POLICY DIRECTION

Slow intrinsic growth rate in forest elephants indicates recovery from poaching will require decades

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Summary

1. African forest elephants Loxodonta cyclotis are experiencing persistent declines driven by illegal killing and range loss. Despite the importance for policy debates regarding elephant trade managed through the Convention on International Trade in Endangered Species (CITES), little is known about forest elephant demography and, consequently, the impacts of offtake and subsequent population recovery potential.

2. Using 23 years of individually based demographic data from Dzanga, Central African Republic, we found low reproductive potential resulting from annual birth rates averaging 4·3% (SD: 1·4%), a median inter-birth interval of 68 months and a median primiparous age of 23 years. Average mortality was 3·1% per year (SD: 1·0%) during the study, with approximately 1·4% of that attributed to human killing.

3. This population of forest elephants demonstrated concerningly slow growth rates, with a doubling time of nearly 60 years under current conditions (41 years excluding human impacts), amounting to three times that reported for savanna elephants. As such, forest elephants appear to be significantly more sensitive to human-induced mortality than their congeneric species.

4. Such slow intrinsic growth challenges current perceptions of historic and contemporary ivory trade impacts on forest elephants, highlighting the urgent need to stem poaching and institute long-term protective measures.

5. *Policy implications.* Debates regarding the sustainability of the ivory trade for the species appear to have overestimated growth rates of forest elephants. The information presented here indicates that sustainable offtake models for forest elephants need reassessment.

Key-words: conservation, demography, forest elephants, illegal killing, *Loxodonta cyclotis*, mortality, poaching, population growth rate, population recovery

Introduction

Determining underlying demographic population processes is fundamental for the management and monitoring of wildlife species (Caughley & Sinclair 1994). Data on demographic processes (fecundity, survival, age of first reproduction, etc.) allow quantification of population trajectories, the identification of population sectors to which growth is most sensitive and determinations of the mechanisms driving population trends (Caswell 2001). In particular, when animal populations have suffered severe declines, demographic data are critical for evaluating what conservation measures might be effective and estimating time to recovery (Beissinger & Westphal 1998). Such information is fundamental to policy debates regarding the viability and benefits of species trade.

The forest elephants *Loxodonta cyclotis* of Central Africa face the threat of extinction, with recent analysis of census data across their range showing a 62% decrease in their numbers for the period of 2002–2011 coupled with a loss of 30% of their geographical range (Maisels *et al*. 2013). Modelling of Monitoring of the Illegal Killing of Elephants (MIKE) data corroborates this, indicating that forest elephants are experiencing the greatest levels of

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poaching in Africa with potentially as much as 10–18% of the population killed per year (Wittemyer *et al.* 2014). This decline is of high conservation concern due to the evolutionary distinctiveness of forest elephants (Ishida *et al.* 2011) and their ecological importance to Central African humid forests (Beaune *et al.* 2013), which serve as the second largest carbon sequestration zone on the planet (Mayaux *et al.* 2013).

Despite the severe threats faced by forest elephants, we lack a basic knowledge of the demography and behaviour of this species. Forest elephants' cryptic nature, dense habitat and logistical constraints on research limit our ability to study this species and understand its conservation status (Wrege *et al.* 2012), resulting in limited knowledge for management decisions. Here, we summarize 23 years of individual-based monitoring data collected on the Dzanga forest elephant population at Dzanga Bai, Central African Republic, the longest running study of its kind on any species in Central African forests (Turkalo, Wrege & Wittemyer 2013). The study site is of high conservation value as part of the UNESCO World Heritage Sangha Tri-national area. We present the first detailed demographic information on forest elephants, including population growth rate, age at first parturition, birth rate, mortality rate and inter-birth interval, and use these data to infer population growth trajectories under different scenarios of human pressure. We discuss the applicability of these data for interpreting population trends more generally for the species and relevance to debates regarding regulated trade in ivory through Convention on International Trade in Endangered Species (CITES).

Materials and methods

STUDY SITE AND INDIVIDUAL IDENTIFICATION

Data presented here are based on individually identified forest elephants visiting the Dzanga forest clearing in south-western Central African Republic (C.A.R.; 2·963°N, 16·365°E) between 1990 and 2013. Observation of individuals at the Dzanga clearing was necessarily opportunistic, dependent on the visiting pattern of each family or adult male. As such, the frequency of observations across individuals differed (Turkalo, Wrege & Wittemyer 2013). To control for these differences, we derived demographic parameters using a cohort representing the best-known adults identified before 1995 and satisfying the following criteria: (i) seen a minimum of 12 times; (ii) observed over three or more years; and (iii) with an average of at least four observations for each year they were alive. All offspring of this cohort of adults were included in analyses. Details of the study site and general methods used in identification and ageing can be found in Turkalo, Wrege & Wittemyer (2013) and Turkalo (2013).

### DEMOGRAPHIC DATA COLLATION AND ANALYSIS

Mortality, natality and changes in population size were calculated from the specified cohort of individuals, ensuring trends were not influenced by immigration of new groups (i.e. groups seen for the first time) during the study. Demographic parameters (mortality, natality and dispersal) were extracted from this cohort between 1995 and 2009, covering the span of most comprehensive data. This sample included 1207 individual elephants, comprised of 349 adults (201 females, 148 males), 242 juveniles or sub-adults (158 females, 84 males) still in the family group when first identified and 616 new offspring observed by the end of 2009. Individuals assumed to have dispersed from the study area (see definition below) were excluded from analyses (demographically censored) from the assigned year of dispersal. Annual population (cohort) size included those individuals born in a given year (despite entering the cohort part way through the year). Thirty-seven calves (6%) were omitted from analysis on account of not being assigned an age accuracy. The first observation was estimated to be within ±1 month for 61% and within ±3 months for 93% of the remaining calves. All age-based analyses used estimated birthdate, with data sets restricted to accuracy cut-offs as stipulated.

We assigned date of death based on (i) observation of carcasses of known elephants (rare – none in the analysed cohort), (ii) very young calves missing when observing their known mother (rare) and (iii) individuals not seen for four times their inter-visit interval. Individuals in the latter category were assigned a death date of twice their inter-visit interval. Juveniles of both sexes were often difficult to identify individually. Sudden disappearance of juveniles (under the age of 15) from their natal groups were assigned as mortalities. Those that progressed through increased independence followed by disappearance were considered dispersal cases (62% of males, 34% of females).

Age at primiparity was determined for the set of females first identified as juveniles younger than 9 years of age (youngest recorded primiparous age was 10; $n = 445$). We included females monitored through 2013 in this analysis. In addition, a parallel analysis using a more conservative cohort of females identified under the age of 7 (based on minimum primiparous age for savanna elephants (Moss 2001; Wittemyer, Daballen & Douglas-Hamilton 2013)) was applied to assess the sensitivity of our analysis to the 9-year age threshold. The accuracy of age estimates of females used was ±6 months for the 97% of individuals whose births were observed during the study (the ages of remaining females was assessed to be ±12 months). Given very high infant survival to 1 year (see results), females coded dead before primiparity were censored on last day of observation. Females appearing with a calf after a gap in sightings were censored if the gap was longer than 22 months (i.e. the length of elephant gestation). The Kaplan–Meier survival method was used to estimate the median female age at first birth and to calculate confidence intervals (Kaplan & Meier 1958). Inter-calving intervals were calculated in the same fashion, with the exception that females with a sighting gap of 365 days that began 22 months from the previous birth were censored.

The total known mortality was partitioned into human and natural causes using elephant carcass data collected in the Dzanga-Ndoki National Park as part of the MIKE Programme, as described in Wittemyer *et al.* (2014). Total known mortality rates m_t were multiplied by the proportion of carcasses for which death was ascribed to be caused by natural processes p_N to derive the natural mortality rate $m_N = m_t p_N$. Because carcass data were not available prior to 2005, we used the average carcass ratio of
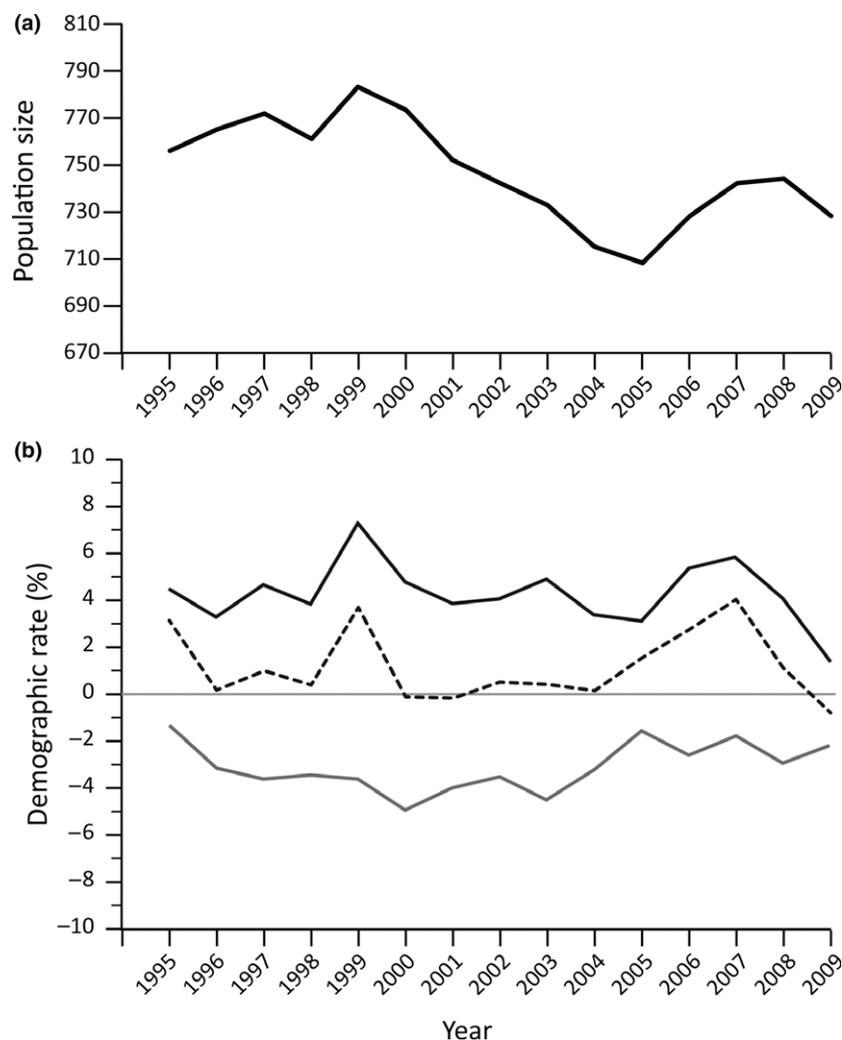
Fig. 1. Population trends collated for the best-known individuals from the Dzanga elephant population. (a) The monitored cohort declined over the study period, primarily on account of dispersal. (b) Natality (black upper line) and mortality (grey lower line) fluctuated weakly across years and typically indicated positive population growth (dashed black line).

$p_N = 0.41$ from 2005 to 2015 to adjust rates prior to 2005. Demographic trends using the observed ($r = 0.012$), estimated without human impacts ($r = 0.026$) and high mortality (assuming all dispersal ended in mortality; $r = -0.002$) growth rates were projected out 70 years using a deterministic exponential population growth model. A logistic growth model was not used on account of a lack of information on carrying capacity of elephants (Armbruster & Lande 1993).

All statistical analyses were run using SAS®9.4 (Cary, NC, USA), and tests were considered significant at an experiment-wise error rate of 0.05.
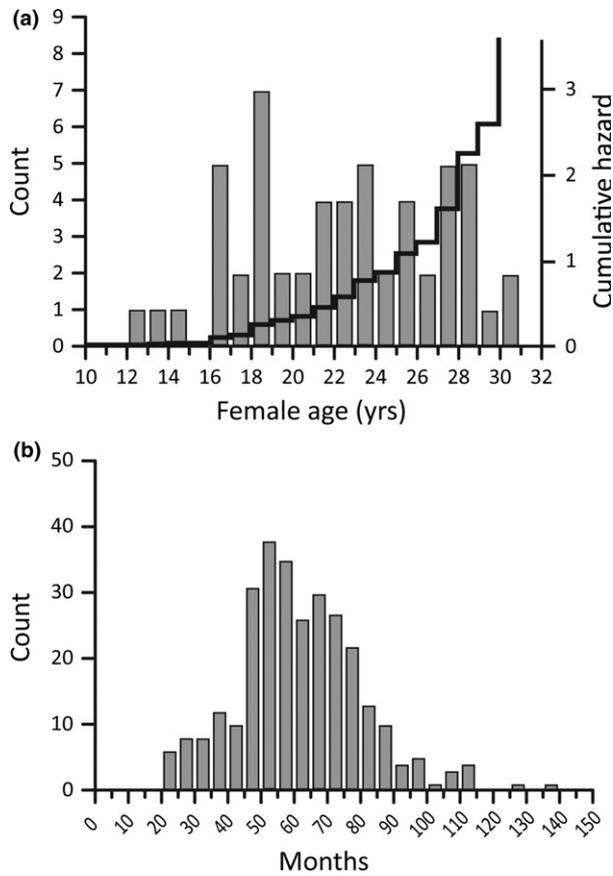
Results

ANNUAL NATALITY AND MORTALITY

The difference in annual natality and mortality suggested an average annual increase of 1.19% (Fig. 1a), but this dropped to −0.19% (SD: 1.9%) when including dispersal (Table S1). Natality averaged 4.28% (SD: 1.35%) per year (Fig. 1b) while annual mortality averaged 3.09% (SD: 1.05%) per year, peaking at 4.92% in 2000 and with a low of 1.32% in 1995 (Fig. 1b). Dispersal averaged 1.38% (SD: 0.68%) per year, comprised of 2.3% of the male population and 0.8% of the female population (Table S1, Supporting Information).

PRIMIPAROUS AGE AND BIRTH INTERVALS

Among the 31 females of known age that gave birth over the study period, mean age at primiparity was 20.4 years (SD: 3.9 years). The youngest primiparous female in this sample was 13 years old, and the oldest was 28 years old (notably, a 10-year-old female outside the cohort gave birth). A Kaplan–Meier analysis of 252 females identified before they were nine years of age indicated that the median primiparous age was 23 years (95% CI: 22–25 years) (Fig. 2a; Table S2). We repeated this analysis for the sample of females first identified before they were 6 years old, with little qualitative change in the estimates ($n = 309$, 31 births; median age = 22 years, CI: 20–23 years). The median inter-birth interval from the sample of 356 pairs of births observed between 1990 and 2013 was 61 months (SD = 19.7 months; Fig. 2b). Kaplan–Meier analysis including females who were lost prior to observation of a

Fig. 3. Population growth projections (black lines) and 95% confidence envelopes (shaded ribbons) for forest elephants under scenarios of 'high mortality' (quantified assuming all losses of individuals in the study were due to mortality, not dispersal), 'observed mortality' (difference between natality and mortality over the 15 year study), 'natural mortality' (mortality calculated after excluding the impacts of humans) and 'average savanna' population growth rates. The starting population size is that recorded during the last survey in the ecosystem, with the horizontal line representing the doubled population size.

Fig. 2. The population growth rate in the study cohort was markedly lower than that found in savanna elephants. (a) The cumulative hazard (black line) overlaid on the distribution of age at first calf and (b) the distribution of inter-calf intervals recorded for the Dzanga population.
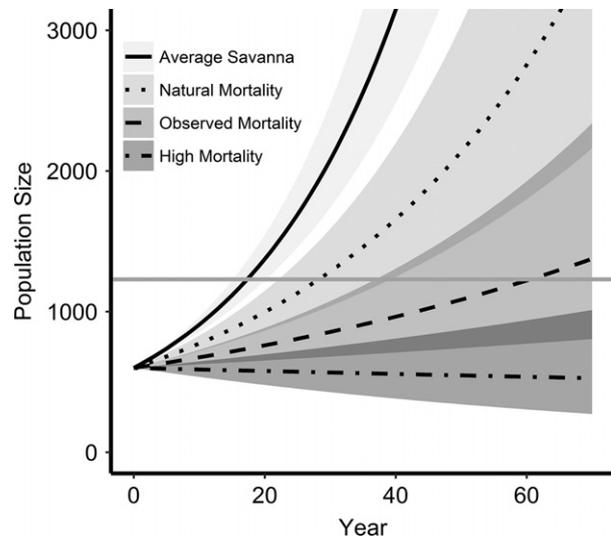
second birth derived a median birth interval of 68 months (95% CI: 65–71 months; Table S3).

POPULATION GROWTH AND ILLEGAL KILLING

Carcass survey data were available for Dzanga from 2005 to 2015, showing an average annual proportion of illegally killed elephant (PIKE) carcasses of 0·47, including an excessive poaching year in 2013 due to a coup in C.A.R. Excluding 2013, PIKE averaged 0·41 per annum. Adjusting annual mortality by PIKE suggested natural mortality in the absence of human impacts was 1·71% (SD: 0·6%) per annum, with illegal killing removing 1·38% of the population per year on average. The doubling time of the population, currently at 58·1 years, is reduced by about a third after excluding illegal killing, though population trajectories remain markedly lower than that found among savanna populations (Fig. 3).

Discussion

Given the precarious status of African forest elephants, deeper understanding of their population biology is invaluable to aid in projecting population trends and characterizing their conservation status. Understanding underlying intrinsic growth potential is fundamental to resolving the impacts and recovery from human offtake and critical to the pervasive debates regarding the viability of ivory trade legislated through CITES (Martin *et al.* 2012). Prior to this study, assessments of the species status were based solely on periodic population surveys, depicting marked declines in populations and the species over the last several decades (Michelmore *et al.* 1994; Beyers *et al.* 2011; Maisels *et al.* 2013). While highlighting the seriousness of their conservation status, these approaches do not offer insight to the demographic underpinnings of the declines and related recovery potential of the species, information fundamental to modelling offtake and management. The data presented here provide the first assessment of basic forest elephant demography, providing the only demographic parameters on mortality, natality and population rates of change for the species and the potential influence of humans on trends. Unfortunately, results from this study demonstrate reproductive potential of forest elephants in the Dzanga system is lower than initially assumed based on savanna elephant demography (Martin *et al.* 2012; Wittemyer *et al.* 2014), even under ideal circumstances (Fig. 3). Magnifying the conservation challenges faced by forest elephants, the results from this study suggest that recovery to population levels in 2000 is likely to require decades (81 years to reverse the reported 62% decline given the current rate of population growth), highlighting the critical importance of stemming

population declines that are primarily driven by poaching for ivory.

POPULATION GROWTH, SURVIVAL AND NATALITY

The Dzanga population increased consistently through the 20 years of this study (Turkalo, Wrege & Wittemyer 2013). However, the demographic parameters estimated here reinforce the interpretation that this increase was driven by immigration more than intrinsic growth. Despite annual natality generally exceeding mortality, dispersal (presumed here given the disappearance of individuals from their natal groups for unknown reasons) caused the size of the core monitored cohort to remain nearly static over the 15 years for which demographic parameters were extracted. It is suspected that at least a portion of the dispersed individuals were actually mortalities. The converse was also true that losses ascribed to mortality may have been emigration, though our approach of focusing on a specific cohort (all regularly observed in Dzanga Bai) was designed to minimize this possibility. Individuals and groups suspected to have emigrated mid study were excluded through our definition of core individuals. As such, we structured our approach to generate conservative estimates of mortality and high reliability estimates of natality.

Observed mortality was adjusted by observed PIKE values to derive a natural mortality rate. It is notable that PIKE in Dzanga is one of the lowest recorded among forest elephant populations (CITES 2012). It is possible the access to and monitoring of bais allows more natural mortalities to be discovered relative to other forested sites, where patrolling may lead to biases in detection of poached carcasses (Wittemyer *et al.* 2014). Given high anti-poaching effort in the Dzanga system, the potential for biases in the detection of poached relative to natural carcasses still exists, which could depress estimates of natural mortality.

The variance around annual natality and mortality rates was low relative to well-studied savanna elephant populations. The influence of strong stochasticity in inter-annual rainfall and resulting primary productivity is widely recognized to drive the variation in savanna systems (Moss 2001; Gough & Kerley 2006; Foley & Faust 2010; Wittemyer, Daballen & Douglas-Hamilton 2013). Similarly, the relative stable ecological conditions, that is constant availability of water and food, in forest settings and relative low variance in inter-annual rainfall likely drive the relative stability in natality and mortality.

SLOW MATURATION AND LONG INTER-CALVING INTERVALS DRIVE LOW NATALITY

The long inter-calving interval and old average age of primiparity (the mother's age at first birth) are the primary factors leading to the markedly slower growth. While much of what has been projected about forest elephant demography has been based off the demography of their savanna counterparts (Martin *et al.* 2012; Wittemyer *et al.* 2014), primiparous age in Dzanga (median of 23 years) exceeded any studied savanna elephant population (Douglas-Hamilton 1972; Laws, Parker & Johnstone 1975; Moss 2001; Freeman, Whyte & Brown 2009; Foley & Faust 2010; Wittemyer, Daballen & Douglas-Hamilton 2013) including those studies deriving the data in the same manner for which median levels were 11·2–14 years (Moss

Table 1. Population size and densities of forest elephant populations

Population	Country	Estimate*	Year	Survey area	Density elephant per km²
Dzanga National Park	**C.A.R.**	**183 (±108)**	**2012**	**497**	**0·368**
Boumba-Bek National Park	Cameroon	2062 (±604)	2012	2079	0·992
Mbam-Djerem National Park	Cameroon	901 (±388)	2009	1433	0·629
Banyang-Mbo Wildlife Sanctuary	Cameroon	153 (±52)	2007	667	0·229
Okapi Faunal Reserve	D.R.C.	1279 (±672)	2011	12 787	0·100
Salonga National Park	D.R.C.	1186 (±692)	2004	22 100	0·054
Lopé National Park	Gabon	4142 (±2167)	2009	4486	0·923
Ivindo National Park	Gabon	2851 (±677)	2009	2996	0·952
Monts Birougou National Park	Gabon	124 (±121)	2007	690	0·180
Mwagné National Park	Gabon	1680 (±499)	2012	1581	1·063
Pongara National Park	Gabon	344 (±152)	2006	380	0·905
Conkouati-Douli National Park	Republic of Congo	947 (±180)	2013	3850	0·246
Nouabalé Ndoki National Park	Republic of Congo	2324 (±565)	2011	3962	0·587
Odzala Kokoua National Park	Republic of Congo	9292 (±2206)	2012	13 525	0·687

*African Elephant Database (AfESG 2013).
Study area in bolded text.

2001; Gough & Kerley 2006; Foley & Faust 2010; Wittemyer, Daballen & Douglas-Hamilton 2013). The relatively old primiparous age could be driven by missed calf mortalities, though results of analysis of the most stringent data set containing calves identified within one month of birth indicate calf mortality was rare during the study. Further, calf survival the first year of life is greater than 97% (A. Turkalo, unpublished data). This 9- to 12-year delay has the potential to reduce natality (and subsequently population growth) by ~2–3% per annum relative to reported rates in savanna populations. In addition, the median inter-calf interval of 5·5 years found at Dzanga was also longer than that reported for similarly monitored savanna populations (3·3–4·5 years) (see summary in Wittemyer, Daballen & Douglas-Hamilton 2013). This further reduces the relative natality by ~1% per annum. Compared to savanna elephants, slower reproduction results in a lower growth rate, despite marginally lower mortality in this forest elephant population.

Only in high-density savanna populations have longer inter-calf intervals, and similar (but younger) primiparous ages been reported (Laws, Parker & Johnstone 1975). As such, the quantified rates in Dzanga would suggest a population of savanna elephants experiencing strong density-dependent impacts (see summary and discussion in Wittemyer, Daballen & Douglas-Hamilton 2013). Observations demonstrate female forest elephants are biologically able to conceive as young as 10 years in Dzanga, suggesting the slower reproductive activity indeed may be related to ecological limitations. However, dung census in Dzanga National Park suggests relatively low densities of elephants (0·37 within the boundaries and 0·16 elephant per km^2 in the broader ecosystem in 2013 and 0·24 in 2004; AfESG 2013), lower than the majority of surveyed forest populations in Cameroon, Gabon and the Republic of Congo (Table 1). Most, if not all, of these populations are experiencing elevated poaching levels, though MIKE data suggest Dzanga experiences lower poaching pressure relative to other forested populations (CITES 2012; Wittemyer *et al.* 2014). As such, it seems unlikely the depressed reproductive potential reported here is a function of density.

It is more likely that these reproductive rates simply reflect the ecological limitations of being terrestrial and (at least partially) reliant on fruit in primary tropical forest areas. Although the forest environment is dense in vegetal matter, much of forest elephant diet consists of browse (leaf matter and bark; White 1994; Blake 2002) which is high in secondary compounds and low in quality (Coley & Barone 1996). Low reproductive rates may in fact be the norm for large-bodied mammals in these rain forests (Tutin 2001). It is possible location specific vegetation characteristics in Dzanga that drive depressed intrinsic growth rates are absent in other forest systems, but this seems unlikely. Data from other populations of forest elephants in the Central Africa region are needed to determine whether forest elephants show variation in reproductive onset and inter-calf intervals as seen across savanna elephant populations.

CONSERVATION STATUS OF FOREST ELEPHANTS

The demographic information presented in this article shows that a slow rate of reproduction and increasing poaching pressure presents a serious obstacle to the recovery of already dramatically reduced forest elephant populations across Central Africa. With the continued poaching pressure in these populations (CITES 2012; Wittemyer *et al.* 2014) and the extended time to recover (based on simple demographic projections using the parameters presented here), the conditions of forest elephants are more precarious than previously thought. We estimate that should poaching be controlled, the doubling time of forest elephant populations is over twice that found in savanna populations (Fig. 3). These data provide a novel context to the impact of ivory offtake on this species, information fundamental to policy debates regarding regulated trade in ivory at CITES. Further, these data suggest that assessment of the species status according to Red List criteria should be conducted for 60-year time periods (approximately twice the generation time for the species). It is important to recognize that protected areas in the Central African forest basin cover the required area for substantial populations of elephants over the long term. It is critical that conservation investments in this region are made that allow sustained efforts for the decades it will require to bring numbers of this species back to levels approaching those historically present.

Data accessibility

Raw data are presented in the supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Annual population count data from the Dzanga elephants.

Table S2. Cohort of monitored females from which ages of primiparity were derived.

Table S3. Cohort of females from which inter-calving intervals for the Dzanga population were derived.