The consequences of poaching and anthropogenic change for forest elephants

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Abstract

Poaching has devastated forest elephant populations (*Loxodonta cyclotis*), and their habitat is dramatically changing. The long-term effects of poaching and other anthropogenic threats have been well studied in savannah elephants (*Loxodonta africana*), but the impacts of these changes for Central Africa's forest elephants have not been discussed. We examine potential repercussions of

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these threats and the related consequences for forest elephants in Central Africa by summarizing the lessons learned from savannah elephants and small forest elephant populations in West Africa. Forest elephant social organisation is little known than for savannah elephants, but the close evolutionary history with savannah elephants suggests that they will respond to anthropogenic threats in broadly similar ways. The loss of older, experienced individuals could disrupt ecological, social and population parameters. Severe reduction of elephant abundance within Central Africa's forests can alter plant communities and ecosystem functions. Poaching, habitat alterations and human population increase are probably compressing forest elephants into protected areas and increasing human-elephant conflict, negatively affecting their conservation. We encourage conservationists to look beyond forest elephant population decline and address these causes of change when developing conversation strategies. We propose research priorities, including assessing the effectiveness of the existing protected area network for landscape connectivity in the light of current industrial and infrastructure development. Longitudinal assessments of landscape changes on forest elephant sociality and behaviour are also needed. Finally, lessons learned from West African population loss and fragmentation should be used to inform strategies for land-use planning and managing the human-elephant interface.

Introduction

African forest and savannah elephants: *Loxodonta cyclotis* and *Loxodonta africana* respectively (Roca et al. 2015) have recently and rapidly declined due to intense ivory poaching (Bouché et al. 2011; Maisels et al. 2013; Wittemyer et al. 2014), especially under weak governance and widespread corruption (Bennett 2015). Protection efforts have included funding anti-poaching, anticorruption and anti-ivory trafficking systems, legal reform in range states and destination countries, and awareness campaigns such as burning ivory stockpiles. Despite these efforts, both

African elephant species continue to decline, particularly forest elephants in Central Africa (Maisels et al. 2013; Wasser et al. 2015).

Poaching, land use change, and human population increases have long-lasting effects on African elephants that extend beyond population declines. These wider impacts and some processes of recovery are documented for savannah elephants (Gobush et al. 2008; Gobush & Wasser 2009; Archie & Chiyo 2012; Shannon et al. 2013), but remain largely unstudied for forest elephants. This paper examines potential repercussions of changes in forest elephant numbers, distribution and behaviour and associated consequences for their conservation in Central and West Africa. We first describe known anthropogenic impacts on savannah elephants and on forest elephants in West Africa, where substantial forest loss and degradation have occurred. We then outline current knowledge of forest elephants, and infer what the next few decades could hold for them throughout their range. Finally, we propose various research questions that should be addressed to safeguard them.

Consequences of anthropogenic disruption for elephants

Free-ranging savannah elephant populations are comparatively rare, as large undisturbed “megaparks” are rather the exception than the rule (van Aarde et al. 2006). Their habitat outside protected areas is increasingly human-dominated, so most savannah elephants must negotiate risky landscapes or face compression. Similarly in West Africa, small forest elephant populations persist mostly in protected areas surrounded by vast agricultural areas. Progressively fragmented populations increase the likelihood of local extinctions, and place increased pressure on the interface between both species of elephants and people (Barnes 1999; Hoare 2000).

Activity patterns and ranging behaviour

Where poaching occurs, elephants regularly hear gunshots, encounter poachers and elephant carcasses and witness the death of conspecifics, including close associates and family members. Savannah elephants alter their behaviour when exposed to these threats; they immediately shift to more nocturnal activity patterns, and increase flight behaviour (Ruggiero 1990; Graham et al. 2009). In order to engage in risky behaviour such as crop raiding, both savannah and West African forest elephants wait until darkness falls, and avoid moonlit nights, before leaving secure areas (Galanti et al. 2006; Wittemyer et al. 2007; Jackson et al. 2008; Gunn et al. 2014). Savannah elephants also travel faster outside protected areas, particularly in areas of "elephant-intolerant" human populations (Douglas-Hamilton et al. 2005; Graham et al. 2009; Granados et al. 2012). Roads are often barriers to movements as savannah elephants generally avoid areas of loud noise and high human density (Boettiger et al. 2011).

Limited safe habitat means that savannah elephant choices to minimize risk can lead to local elephant super-abundance, compression into secure areas, and the possibility of vegetation damage (Barnes 1983; Lewis 1986). The role of savannah elephants as keystone species remains controversial (O'Connor et al. 2007). While savannah elephant feeding can reduce woody plant diversity and vegetation structure in some areas (Lombard et al. 2001), other studies have shown more positive effects on biodiversity (Yessoufou et al. 2013). Savannah elephant impact may be as diverse as the habitats they occupy and defy simple categorisation into "good" or "bad" (van Aarde et al. 2006).

Where people live alongside elephants, conflict between the two species can harden the boundaries limiting elephant movements (Barnes 1999; Bouché et al. 2011). Crop raiding, destruction of homes, injury and death to livestock or people creates hostility towards conservation programmes and even physical attacks on savannah elephants (Hoare 2000; Lee & Graham 2006). Many studies have proposed solutions, but strategies remain complex and require continuous management at multiple levels (Boafo et al. 2004; Hoare 2015). Both savannah and West African forest elephants adapt quickly to attempts to reduce their crop raiding (Barnes 2002), especially males (Hoare 1999; Jackson et al. 2008) who can learn techniques from others (Chiyo et al. 2011; 2012). Ensuring the survival of African elephants in human-dominated landscapes therefore requires anti-poaching measures, land use planning, and managing the human-elephant interface across elephant habitats.

Poaching impacts on savannah elephant social organization and behaviour

Savannah elephants' complex social systems include lifelong individual bonds and friendships (Wittemyer & Getz 2007; Moss & Lee 2011). At puberty, males disperse and become socially independent, whereas females remain in their natal families throughout their lives (Lee et al. 2011; Moss & Lee 2011) where they can benefit from the social, spatial, and ecological knowledge of experienced female relatives (McComb et al. 2001, 2011). Elephant fission-fusion sociality is maintained by sophisticated communication systems and excellent social and spatial memory (McComb et al. 2003; Bates et al. 2008b). Older females play an important role in decision-making in relation to predation and risk (McComb et al. 2001) and in finding scarce water sources (Foley et al. 2008). Male savannah elephants are sexually mature by age 17, but cannot compete until their thirties and do not reach reproductive prime until in their forties (Lee et al. 2011). Savannah elephant paternity is largely determined by age and musth (Hollister-Smith et al. 2007; Rasmussen et al. 2007); in the presence of large musth males, musth in younger males is suppressed (Poole 1987; Slotow et al. 2000). Poaching alters elephant population dynamics, reducing survivorship and life expectancy, skewing sex ratios, increasing the number of orphans and preferentially removing old, experienced individuals (Wittemyer et al. 2013): this removal can compromise survival and reproductive success amongst survivors. Loss of large prime males leads to increased harassment of females by younger, inexperienced males, and in those younger males siring offspring, altering reproductive skew (Rasmussen et al. 2007; Owens & Owens 2009; Archie & Chiyo 2012). Loss of experienced female leaders disrupts social and ecological knowledge (Foley et al. 2008) and the adaptive value of female relationships, increasing agonism between females (Gobush & Wasser 2009; Archie & Chiyo 2012). Post-poaching, savannah elephants increase their reproductive rates by reducing both age at first reproduction in females and interbirth intervals (Owens & Owens 2009; Wittemyer et al. 2013), which results in rapid population growth in some (Foley & Faust 2010), but not all populations (Gobush et al. 2008; Owens & Owens 2009).

Savannah elephants exposed to anthropogenic threats experience physiological stress (Jachowski et al. 2012). Poaching risk is positively correlated with females' glucocorticoid levels, especially in disrupted family groups. Females lacking close kin experience chronic stress, with subsequent effects on reproductive output (Gobush et al. 2008). Savannah elephants show empathy (Bates et al. 2008a), strong interest in the remains of conspecifics (Douglas-Hamilton et al. 2006), mourning and the ability to recognize dead family members (McComb et al. 2006). Survivors of traumatic events experience psychosocial effects well beyond altered reproductive parameters and population structure (Bradshaw et al. 2005), which may last for decades (Shannon et al. 2013). Young males that witnessed the deaths of family members through culling and were subsequently translocated behaved hyper-aggressive as they matured, before the introduction of older males to suppress their abnormal behaviour (Slotow et al. 2000). Absence of older elephants in a population makes it possible for disruptive or aberrant behaviour to be retained. As females become more frequent poaching targets, downstream population consequences may escalate. In young savannah elephants, loss of a mother elevates mortality risks, and these effects persist until orphans are in their twenties- well beyond the age at which males disperse from families and females commence reproduction (Lee et al. 2013). This occurs despite orphans remaining within the family unit, where other female relatives and allomothers protect and care for them (Lee 1987).

Inferring the consequences of anthropogenic threats for forest elephants

Within ten years, ivory poaching reduced Central African forest elephant populations by 62%. Their range shrank by 30% over the same period, facilitated by increased access along new forest roads, corruption, and the lack of law enforcement (Blake et al. 2008; Maisels et al. 2013). Current offtake levels are unsustainable (Wittemyer et al. 2014) with potentially profound consequences for forest ecosystems and local people´s livelihoods. Most forest elephants are now found in the larger intact forests of Gabon, northern Republic of Congo and southeast Cameroon with low human population density; mostly in well-guarded protected areas surrounded by logging concessions with at least some antipoaching effort (Maisels et al. 2013). Smaller populations still survive throughout Central Africa, although often these are in protected areas surrounded either by "empty forest" or by human-dominated land-use areas. The remnant West African forest elephant populations - fragmented, isolated and compressed over the past century - show an alarming trajectory for forest elephants elsewhere.

The expansion of industrial logging has dramatically changed Central African elephant habitats (Laporte et al. 2007). Two decades ago, roads and settlements were few, and forest elephants favoured secondary forests with open canopies and dense herbaceous vegetation (Barnes et al. 1991). Well-protected logging concessions can support locally high elephant populations (Stokes et al. 2010), and high protection around oil concessions provides refuges for elephants (Kolowski et al. 2010). However in reality protection resources are often lacking and all populations without protection have dramatically declined in the last decade (Maisels et al. 2013). Further habitat fragmentation and alteration is likely in the near future, as most forest is suitable for palm oil plantations (Wich et al. 2014) and mining (Edwards et al. 2014), converting existing habitats and expanding infrastructure (Laurance et al. 2015).

Relatively little is known about forest elephants, because rainforest visibility is poor; most of what we know comes from dung and DNA work, telemetry, or direct observations at forest clearings (e.g. Blake & Hedges 2004; Fishlock & Breuer 2015). Forest and savannah elephants share enough characteristics that insights from savannah elephants can inform where human pressure might threaten forest elephants throughout their range.

Impacts on forest elephant ranging and distribution

Forest elephant movements are directly influenced by human activity even in intact habitats; road and human settlement distribution and density are negatively correlated with elephant density (Blake et al. 2008; Vanthomme et al. 2013; Maisels et al. 2013). Forest elephants become compressed into "safe" places, particularly effectively protected areas (Yackulic et al. 2011; Jachowski et al. 2012), As for savannah elephants, roads in Central Africa act as barriers to forest elephant movements and provide access for poachers (Blake et al. 2008), reducing population connectivity across the Congo Basin. Forest elephants are strongly attracted to mast fruiting events (White 1994; Blake & Fay 1997; Morgan & Lee 2007) so human activities near these resources might impact wider elephant ranging and feeding behaviour.

Impact on forest elephant behaviour and social organisation

Forest elephants range in small groups consisting of a mother with one or several offspring, suggesting that dispersal from the natal group occurs for both males and females (Morgan & Lee 2007; Turkalo et al. 2013). Forest elephants have a fission-fusion society shaped by female choice and intense male-male competition (Fishlock 2010); although social networks appear less dense than for savannah elephants, forest elephants nonetheless aggregate in open areas across their range (Fishlock et al. 2008; Turkalo et al. 2013; Schuttler et al. 2014). They use aggregations to maintain relationships and to maximise social opportunities rather than minimise competition (Fishlock & Lee 2013). Aggregations are opportunities to exchange information and may be hubs for social learning and the establishment of traditions (Fishlock et al. 2015). Like savannah elephants, forest elephants are slow-maturing, long-lived and reliant on dispersed resources suggesting that older forest elephants accrue experience that younger individuals can benefit from.

Despite the ecological distinctions between the two elephant species and our knowledge gaps in life history parameters, we already see similarities in their responses to anthropogenic disturbance: forest elephants become increasingly nocturnal due to poaching (Vanleeuwe et al. 1997; Wrege et al. 2012) and seismic activities (Wrege et al. 2010). They shorten their visits to forest clearings ("bais") when poachers are active, and flee when they detect humans (Maisels et al. 2015). Post-poaching, it can take years for elephants to become diurnal and habituate to humans, which can impact tourism potential.

Forest elephant population structures have already been altered by selective removal of large-tusked individuals for the ivory trade (Turkalo et al. 2013; Griffith 2014). The degree of male reproductive skew is not known for forest elephants, but intense male-male competition (musth, fights, mate-guarding) suggests that it continues to be a selective pressure. Mature males reduce female harassment and suppress younger males (Fishlock 2010). It is unknown how the removal of old females has affected forest elephant population structure, nor whether these females play a key role for society in the same way that older savannah females buffer risks for families. Orphan creation and subsequent orphan survival rates are also unknown, as predation risks differ between forest and savannah (lions are absent in forests, but leopards are ubiquitous, and spotted hyenas present in some forests). Overall we suggest that the loss of older, experienced individuals of both sexes is likely to alter knowledge transfer, reproductive skew and life history patterns in forest elephants and that traumatic individual experiences may lead to chronic stress, and elevated stress responses.

Ecological impacts

Forest elephants play a key role in maintaining important landscape features which other wildlife depends on (Blake & Inkamba-Nkulu 2004; Turkalo et al. 2013). Where forest elephants avoid bais, dramatic vegetation changes result, radically altering habitat structures (Maisels et al. 2015). Forest elephants are highly frugivorous (Short 1981; White et al. 1993; Blake 2002; Morgan & Lee 2007) and changes in their density, distribution and ranging can affect ecological processes. Defaunation of large seed disperser is likely to erode carbon storage (Bello et al. 2015). Among these large trees species several "elephant-obligate" species have been identified (Babweteera et al. 2007; Blake et al. 2009). Other "non-obligate" species (dispersed by elephants and other animals) are "elephant facilitated" when passed through an elephant's gut (Nchanji & Plumptre 2003). While elephant-obligate species comprise only a portion of large tree species diversity (Blake et al. 2009), one study showed that elephant loss resulted in lowered sapling diversity and a shift towards smaller, faster-growing trees that store less carbon (Beaune et al. 2013). Forest elephant abundance can therefore affect plant community structure and lateral nutrient transport, with associated consequences for agriculture (Wolf et al. 2013).

The human-elephant interface in forest environments

As forest elephants become compressed into a few safe havens within protected area networks, the edges harden between where wildlife is tolerated and not (Barnes et al. 1995). Human-elephant conflict in Central Africa is on the rise (Barnes 1996). Increased contact with increasing local populations amplifies the potential for conflict, and successful conservation efforts may actually exacerbate these effects, because elephants understand which areas are safe and lose their fear of humans in those zones. Crop-raiding events are often heightened in the vicinity of protected areas, fuelled by land-use change and increasing human populations. Often protected areas lack support from national conflict mitigation strategies, which are either entirely lacking, or failing.

The effects of hostility work in both directions. Elephants traumatised by poaching become more destructive to infrastructure and aggressive to people. When human injuries or deaths are attributable to elephants, hard-won support for conservation efforts is eroded, hostility towards park and wildlife authorities becomes entrenched and poachers can profit from jaded attitudes by offering "problem animal control" solutions. Local people, researchers and tourists may be exposed to increased risk of elephant attacks. Significant economic impacts of this "downward spiral" occur as ecotourism suffers from reduced security and infrastructure damage, further reducing the (already limited) benefit-sharing ratios that conservation initiatives operate on.

Human influences on forest elephants in Central Africa - implications for conservation

Forest elephant populations and their habitats have undergone dramatic change in West Africa, which provides lessons for the conservation challenges in Central Africa, particularly where forest elephants occur in small isolated populations and regularly range outside protected areas. Rather than focus on efforts that address consequences (Hoare 1999; Barnes 2002; Jackson et al. 2008) such as altering crop raiding patterns, here we outline research questions that address the causes of challenge and change that might allow for structured scenario planning and long-term conservation activities to support a future for forest elephants, rather than the continued documenting of declines. The actions needed to safeguard Central Africa´s forest elephants will require strong (inter-) governmental commitment, collaboration with extractive industries, foreign aid funds, and engagement of local communities.

Protected area network

Does the existing protected area network capture the landscape connectivity needed by forest elephants to access critical resources such as bais and important foods? How will this change in the next century, given expanding industrial and infrastructure development? Outside protected areas, where are the remaining significant elephant populations? Where populations are already isolated, how feasible is it to maintain minimum viable populations? How expensive will this be, and who will pay? Is there a threshold of human density beyond which forest elephants disappear (Barnes 1999; Hoare & Du Toit 1999) and how do the spatial arrangements of infrastructure and cultivation affect this? Can we restore carbon-sequestering potential in areas where forest elephants have become locally extinct?

Land use planning and managing the human-elephant interface

How compatible is current land use with forest elephant conservation plans? How do forest elephants and humans compete for space and resources and how can we reduce the likelihood of attracting elephants to areas of human settlement? How might this change with accelerated rates of climate change? How do extractive industries impact forest elephant density, ranging, and distribution? What laws do range states need to adequately protect humans and wildlife from the negative effects of burgeoning infrastructure?

Impacts on forest elephant sociality and ecology

Are forest elephants changing their diet and behaviour to exploit new resources? Does this affect management of the human-elephant interface? What are the effects of removal of old, experienced forest elephants? Does poaching alter life history parameters (e.g. inter-birth interval, age at first birth), social organization, population dynamics? What does this mean for the recovery potential of populations already affected, assuming security threats can be addressed?

While we have emphasised anthropogenic impacts of forest elephants in Central Africa, these research questions have implications for all forest elephants, including those residing in small populations in West Africa.

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