


LETTER

Informing Aerial Total Counts with Demographic Models: Population Growth of Serengeti Elephants Not Explained Purely by Demography

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Abstract

Conservation management is strongly shaped by the interpretation of population trends. In the Serengeti ecosystem, Tanzania, aerial total counts indicate a striking increase in elephant abundance compared to all previous censuses. We developed a simple age-structured population model to guide interpretation of this reported increase, focusing on three possible causes: (1) in situ population growth, (2) immigration from Kenya, and (3) differences in counting methodologies over time. No single cause, nor the combination of two causes, adequately explained the observed population growth. Under the assumptions of maximum in situ growth and detection bias of 12.7% in previous censuses, conservative estimates of immigration from Kenya were between 250 and 1,450 individuals. Our results highlight the value of considering demography when drawing conclusions about the causes of population trends. The issues we illustrate apply to other species that have undergone dramatic changes in abundance, as well as many elephant populations.

Introduction

Effective conservation is contingent upon obtaining accurate and up-to-date information on the status of populations. Demographic assumptions and counting methodologies can strongly alter conclusions about populations in ways that affect conservation actions. Distrust of survey results can enable management inaction, despite evidence that real population changes have occurred (Wasser *et al.* 2010). There is often a need to differentiate demographic processes, such as birth, death and migration, from fluctuations related to survey practices (Doak and Cutler 2014), such as changes to counting meth-

ods (Sinclair 1973), inconsistent sampling of the population (Milner-Gulland *et al.* 2001), imprecise estimates (Fisher *et al.* 2000), or changes in analytical assumptions (Morrison *et al.* 2016). Demographic models provide a powerful and relatively simple method for gaining insight into the causes of apparent changes in populations by allowing the quantification of biological and external contributions to growth and decline, under different assumptions (Morris and Doak 2002).

Here, we illustrate the application of a simple demographic model to a series of censuses of African savanna elephants (*Loxodonta africana*) in the Serengeti-Mara Ecosystem (SME) on the Tanzania-Kenya border. Census

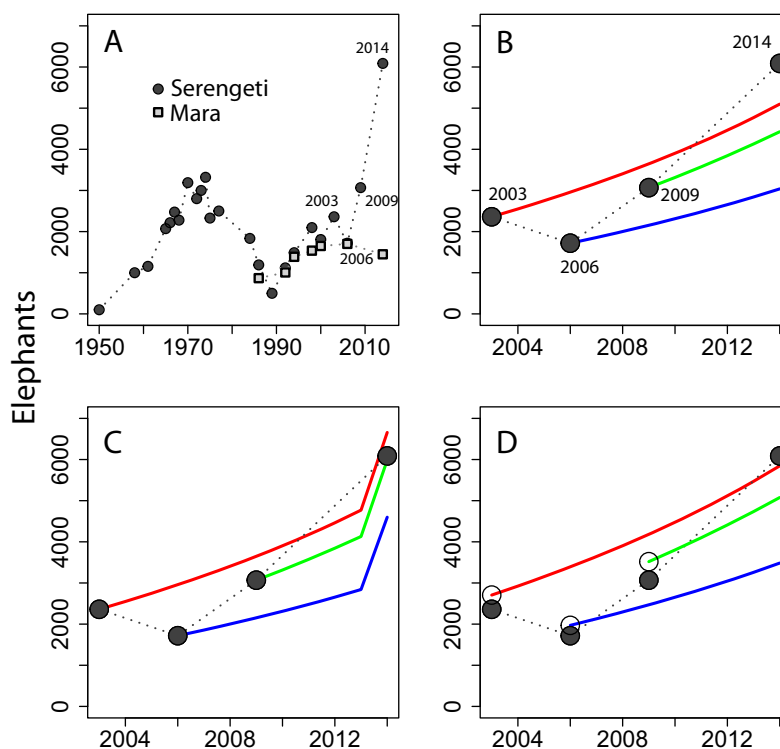


Figure 1 (A) Reported population trends of Serengeti and Mara elephants over time (Mduma *et al.* 2014). Projected population growth of Serengeti elephants under (B) high growth rates (7% per year; solid lines), (C) high growth rates and high immigration from the Mara in 2014, and (D) high growth rates and bias-corrected counts from previous surveys (open circles). Reported censuses (2003–2014) shown in background, with each census projection differing by color (2003 red, 2006 blue, and 2009 green).

results from 2014 in the SME indicate that elephants have increased to over 7,500 animals, or nearly twice as many than has ever been recorded since periodic surveys began in the 1950s (Mduma *et al.* 2014) (Figure 1A). While this trend provides a measure of hope in an otherwise grim narrative about the status of wild African elephants (Thouless *et al.* 2016), including dramatic losses in portions of Tanzania (Wasser *et al.* 2015), most of the apparent population growth in SME occurred within Serengeti National Park on the Tanzanian side of the ecosystem (hereafter “Serengeti”), fueling speculation about the underlying causes of the increase (Nkwame 2014). We explore three broad explanations for the observed population growth: (1) high in situ survival and birth rates, (2) immigration from the Kenyan side of the ecosystem (hereafter, the “Mara”), and (3) variable survey design across time. We use an age-structured population model, informed with age composition data from Serengeti. Our goal is to enhance the interpretation of this and future wildlife total counts.

Methods

Background

Elephants throughout East Africa, including the SME, experienced extensive ivory exploitation during the latter

half of the 1800s (Spinage 1973; Sinclair *et al.* 2008). At the time of the first aerial census in the SME in the 1950s, only ~100 elephants resided in Serengeti (Sinclair *et al.* 2008), though an unknown number resided outside of the park boundaries. The Serengeti population increased to roughly 3,000 individuals by the mid-1970s following high in situ growth and immigration from areas south of Serengeti and the Mara, to the north (Lamprey 1964; Dublin and Douglas Hamilton 1987). Poaching in the late 1970s and early 1980s reduced the Serengeti population by roughly 80% (Dublin and Douglas Hamilton 1987; Sinclair *et al.* 2008). Following the 1989 international ban on ivory trade by the Convention on International Trade in Endangered Species (CITES), the Serengeti population increased steadily to over 3,000 animals by 2009 (Figure 1). Over the past 30 years, the elephant population in the Mara has remained relatively stable, with higher densities (but lower absolute abundances) than Serengeti (Figure 1).

Elephant surveys

Census planners in Serengeti rely on “total” counts in which surveyors search the entire known elephant range and assume complete detection of all individuals (Norton-Griffiths 1978; Douglas-Hamilton 1996). While the assumption of perfect detectability is unrealistic even

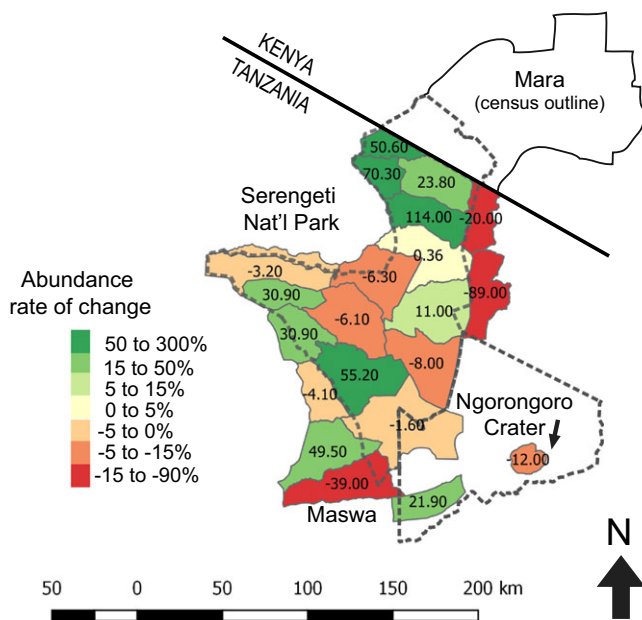


Figure 2 Map of the Serengeti Ecosystem with divisions of major protected areas and survey blocks in Serengeti, shaded by abundance rate of change (% per year) of the elephant population between 2009 and 2014.

with large-bodied animals in open savanna (Hedges 2012), total counts remain the preferred survey method in SME because the clumped distribution of elephants generates large uncertainty in sample-based estimates (e.g., using systematic reconnaissance flights) (Caughley 1974; Norton-Griffiths 1978). This uncertainty can inhibit detection of temporal trends (Hedges and O'Brien 2012) which are often more important than accurate abundance estimates in conservation and management settings.

Recent aerial total counts of elephants were conducted in 2003, 2006, 2009, and 2014 in Serengeti, and in 2006 and 2014 in the Mara. The joint Serengeti-Mara count in 2014 was undoubtedly the most extensive in the ecosystem to date, requiring ~250 flight hours in fixed wing aircraft to cover 30,950 km² (Mduma *et al.* 2014). The 2014 count occurred between May 19 and June 6 and covered all areas in the greater Serengeti-Mara Ecosystem known to support elephants. On the Mara side, surveyors used similar methodologies as previous total counts, relying on visual counts of observed herds and 1.0 km intertransect spacing, with transects covering the Masai Mara National Reserve and a large dispersal area to the north and east of the reserve on group ranches and private conservancies (Mduma *et al.* 2014) (Figure 2). On the Tanzanian side, the survey occurred within 18 distinct blocks, most of which had been surveyed in previous censuses, and included Serengeti National Park, Maswa, Grumeti and Ikorongo Game Reserves, and portions of Ngorongoro Conservation Area and Loliondo (Figure 2). Within blocks, transect density was higher than in pre-

vious counts, with intertransect distances ranging from 0.6 km in woody habitat to 2 km in open grasslands where visibility was much greater (Mduma *et al.* 2014). When observers spotted groups of ≥ 10 individuals, pilots flew inward circles above the group until observers had achieved consistent visual counts (Mduma *et al.* 2014). Digital photos were also taken of each elephant group and compared to observer counts at the end of each flight. Photographs were used to verify numbers in each herd, especially for large groups, though age/sex composition was not collected. Most total counts prior to 2014 were based on visual counts and did not use digital photos to verify group sizes.

Population model

Elephant populations have the lowest growth potential of any terrestrial mammal, limited by a 22-month gestation and a 3- to 4-year minimum interbirth interval (Estes 1992). Consequently the maximum theoretical long-term growth rate for populations (Calef 1988), and the highest sustained rate (over 12 years) recorded in the wild (Foley and Faust 2010) is around 7% per year. While these high growth conditions are unlikely in wild populations over long periods of time, they serve as a starting point for understanding the potential (i.e., conservative) magnitude of other processes driving apparent population increases (i.e., immigration and undercounting) and are not atypical for populations recovering from poaching (Douglas-Hamilton 1987). We used a deterministic, stage-structured population model to ask whether the

Table 1 Vital rates and age structure used here to project the population growth of Serengeti elephants, modified from elephants in Amboseli National Park, Kenya (Moss 2001). Fecundity (calves/female/year) of breeding-age females was increased to reflect the maximum possible birth rate (3-year birth intervals). Survival values were increased in proportion to their elasticities. Age class proportions based on field data collected in Serengeti in 2006 ($n = 211$)

Age class	Fecundity	Annual survival	Proportion age class (t_1)
0–1	0.000	0.948	0.038
2–5	0.000	0.994	0.223
6–10	0.021	1.000	0.227
11–15	0.333	0.999	0.071
16–20	0.333	0.998	0.047
21–35	0.333	0.989	0.237
35+	0.333	0.934	0.156

observed increases in the Serengeti population were plausible under growth conditions of 7% growth per year between 2003 and 2014, based on the dominant eigenvalue of the projection matrix (Caswell 2001). Our model relied on published elephant survival estimates from a long-term (>40 years) study in Amboseli National Park, Kenya (Table 1) (Moss *et al.* 2011). To achieve a 7% annual growth rate in our model, fecundity rates of all females > 11 years old were set to 0.333, to reflect an interbirth interval of 3.0 years (Calef 1988; Foley and Faust 2010). Next, we increased survival rates in proportion to their elasticities to achieve an annual growth rate of 7% per year. We also considered a more moderate annual growth rate (3% per year). We did not consider the possibility of higher fecundity due to twinning because twins are relatively rare in most elephant populations, accounting for < 1% of conceptions in Amboseli (Moss 2001) and 5% of conceptions in Tarangire National Parks (Foley 2002).

Our demographic model used age-sex structures that were based on ground-based surveys conducted in Serengeti in 2006 (Table 1). These surveys used visual indicators of age-sex based on head morphology and body size to classify individuals into seven age-classes: 0–1 years, 2–5 years, 6–10 years, 11–15 years, 16–20 years, 21–35 years, and 35+ years. Females comprised 65% of the population. Our model assumed equal survival rates among sexes within age classes.

We projected populations forward in time starting from three previous census estimates: 2,360, 1,718, and 3,068 individuals, corresponding to aerial surveys in 2003, 2006, and 2009, respectively (Figure 1). This provided a comparison between our model projections and the observed 2014 count in Serengeti ($n = 6,087$ elephants). We did not test the sensitivity of results to particular vital rates because all rates were near their theoretical maximum (Table 1). Because total counts (such as those from

the Serengeti-Mara) lack error estimates, they do not provide distributions from which to sample stochastically; thus, our model projections were necessarily deterministic.

We introduced immigration into the model by projecting the Mara population from its most recent total count in 2006 (1,701 individuals) and allowing it to grow at 7% per year until 2014, as above, at which point we assumed all net differences between the number of projected and observed individuals in the Mara immigrated to the Serengeti. Our goal was to represent the most extreme conditions of population growth and immigration. We did not correct the Mara counts for bias due to visual counting (see below). Few neighboring areas outside of the survey area are suitable for elephants because of high human densities, and while sizeable elephant populations still occur in other parts of Northern Tanzania and Southern Kenya, such as Tarangire, Lake Manyara and Amboseli National Parks, we expected these to be too distant (100–250 km) and too isolated by intensive human activities to contribute in a demographically meaningful way to the Serengeti or Mara populations. This expectation is supported by genetic analysis that shows strong female philopatry in elephant populations east of the Gregory Rift Wall (Amboseli and Tarangire), with limited recent genetic exchange between Tarangire and the Serengeti-Mara population (Ahlering *et al.* 2012). While data on movement of individuals within SME was unavailable, we quantified temporal trends within survey blocks to understand potential spatial drivers of population change.

To understand the effect of undercounting in previous surveys, we calculated the mean difference between photo counts and visual counts from the 2014 survey after accounting for increasing error rates in larger group sizes (c.f. Figure 3). We applied this mean error as a correction to previous counts in 2003, 2006, and 2009, under the assumption that the distribution of group sizes in previous counts was approximately similar to 2014 (group size data were unavailable from previous surveys). We fit a log-linear model to the counting data (visual vs. photo counts) and compared this model's slope to a 1:1 line. We then projected these corrected counts with a high in situ population growth (7% per year).

Results

Assuming high in situ growth, the projected population size of Serengeti elephants fell short of the 2014 census (6,087 individuals) by a minimum of ~1,000 elephants when projected from 2003 and a maximum of ~3,100 elephants if projected from 2006 (Figure 1B). The addition of immigration into our model only allowed the

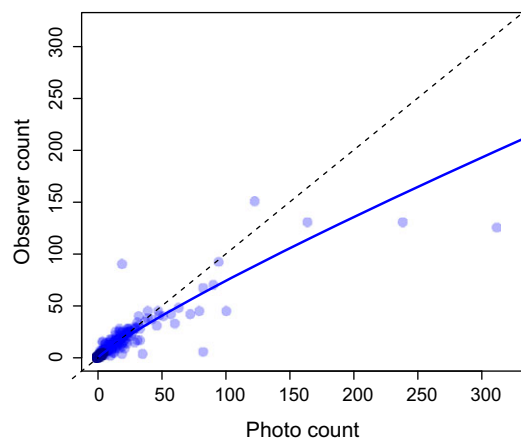


Figure 3 Photographic counts versus observer counts of Serengeti elephants. Each data point represents a group encountered during the 2014 aerial survey in Serengeti National Park. Dotted line is the 1:1 line indicating perfect agreement between observer and photo counts, and blue line is the fitted log-linear relationship.

projected population size to reach the 2014 census estimate when the starting year was 2003 and elephants grew at 7% per year (Figure 1C). At most, immigration from the Mara was ~1,450 individuals under the assumptions that both the Mara and Serengeti populations grew at 7% per year and between 60% and 100% of the net differences in the Mara population (between the projected population and its 2014 census) immigrated to Serengeti. Under less extreme rates of in situ population growth (3% per year) in Serengeti, the net immigration from the Mara would have to be in the range of 2,000–3,500 individuals, which is implausible given the size of the Mara population. Thus, high rates of in situ population growth are required in both the Serengeti and Mara populations to reach the 2014 census estimate. Changes in population size within survey blocks further confirmed that the spatial distribution of elephants has changed considerably since 2009 (Figure 2). The northernmost blocks along the Tanzania-Kenya border experienced an 11.6-fold increase (from 195 to 2,256 individuals) in the number of elephants observed in the 2009 versus 2014 census.

Comparisons of the number of elephants observed per group using the two counting methodologies (visual counting vs. photographic counting) in the 2014 census (Figure 3) suggest that visual counting resulted in a mean bias of $-12.7 \pm 1.9\%$ (equivalent to 691 undetected elephants in 2014). Undercounting was most severe in large groups (ca. >40 individuals) and the predicted relationship between observer and photo counts is well below the 1:1 line (slope for log-linear relationship: 0.87 ± 0.02 ; Figure 3). Note this formula provides an estimate of bias for different group sizes. Because the three most recent

previous censuses (2003, 2006, and 2009) only used visual counting methods, we corrected the initial population sizes by -12.7% and projected each to 2014, again assuming high in situ growth (7% per year), but no immigration. Only projections from 2003 reached close to the 2014 census level, falling short by about 250 individuals (Figure 1D). Population projections from the 2006 and 2009 censuses fell short by 2,603 and 1,010 individuals, respectively. Thus, to reach the 2014 census count required a combination of high in situ growth on both sides of the border, undercounting in previous censuses and hundreds of elephants immigrating from the Mara. The 2006 count appears to be incompatible with the 2014 count, even under these extreme assumptions.

Discussion

Concern over the status of elephants triggered a recent, ambitious effort by African wildlife agencies and non-governmental partners to carry out population counts across the continent in areas supporting major concentrations of elephants (Chase *et al.* 2016; Thouless *et al.* 2016). Results from these counts have had far-reaching implications for conservation, tourism and socioeconomic policies and they provide the most important direct evidence of the scope of the current elephant crisis. Surveys in the SME demonstrate that elephants have undoubtedly increased over the past 25 years, a pattern that coincides with increased antipoaching efforts in the ecosystem (Hilborn *et al.* 2006) and global restrictions on ivory trade (Sinclair *et al.* 2008). Results presented here suggest that recent apparent growth in Serengeti elephants is likely due to a combination of high in situ growth, immigration from the Mara and improved detection of individuals.

Between 250 and 1,450 elephants have immigrated from the Mara to Serengeti since 2003, a conclusion supported by the 11.6-fold increase in elephants in Northern Serengeti near the Tanzanian-Kenyan border (Figure 2). Several factors may be contributing to this high level of immigration. The 2014 aerial survey found a higher abundance of carcasses on the Kenyan than the Tanzanian side of the ecosystem (117 vs. 75 carcasses, corresponding to ratios of dead:live animals of 8.1% and 1.2%, respectively) (Mduma *et al.* 2014). This suggests that mortality (including from poaching) is greater in the Mara than Serengeti, at least in the several years prior to the survey, and that immigration to Serengeti could be driven in part by elephants vacating areas they perceive as more dangerous. Increasing human and livestock densities outside of the core protected areas may also be increasing direct disturbance and exacerbating food competition outside these areas, leading to a compression of

elephant ranges (Ogutu *et al.* 2011; Ogutu *et al.* 2016). Examples of distributional shifts by elephants in response to human disturbances have been well-documented in other ecosystems (Douglas-Hamilton 1987; Graham *et al.* 2009; Goheen and Palmer 2010). Nonetheless, the Serengeti and the Mara populations are undergoing a period of rapid in situ growth, evidenced by relatively low elephant carcass ratios compared to many ecosystems in Africa (Chase *et al.* 2016), a young age structure, and densities much lower than those observed in some areas (Robson *et al.* 2017). The Mara elephant population has remained relatively stable in size during the past 15 years, with higher densities than the relatively unpopulated Serengeti (Figure 1A). Thus, immigration from the Mara to Serengeti may be a natural consequence of density-dependent dispersal from areas of higher density to lower density. Without data on movement of individual animals between Serengeti and elsewhere, and without counts in both wet and dry seasons, migration or range contractions will be difficult to distinguish from in situ change.

Increased detectability of elephants in the 2014 census (on the Serengeti side) likely increased the apparent growth in the population. Transect spacing was denser in the 2014 survey than previous surveys, and this likely increased detectability, particularly of small groups. Detection bias is strongly affected by the distribution of group sizes: larger groups (>40 individuals) generate the majority of bias (Figure 3) so surveys involving many large herds, as often observed in the wet season, will be more biased than those involving many small herds. We suggest that the main challenge in accurately counting large groups is the detection of calves which tend to move near or under their mothers when low-flying planes pass overhead (Figure A1). The Serengeti elephants have a relatively young age distribution (based on ground surveys), with 26.1% ($\pm 3\%$) of elephants under the age of 5 in 2006 (Table 1). Thus, significant undercounting of calves in all surveys since 2003 seems likely. Future efforts to collect age data during aerial surveys and compare this to ground based surveys would be useful to determine the extent of undercounting of young animals.

Policy implications

Changes to survey practices can have important consequences for conservation policies. For instance, in the Greater Yellowstone Ecosystem, apparent growth in the number of grizzly bears (*Ursus arctos horribilis*) served as the basis for efforts to remove protections of grizzly bears under the U.S. Endangered Species Act. However, the apparent population growth may, in part, be due to changes in observation effort over time and inadequate consid-

eration of grizzly life histories, rather than actual demographic growth (Doak and Cutler 2014). Likewise, unregulated hunting of saiga antelope (*Saiga tatarica*) in Central Asia resulted in dramatic population declines in the 1990s (Milner-Gulland *et al.* 2001). When saiga reached low densities, declines in detectability due to smaller group sizes likely overestimated the severity of population declines, and consequently suggested that ongoing conservation measures were less effective than in reality (McConville *et al.* 2009). The failure to account for improved detectability will imply that populations have increased more (in the case of Serengeti elephants), or decreased less, than has actually occurred (McConville *et al.* 2009). The latter of these possibilities is particularly worrying given the severity of elephant population declines reported elsewhere (Chase *et al.* 2016; Thouless *et al.* 2016).

The Serengeti elephants typify the challenges of monitoring wildlife populations in ecosystems that span multiple jurisdictions, particularly international boundaries (Kark *et al.* 2015). Of the 769 km of shared border between Kenya and Tanzania, 37% lies within transboundary protected areas, and much more serves as habitat for free-ranging wildlife. Elephants in the SME continue to move freely across this border and constitute a single, transnational population (Ahlering *et al.* 2012). Given the large numbers of animals that live near the border (Dublin and Douglas Hamilton 1987; Mduma *et al.* 2014), simultaneous counts on both sides and standardized methodologies will be necessary for producing accurate ecosystem-wide counts (Mduma *et al.* 2014) and reliable long-term trend data.

Unfortunately, financial and institutional commitment for coordinated, multi-national species surveys, such as the Great Elephant Census (Underwood *et al.* 2015), and the subsequent acceptance of survey results by policymakers often only occurs after species reach crisis points. Mounting evidence from other ecosystems in Tanzania suggests that savanna elephants are under extreme pressure from poaching (Wasser *et al.* 2015) and this only magnifies the importance of accurate census results using consistent methodologies, which can be aided by demographic analysis. In the Selous-Niassa Ecosystem along the border of Tanzania and Mozambique, elephant censuses suggested dramatic declines in elephants in the mid to late 2000s (Thouless *et al.* 2016), but distrust of survey results may have contributed to a slow response to the crisis locally, and helped prolong efforts in Tanzania to lift the international CITES ban on ivory sales (Wasser *et al.* 2010). Our study provides a small illustration of the challenges of interpreting population trends from the largest of all terrestrial species in one of Africa's best-studied ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1 Aerial image of elephants in Serengeti from the 2014 census, showing the bunching behavior of elephants that makes counting individuals from the air difficult.

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