Can we sustainably harvest ivory?¹

David Lusseau*¹ & Phyllis C. Lee²

¹Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK
²Faculty of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK
*Correspondence: d.lusseau@abdn.ac.uk

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SUMMARY
Despite the 1989 ivory trade ban, elephants continue to be killed to harvest their tusks for ivory. Since 2008, this poaching has increased to unprecedented levels driven by consumer demand for ivory products. CITES is now considering to develop a legal ivory trade [1,2]. The proposal relies on three assumptions: i) harvest regulation will cease all illegal activities; ii) defined sustainable quotas can be enforced; iii) we can define meaningful sustainable quotas that come close to the current demand. We know that regulating harvest does not stop illegal takes. Despite whaling regulation after WWII, illegal whaling continued for decades [3]. The introduction of wolf culls in the USA actually increased poaching activities [4] while one-off ivory sales in 1999 and 2008 did nothing to halt elephant poaching. Governance issues over the ivory supply chains, including stockpiling, make enforcing quotas challenging if not impossible [5,6]. We have not yet adequately assessed what could be a sustainable ivory yield. To do so, we develop a compartmental model composed of a two-sex age-structured demographic model and an ivory production and harvest model. We applied several offtake and quota strategies to define how much ivory could be sustainably harvested. We found that the sustainability space is very small. Only 100 to 150kg of ivory could be removed from a reference population of 1360 elephants, levels well below the current demand. Our study shows that lifting the ivory ban will not address the current poaching challenge. We should instead focus on reducing consumer demand.

RESULTS AND DISCUSSION
Harvest model development
In order to develop a harvest model, we must first understand the process by which ivory is obtained. We can apply one of the many approaches used in wildlife management to define these sustainable quotas. However, much of the debate surrounding the sustainability of ivory harvest overlooks one key point: hunters do not want to kill elephants; they want to harvest ivory. Yet, we attempt to inform this harvest using one of two approaches, neither suited to the challenge. It is misguided to use classical population models to try and predict what level of elephant removal population(s) can sustain so as to provide the ivory needed for the market because ivory requires selective harvesting from a sexually dimorphic trait [7]. It is also misguided to use classical resource extraction models, which the current CITES “Decision-Making Mechanism for a Process of Trade in Ivory” is considering, because ivory is a renewable resource made by elephants which increases in mass as elephants age [2]. If the take does not match the demographic pace of elephant populations, a given amount of ivory harvested by removing a few large elephants from the population will require killing more, smaller, elephants the next year. We faced a similar hurdle in the early 20th century when trying to manage whaling by reducing the harvest to the amount of whale oil produced when that oil was extracted from different age-sex classes, different populations, and even different species [8].

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We developed a compartmental model (Figure 1) to deal with these problems which accounts for the two steps involved in ivory harvesting. We aimed to determine how much ivory could be harvested sustainably for a typical demographically-healthy elephant population under different realistic management and hunting strategies. We defined sustainability here as the ability to not significantly alter the elephant population growth rate as well as an ability to maintain a stable or increasing annual ivory harvest.

Figure 1. Conceptual model. A. Diagram representing the compartmental model and its dynamics (top panel). A 5-year bin age-structure was applied to both males (light) and females (dark) who then contributed to demography through survival and reproduction (arrow to the central square). The model was parameterised using long-term focal follow observations from the Amboseli, Kenya, population (Table S3). The ivory standing stock (B) was then estimated for each age/sex classes (circles; Figure S5) and a harvest was introduced which lead to further mortality. C. The realised population growth rate was representative of the observed annual population growth (black line). The dashed lines represent the mean – over all control simulations – simulated population growth over 100 years (black), the mean 2.5% quantile over 100 years (light grey), and the mean 97.5% quantile over 100 years (light grey). Bands represent the 95% confidence intervals over all control simulation runs for each estimate (n=9000).
We first used a two-sex stochastic age-structured population model to simulate the demographic dynamics of an elephant population [9] (Figure 1, see Supplemental Experimental Procedures for a full description of the model). A two-sex model is important because of the sexual dimorphism in ivory production and the density-dependent differential reproductive success in males correlated with age and therefore tusk size [10]. In this instance, the population model was parameterised using information from the longest running research programme on African elephants. It is important to note that in this model we accounted for neither stochastic environmental impacts on demographic rates (droughts [11]), nor indirect social demographic effects (e.g., the impact of matriarchs on survival probability in their matrilines [12]). Therefore, the population trajectory we simulate is the best this population can achieve.

We then model the standing stock of ivory from the simulated age- and sex-class structure of the population at each year and introduced a harvest model for this stock (Figure 1). We could use one of three tactics to harvest ivory: i.) hunters try to maximise ivory gain per kill by selectively targeting larger animals, ii.) hunters do not have a complete knowledge of the population and therefore using the same tactics but kill selectively the larger animals whenever they find them (partially selective), and iii.) hunters randomly harvest elephants (Supplemental Experimental Procedures). This harvest was managed with a quota defined as the proportion of one of three ivory stocks. The first management scheme using the original stock available at the beginning of the simulation to define the quota. The second scheme used either the original stock or the standing stock, whichever was the largest, in order to account for the difficulty in reducing quotas once they are established [13]. The last scheme assumed perfect governance and therefore an ability to define an annual quota based on the annual standing ivory stock. We did not account for the possibility of defection from these management schemes (poaching), hence only examining the best case scenarios, even though defection will influence significantly management success [14].

**Harvest sustainability**

For all harvest scenarios, the harvest quickly becomes unsustainable (Figure 2, see also Table S1-S2 and Figures S1-S3). Increasing the allowed take level decreased the capacity for the harvest to remain stable or increase (ivory harvest growth ≥ 0; Table S1, Figure S1). We determined population trajectory changes by comparing population growth rate under the different scenarios to what the population growth rate was in control conditions (no take). The response variable was therefore binary (binomial error distribution): if the 97.5% quantile of population growth rate realised over 100 years in a simulation was lower than the 2.5% quantile of population growth rate in the 9000 control simulations then the population trajectory was deemed significantly changed. If not, then it was deemed unchanged (similar to control simulations). The probability that the population trajectory would be significantly altered increased rapidly with take levels (Table S2, Figure S2). The better outcome emerged when annual quotas were defined and the hunt was selective (Figure S2).
Figure 2. The fate of the ivory harvest under the combination of the three hunting strategies and the three quota definition strategies for varying proportion of quota take allowed (from 0 to 10% of ivory stock). Annual: quota defined as a proportion of the annual standing stock of ivory; Original: quota defined as a proportion of the standing stock of ivory at year 2; Maximum: quota defined as the maximum of Annual and Original. Selective: preferential hunt of largest animals; Random: animals randomly selected; Partially Selective: more common larger animals preferential hunted. See also Tables S1-S2 and Figures S1-S3.

For each simulation we could determine whether the population was extirpated (when abundance fell to zero). We could therefore determine how many replicate simulations (out of 1000 replicates for each take, hunting and quota scenarios) led to extirpation (Figure 3). The probability to extirpation increased very rapidly with take levels. The ability to define annual quota decreased the probability of extirpation with take levels, and so did some selectivity in harvest (Figure 3). The ability to vary the harvest intensity annually does allow offtake to increase compared to other quota definition scheme (Figure 2) and decreases the risk that the harvest would lead to the population’s extinction.
Figure 3. Observed proportion of 1000 simulations that ending in population extinction for each hunting (Partially selective, Selective, and Random) and quota (Annual, Original, Maximum) scenarios and allowed take level.

**Maximum sustainable ivory yield**

We retained the ivory yield for all simulations that match our sustainability criteria in both population growth rate change from baseline as well as ivory production over the entire simulated period. These sustainable harvests would allow the retrieval of at most 100 to 150kg of ivory annually from initially 1360 individuals depending on the quota and hunting strategy (Figure 4). This outcome is contingent on no poaching occurring. However, even with these very small takes, sustainability is only possible if the maximum harvest size decreases through time when individuals hunt randomly regardless of the quota definition (Figure 4). The maximum harvest size can be marginally increased if annual quotas are defined (Figure 4). That is because the population itself is allowed to increase (Figure S2).
Figure 4. The amount of ivory that could be sustainably harvested from our reference elephant population. Violin and bar plots of the scenarios that were sustainable (Figure 2): A. annual ivory harvest at year 2, B. annual ivory harvest at year 50 when continuously adhering to quota and hunt strategy (grouped and coloured by quota strategy). The maximum sustainable harvest (in kg) is given about each violin plot.
We do not have a current estimate of the ivory annual consumer demand, but from seizures we can estimate that around 210 tonnes of ivory are poached each year [15]. Given a population of around 700,000 African elephants; this would be equivalent to having to harvest c. 410kg annually from our simulated reference population. Given the current lower abundance estimate of 473,000 (2013 estimate); we would need to harvest c. 600kg from the reference population [1]. This is very far from our sustainable harvest estimates (Figure 4). These estimates do not account for population variance in tusk size and tusklessness [16], indirect social effects of the harvest [17] and abiotic effects on demography [11]. Climate predictions show that droughts will intensify and become more frequent [18] hence the population trajectory we simulated is liberal (note how we are not capturing extreme changes, Figure 1C). In addition, the margin of error in this harvest is very small (Figure 2); we quickly run the risk of extirpating the population under overexploitation (Figure S4).

CONCLUSION
In 2007, a CITES working group was mandated to determine mechanisms for ensuring that a legal trade in ivory could be controlled and policed in relation to regulated demand (Decision-Making Mechanism for a Process of Trade in Ivory – DMM [2]). Key features were (1) reaching a realistic estimate of legitimate, sustainable demand from Asian markets for ivory; (2) a mechanism for permanently marking ivory and developing a permit system not open to either corruption or counterfeiting; (3) population modelling for ivory offtake (from natural mortality and/or directed harvesting) to meet the planned or estimated demand. The success of this plan clearly hinges on a number of assumptions, one of which is an ability to match demand with an ivory yield which can be sustained by elephants. Given the large discrepancy between current illegal demand and what can be sustainably harvested from African elephants, we cannot see a way by which ivory harvesting can resume and be sustainable. Thus, there is a very high risk that lifting the ivory ban will lead to the rapid disappearance of African elephants. At the same time, we cannot brush aside the fact that poaching has reached industrial scale fuelled by an increase in consumer demand driven by the rise of the middle class in countries like China [5]. We must urgently work on finding ways to change consumer behaviour as the only avenue by which we can resolve the ivory trade tragedy.

EXPERIMENTAL PROCEDURES
Demography
Demographic parameters were estimated from individual follows in Amboseli, southern Kenya, from 1972 to 2014 and ongoing (Table S3) [19]. The study was entirely observational and had full clearance from relevant authorities.

We developed a two-sex population model structured in 5-year age classes (Figure 1). This model was projected for 100 years, starting with sex/age distribution estimated from the Amboseli study. This 100-year simulation was replicated 1000 times for each combination of take level, hunting and quota scenarios. Survival probabilities and female fertility rates were drawn each year from beta distribution with mean and variance estimated from the Amboseli study. Age-specific male fertility rates were drawn each year from log-normal distribution with parameter estimates taken from [10]. Fertility rates were density-dependent (see Supplemental Experimental Procedures).

Harvest model
Each year, the standing stock of ivory was estimated by randomly drawing the contribution of each individual using an age-sex specific ivory growth model (Figure S5). A quota was then defined depending on take level allowed (ranging from 0 to 10% of the stock) and the quota definition for year
Hunting then took place by randomly killing individuals and harvesting their ivory. Individual elephants were selected using one of three hunting scenarios:

i. Random: an individual (>5 years) was randomly selected from the population with a probability weighted by the abundance of the age-sex class. This provided a mean to random select individuals that hunters were more likely to find by chance.

ii. Selective: an individual was randomly selected from the population with a probability weighted by tusk size

iii. Partially selective: an individual was randomly selected from the population with a probability weighted by tusk size and abundance of age-sex class.

The hunt continued until the quota was met.
Each combination of take level, hunting and quota strategies was replicated 1000 times.

AUTHOR CONTRIBUTIONS
PL collected the data. PL and DL designed the population and harvest models. DL implemented the models and carried out the simulations and analyses. DL and PL wrote the manuscript.

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REFERENCES


