability to identify strong spatial correlates for HEC, HEC was as much a feature of unpredictable male elephant behaviour than underlying spatial patterns. This once again reflects that males may be more willing to take risks for nutritional rewards than females (Sitati et al., 2003, p. 668). A study by Sitati et al. (2003) also revealed that it is very likely that all-male groups are less predictable than female-led groups (p. 671). They concluded that single males are likely even less predictable, therefore in areas with higher proportions of single males involved in HEC there may be few, if any, spatial correlates identifiable (Sitati et al., 2003, p. 671). This is important when we consider that male elephants are known to stock up on nutrients before entering musth in order to prepare for the period of nutrient withdrawal. Thus, single, pre-musth male elephants may present a specific crop-raiding threat due to their unpredictable nature, risk-taking behaviour, and need to intake high amounts of energy.

While HEC is an extremely complicated issue, if we base our understanding of the driving factors of habitat loss, alteration, and fragmentation, as well as the spatial, temporal, and demographic patterns in the dynamics of elephant behaviour we begin to understand how and why it happens. This in turn gives us important insight into how certain factors - such as the ivory trade - may actually accentuate the issue. We will now turn to this connection, and examine the way that the disruption of bull adolescence through the removal of older males may in fact exacerbate crop-raiding behaviour and compound the problem.

Convergence: How Poaching May Exacerbate HEC

The relationship between the ivory trade, elephant behaviour, and HEC begins with the removal of older males by poachers. As highlighted in the overview of the ivory trade, the desire to supply ivory is driven by low economic opportunities, poor governance, and high corruption. As such, poaching rates are highest in areas where governance is lacking and economies are poor. As a result of ivory pricing, preference for males with the largest tusks causes poachers to select for older bulls, due to the indeterminate growth of elephants. Following heavy poaching pressure, we can assume the demographic distribution of elephant populations will begin to change in hot spot poaching areas as the number of older males decline. As a result of such demographic alterations we can also assume that, much as in cases where older males have been culled, we will begin to see negative behavioural changes in younger males.

Specifically, two changes are important: the removal of the adolescent learning phase and early entry into musth. The removal of an adolescent learning phase means that younger males will have less, if any, access to the cultural transmission of knowledge from older males that allow them to learn important behavioural strategies, namely how to properly forage. Additionally, it removes the sexually mature yet non-reproductive stage that is believed to aid in brain development and social growth. As such, younger males without the association with older males are denied this critical period of development and the benefits it offers for both long-term survival and reproductive success.

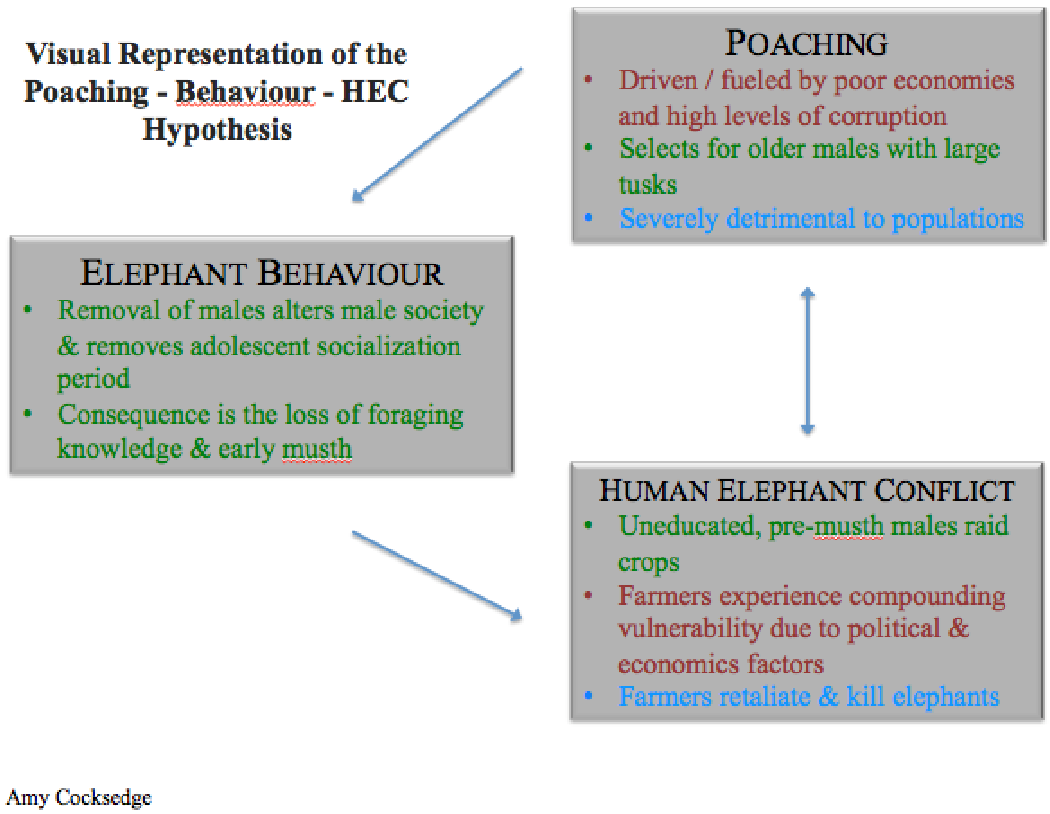

Figure 7. VISUAL REPRESENTATION OF THE RELATIONSHIP BETWEEN POACHING, ELEPHANT BEHAVIOUR, AND HUMAN-ELEPHANT CONFLICT.

In addition to the removal of the adolescent learning period, young males without normal interactions with older males are likely to enter musth early. As demonstrated in Pillanesberg, the removal of older males also removes the chemical control of this phenomenon in younger males. Without contact with older, musth males, younger males enter musth early and for extended periods of time. As pre-musth males must significantly increase their nutrient intake, we understand how this issue compounds with the removal of the adolescent learning period to impact HEC. Young males entering musth due to the lack of older musth males while simultaneously being denied the cultural learning period about foraging skills may present a unique crop raiding threat. The need to excessively forage combined with the lack of knowledge on profitable areas may make young, musth males more prone to crop raid.

The dynamics of HEC also offer insight this relationship. As studies have found, bulls demonstrate more unpredictable behaviour than females, and are also more likely to partake in risky behaviour for the reward of food. These behaviours are often considered influential to crop raiding by male elephants. Combined with the loss of an adolescent learning period and early entry into musth, this presents a compounding issue to crop raiding management.

Understanding the dynamics of HEC offers further insight into the spatial occurrence of crop raiding and its relationship with poaching. As highlighted, small-scale farmers at the edges of reserves are not only at the highest risk of HEC but are most likely to conduct retaliatory actions. This placement and vulnerability is a result of low economic opportunities to purchase better land and protection measures. They are also more likely to retaliate against problem elephants due to the lack of support from the government following such detriment. Significantly, low economic status and poor governance are the same situations that drive the desire to participate in the illegal ivory trade. As such, the hot spots for poaching are likely to overlap with areas where farmers are at highest risk for crop raiding and highest likelihood for retaliatory actions.

The likelihood thus exists that the issues of poaching and HEC are in fact related, compounding threats to elephant conservation. Understanding the dynamics of ivory supply, human-elephant conflict, and elephant behaviour demonstrates that these issues likely have an intimate relationship wherein poaching influences the likelihood of crop raiding, thus exacerbating levels of HEC and retaliatory actions.

Conclusions

Taking a multidisciplinary approach through a political ecology framework while incorporating animal behaviour demonstrates how the ivory trade presents a unique issue to elephant conservation. Not only does it present the direct threat of offtake for the ivory trade, but the disruption of male society presents challenges to young males which may lead to higher instances of crop raiding and retaliation killings. Significantly, poaching, farmers' vulnerability, and the likelihood of retaliation are all consequences of the political and economic situations in countries where elephants range. As such, the ivory trade, elephant societies, and human-elephant conflict all exist in a compounding and negative relationship as highlighted by a political ecology approach to conservation. With the current myriad of threats to the survival of African elephants, understanding the dynamics of these threats is vital to their conservation. As both the ivory trade and HEC present the two most prominent threats to elephant survival, the possibility that they are connected through elephant behaviour and driven by politics and economics is an important realization for conservation and highlights the importance of multidisciplinary approaches to wildlife conservation.

Appendix

A. Classification of hot spot countries by GDP

Country Classification	Country	GDP per capita 1981 (USD)	GDP per capita 2014 (USD)	Graphical Movement	Income Classification 2015
Supply/Hot Spot					
	Gabon	5,166.3	10,208.4		Upper Middle
	Republic of the Congo	1,074.4	3,137.8		Lower Middle
	Cameroon	829.9	1,429.3		Lower Middle
	Equitorial Guinea	157.7	17,430.1		High
	Central African Republic	269.9	371.1		Low
	Chad	190.2	1,024.7		Low
	DR Congo	463.5	440.2		Low
	South Sudan	482.1	1,097.3		Low
	Kenya	405.6	1,358.3		Lower Middle
	Tanzania	No Data	998.1		Low
	Mozambique	288.8	602.1		Low
Intermediary					
	Hong Kong/China	5,991.3	40,169.6		High
	Thailand	720.9	5,519.4		Upper Middle
	Kenya	405.6	1,358.3		Lower Middle
	Tanzania	No Data	998.1		Low
Demand	China	5,991.3	40,169.6		High

	Philippines	731.7	2,870.5		Lower Middle
	Thailand	720.9	5,519.4		Upper Middle
	Viet Nam	No Data	2,052.3		Lower Middle
	United States	13, 993.1	54,629.5		High

(Christy, 2015; GDP Per Capita, 2017; Patela et al., 2015, p. 7949; Strauss, 2015)

B. Transparency International's Corruption Perception Index 2016 – Country Ratings

RANK	COUNTRY/TERRITORY	SCORE	RANK	COUNTRY/TERRITORY	SCORE
1	Denmark	90	24	Bahamas	66
1	New Zealand	90	24	Chile	66
3	Finland	89	24	United Arab Emirates	66
4	Sweden	88	27	Bhutan	65
5	Switzerland	86	28	Israel	64
6	Norway	85	29	Poland	62
7	Singapore	84	29	Portugal	62
8	Netherlands	83	31	Barbados	61
9	Canada	82	31	Qatar	61
10	Germany	81	31	Slovenia	61
10	Luxembourg	81	31	Taiwan	61
10	United Kingdom	81	35	Botswana	60
13	Australia	79	35	Saint Lucia	60
14	Iceland	78	35	Saint Vincent and The Grenadines	60
15	Belgium	77	38	Cape Verde	59
15	Hong Kong	77	38	Dominica	59
17	Austria	75	38	Lithuania	59
18	United States	74	41	Brunei	58
19	Ireland	73	41	Costa Rica	58
20	Japan	72	41	Spain	58
21	Uruguay	71	44	Georgia	57
22	Estonia	70	44	Latvia	57
23	France	69	46	Grenada	56

RANK	COUNTRY/TERRITORY	SCORE	RANK	COUNTRY/TERRITORY	SCORE
47	Cyprus	55	69	Greece	44
47	Czech Republic	55	70	Bahrain	43
47	Malta	55	70	Ghana	43
50	Mauritius	54	72	Burkina Faso	42
50	Rwanda	54	72	Serbia	42
52	Korea (South)	53	72	Solomon Islands	42
53	Namibia	52	75	Bulgaria	41
54	Slovakia	51	75	Kuwait	41
55	Croatia	49	75	Tunisia	41
55	Malaysia	49	75	Turkey	41
57	Hungary	48	79	Belarus	40
57	Jordan	48	79	Brazil	40
57	Romania	48	79	China	40
60	Cuba	47	79	India	40
60	Italy	47	83	Albania	39
62	Sao Tome and Principe	46	83	Bosnia and Herzegovina	39
62	Saudi Arabia	46	83	Jamaica	39
64	Montenegro	45	83	Lesotho	39
64	Oman	45	87	Mongolia	38
64	Senegal	45	87	Panama	38
64	South Africa	45	87	Zambia	38
64	Suriname	45	90	Colombia	37
			90	Indonesia	37

RANK	COUNTRY/TERRITORY	SCORE
90	Liberia	37
90	Morocco	37
90	The FYR of Macedonia	37
95	Argentina	36
95	Benin	36
95	El Salvador	36
95	Kosovo	36
95	Maldives	36
95	Sri Lanka	36
101	Gabon	35
101	Niger	35
101	Peru	35
101	Philippines	35
101	Thailand	35
101	Timor-Leste	35
101	Trinidad and Tobago	35
108	Algeria	34
108	Côte d'Ivoire	34
108	Egypt	34
108	Ethiopia	34
108	Guyana	34
113	Armenia	33
113	Bolivia	33
113	Vietnam	33
116	Mali	32
116	Pakistan	32
116	Tanzania	32
116	Togo	32
120	Dominican Republic	31
120	Ecuador	31
120	Malawi	31
123	Azerbaijan	30
123	Djibouti	30
123	Honduras	30
123	Laos	30
123	Mexico	30
123	Moldova	30
123	Paraguay	30
123	Sierra Leone	30
131	Iran	29
131	Kazakhstan	29
131	Nepal	29
131	Russia	29
131	Ukraine	29
136	Guatemala	28
136	Kyrgyzstan	28
136	Lebanon	28
136	Myanmar	28
136	Nigeria	28
136	Papua New Guinea	28
142	Guinea	27
142	Mauritania	27
142	Mozambique	27
145	Bangladesh	26
145	Cameroon	26
145	Gambia	26
145	Kenya	26
145	Madagascar	26
145	Nicaragua	26
151	Tajikistan	25
151	Uganda	25
153	Comoros	24
154	Turkmenistan	22
154	Zimbabwe	22
156	Cambodia	21
156	Democratic Republic of Congo	21
156	Uzbekistan	21
159	Burundi	20
159	Central African Republic	20
159	Chad	20
159	Haiti	20
159	Republic of Congo	20
164	Angola	18
164	Eritrea	18
166	Iraq	17
166	Venezuela	17
168	Guinea-Bissau	16
169	Afghanistan	15
170	Libya	14
170	Sudan	14
170	Yemen	14
173	Syria	13
174	Korea (North)	12
175	South Sudan	11
176	Somalia	10

("Corruption Perceptions Index", 2017)

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