



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 examined potential repercussions of 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 organization is less known than the social organization of savannah elephants, but the close evolutionary history of these species suggests that they will respond to anthropogenic threats in broadly similar ways. The loss of older, experienced individuals in an elephant population disrupts 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, which negatively affects their conservation. We encourage conservationists to look beyond documenting forest elephant population decline and address the causes of these declines when developing conservation strategies. We suggest assessing the effectiveness of the existing protected-area networks for landscape connectivity in light of current industrial and infrastructure development. Longitudinal assessments of the effects of landscape changes on forest elephant sociality and behavior are also needed. Finally, lessons learned from West African elephant population loss and habitat fragmentation should be used to inform strategies for land-use planning and managing human–elephant interactions.*

Keywords: Central Africa, habitat alteration, human–elephant conflict, land-use planning, *Loxodonta africana*, poaching, social disruption

Las Consecuencias de la Caza Furtiva y el Cambio Antropogénico para los Elefantes del Bosque

Resumen: *La caza furtiva ha devastado a las poblaciones de los elefantes del bosque (*Loxodonta cyclotis*) y su hábitat está cambiando dramáticamente. Los efectos a largo plazo de la caza furtiva y de otras amenazas antropogénicas han sido estudiadas profundamente en los elefantes de la sabana (*Loxodonta africana*), pero el impacto de estos cambios sobre los elefantes del bosque del centro de África no ha sido discutido. Examinamos las repercusiones potenciales de estas amenazas y las consecuencias relacionadas para los elefantes del bosque del centro de África al resumir las lecciones aprendidas de los elefantes de la sabana y las pequeñas poblaciones de elefantes del bosque en el oeste de África. La organización social de los elefantes del bosque es menos conocida que la organización social de los elefantes de la sabana, pero la cercanía de la historia evolutiva de estas dos especies sugiere que responderán a las amenazas antropogénicas de maneras generalmente similares. La pérdida de individuos más viejos y con mayor experiencia en una población de elefantes causa disrupciones en los parámetros ecológicos, sociales y poblacionales. La reducción severa de la abundancia de elefantes dentro de los bosques del centro de África puede alterar a las comunidades vegetales y a las funciones del ecosistema. La caza furtiva, las alteraciones del hábitat y el incremento de la población humana*

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probablemente estén orillando a las poblaciones de los elefantes del bosque hacia las áreas protegidas, e incrementado el conflicto humano-elefante, el cual afecta negativamente a su conservación. Alentamos a los conservacionistas a ver más allá de la documentación de la declinación de la población de elefantes del bosque y a enfocarse en las causas de esta declinación cuando se desarrollen estrategias de conservación. Sugerimos que se evalúe la efectividad de las redes existentes de áreas protegidas para la conectividad de paisajes de frente al desarrollo actual de industrias e infraestructuras. También es necesario realizar evaluaciones longitudinales de los efectos del cambio de paisaje sobre la organización social y el comportamiento de los elefantes del bosque. Finalmente, las lecciones aprendidas de la pérdida de poblaciones de elefantes del oeste de África y de la fragmentación del hábitat deberían usarse para informar a las estrategias de planeación del uso de suelo y de manejo de interacciones humano-elefante.

Palabras Clave: África central, la alteración del hábitat, los conflictos entre humanos y elefantes, la planificación del uso del suelo, *Loxodonta africana*, la caza furtiva, los trastornos sociales

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 currently include funding anti-poaching, anti-corruption, and anti-ivory trafficking systems; legal reform in range states and ivory-traffic destination countries; and awareness campaigns (e.g., 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 they remain largely unstudied for forest elephants. We examined potential repercussions of changes in forest elephant numbers, distribution, and behavior and associated consequences for their conservation in Central and West Africa. We first studied known anthropogenic impacts on savannah elephants and on forest elephants in West Africa, where substantial forest loss and degradation have occurred. We then examined current knowledge of forest elephants and inferred what the next few decades could hold for them throughout their range. Finally, we considered research questions that should be addressed to safeguard them.

Consequences of Anthropogenic Disruption

Free-ranging savannah elephant populations are comparatively rare because large undisturbed megaparks are the exception rather 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 population com-

pression. Similarly, in West Africa, small forest elephant populations persist mostly in protected areas surrounded by vast agricultural areas. For both species, progressively fragmented populations increase the likelihood of extirpation and increase human–elephant conflict (Barnes 1999; Hoare 2000).

Activity Patterns and Ranging Behavior

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 behavior when exposed to these threats; they immediately shift to more nocturnal activity patterns and increase flight behavior (Ruggiero 1990; Graham et al. 2009). To engage in risky behavior, such as crop raiding, both savannah and West African forest elephants wait until darkness falls before leaving secure areas and avoid crop raiding on moonlit nights (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 movement because savannah elephants generally avoid areas of loud noise and high human density (Boettiger et al. 2011).

Limited safe habitat means savannah elephant choices to minimize risk can lead to population super abundance locally, compression into secure areas, and vegetation damage (Barnes 1983; Lewis 1986). The role of savannah elephants as keystone species remains controversial (O'Connor et al. 2007). Although savannah elephant feeding can reduce woody plant diversity and vegetation structure in some areas (Lombard et al. 2001), sometimes it has more positive effects on biodiversity (Yessoufou et al. 2013). The effects of savannah elephants are as diverse as the areas they occupy and defy simple categorization as either positive or negative (van Aarde et al. 2006).

Where people live alongside elephants, conflict between the 2 species can harden the boundaries limiting

elephant movements (Barnes 1999; Bouché et al. 2011). Crop raiding, destruction of homes, and injury and death to livestock or people create hostility toward conservation programs and can lead to physical attacks on savannah elephants (Hoare 2000; Lee & Graham 2006). Many solutions have been proposed, 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 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 human–elephant conflict.

Poaching Impacts on Social Organization and Behavior

Savannah elephants' complex social systems include life-long 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. 2008*b*). Older females play an important role in decision making related to predation and risk (McComb et al. 2001) and to finding scarce water sources (Foley et al. 2008). Male savannah elephants are sexually mature by age 17, but they cannot compete with dominant males 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 by 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 among 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, which increases agonism between females (Gobush & Wasser 2009; Archie & Chiyo 2012). After population-wide poaching, the reproductive rates of savannah elephants increase as age at first reproduction in females

and interbirth intervals decreases (Owens & Owens 2009; Wittemyer et al. 2013). This results in rapid population growth in some (Foley & Faust 2010) but not in other 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. 2008*a*), have a strong interest in the remains of conspecifics (Douglas-Hamilton et al. 2006), mourn, and recognize dead family members (McComb et al. 2006). Survivors of traumatic events experience psychosocial effects well beyond altered reproduction and kin structure (Bradshaw et al. 2005) that may last for decades (Shannon et al. 2013). Young males that witnessed the deaths of family members through culling and were subsequently translocated exhibited hyperaggressive behaviors as they matured before the introduction of older males to suppress their abnormal behavior (Slotow et al. 2000). Absence of older elephants in a population makes it possible for disruptive or aberrant behavior 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, which is 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 Effects of Anthropogenic Threats

Within 10 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) and may have 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 southeastern Cameroon, where human population density is low. These populations exist mostly in well-guarded protected areas that are surrounded by logging concessions, where there is at least some anti-poaching effort (Maisels et al. 2013). Smaller populations survive throughout Central Africa, although often these are in protected areas surrounded either by forests with few wildlife or areas dominated by human land use. The remnant West African forest elephant populations—fragmented, isolated, and compressed over the past century—are on an alarmingly

downward trajectory, as is the case 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 favored 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 levels of protection around oil concessions provide 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 (Laurance et al. 2015) because most forest is suitable for palm-oil plantations (Wich et al. 2014) and mining operations (Edwards et al. 2014), the establishment of which will convert existing habitats.

Relatively little is known about forest elephants because visibility in rainforests is poor. Most of what is known comes from dung and DNA analyses, radiotelemetry data, and direct observations of elephants 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 Elephant Ranging, Distribution, Behavior, and Social Organization

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; Maisels et al. 2013; Vanthomme et al. 2013). Forest and savannah elephants become compressed into relatively safe places, particularly effectively protected areas (Yackulic et al. 2011; Jachowski et al. 2012). Roads in Central Africa act as barriers to forest elephant movements, provide access for poachers (Blake et al. 2008), and thus reduce 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 may affect wider elephant ranging and feeding behavior.

Forest elephants occur in small groups 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 maximize social opportunities rather than to minimize 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. 2016). Like savannah elephants, forest elephants mature slowly and are 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 2 elephant species and knowledge gaps in life-history parameters, their responses to anthropogenic disturbance are similar. 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 natural forest clearings when poachers are active and flee when they detect humans (Maisels et al. 2015). After a poaching event, it can take years for elephants to become diurnal and habituate to humans, which may affect tourism.

Forest elephant population structures have 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, and 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 or whether these females play a key social role in the same way older savannah females do. Orphan creation and orphan survival rates are also unknown because predation risks differ between forest and savannah (lions [*Panthera leo*] are absent in forests, but leopards [*Panthera pardus*] are ubiquitous, and spotted hyenas [*Crocuta crocuta*] are present in some forests). In general, we suggest that the loss of older, experienced individuals of both sexes likely alters 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 that other wildlife depends on (Blake & Inkamba-Nkulu 2004; Turkalo et al. 2013). Where forest elephants avoid forest clearings, 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 range can affect ecological processes. Defaunation of large seed dispersers is likely to erode carbon storage

(Bello et al. 2015). Among these large tree species, there are several elephant-obligate species (Babweteera et al. 2007; Blake et al. 2009). Some species that are not dispersed by elephants and other animals are elephant facilitated when passed through an elephant's gut (Nchanji & Plumptre 2003). Although elephant-obligate species compose only a portion of large tree species diversity (Blake et al. 2009), one study showed that elephant loss resulted in lower sapling diversity and a shift toward 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 and have associated effects on agriculture (Wolf et al. 2013).

Human–Elephant Interactions 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 where it is not (Barnes et al. 1995). Human–elephant conflict in Central Africa is on the rise (Barnes 1996). Increased contact with 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, fueled 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 conflict work in both directions. Elephants traumatized 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 is eroded, hostility toward park and wildlife authorities becomes entrenched, and poachers can profit from the jaded attitudes of locals 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.

Further Research Topics for Forest Elephant 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 of compression and human–elephant conflict (Hoare 1999; Barnes 2002; Jackson et al. 2008), such as

altering crop-raiding patterns, we outline future research needs, the results of which may inform structured scenario planning and long-term activities that could lead to successful forest elephant conservation. The actions needed to safeguard Central Africa's forest elephants will require strong 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 forest clearings and important foods? How will connectivity change in the next century, given expanding industrial and infrastructure development? Outside protected areas, where are the remaining relatively large elephant populations? Where populations are already isolated, how feasible is it to maintain minimum viable populations? How expensive will maintaining these populations be, and who will pay for their maintenance? 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 carbon-sequestering potential be restored in areas where forest elephants have become locally extinct?

Land-Use Planning and Managing Human–Elephant Conflicts

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

Forest Elephant Sociality and Ecology

Are forest elephants changing their diet and behavior to exploit new resources? How would such changes affect management of human–elephant conflict? What are the effects of removal of old, experienced forest elephants from a family group? Does poaching alter life-history parameters (e.g., interbirth interval, age at parturition, social organization, or population dynamics)? What do alterations to life-history parameters mean for the recovery of already diminished populations, assuming security threats can be addressed?

Although we emphasized 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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