Current Status of the African elephant (*Loxodonta africana*) EEP and projections for the future

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Abstract

Elephants are notoriously difficult to maintain in captivity and only recently has establishing and maintaining self-sustaining captive populations become a priority for zoological institutions. Demographic analysis of the African elephant population in European zoos using studbook data indicates that the population is not self-sustaining and could be demographically extinct within 50 years. Model predictions suggest a fecundity rate of M_x=0.06 is needed to establish and maintain a self-sustaining population. This is achievable if efforts are directed towards reproduction. To date, birth rates have been extremely low (Mx=0.01-0.02) as a result of management practices. Emerging techniques such as artificial insemination may aid breeding by allowing females that do not have physical access to males to reproduce. However, a self-sustaining population will create other challenges including a surplus of male offspring which will require a significant change in elephant-management practices. Captive elephant management is now a highly controversial issue and many have suggested abandoning the goal of maintaining a self-sustaining African elephant population. This study highlights that the African elephant population has the potential to become self-sustaining if zoos focus efforts on breeding and demonstrate their commitment by developing facilities for excess bulls.

Introduction

Although once widely distributed throughout Africa, the African elephant (*Loxodonta africana*) has suffered large scale declines and local extirpation over the past two centuries (**Bouche *et al.,* 2011; Wasser *et al.,* 2008**). The escalating trade in illegal elephant ivory and rapid human population growth and expansion have reduced the species range and numbers drastically. The majority of the remaining elephants in Africa exist in small fragments of protected land isolated by human developments, thus human-elephant conflicts are a common occurrence (**Naughton *et al.,* 1999; Poole, 1996**).

The African elephant plays a keystone role (**Power *et al.,* 1996**) in the diversity of habitats it occupies by influencing canopy cover (**Dublin *et al.,* 1990**), affecting species distribution (**Pringle, 2008**) and seed dispersal (**Blake *et al.,* 2009**). The loss of elephants throughout Africa will therefore have detrimental consequences to the integrity of entire ecosystems and their resources (**Coppollilo *et al.,* 2004; Laws, 1970**).

It is now acknowledged that conservation efforts need to focus on African elephants to ensure their survival in the wild for future generations. Zoos have the potential to play a role in this through public education, raising conservation funds, professional training, scientific research and political action. Furthermore, zoo elephants can help visitors make emotional connections and change behaviours that positively impact elephant conservation (**Smith & Hutchins, 2000; Keele et al 1999; Sukumar, 2003**). With elephant numbers declining, elephants in zoos may also serve as potential genetic or demographic resources that provide insurance against loss or degradation of *in situ* populations (**Faust *et al.,* 2006**).

For zoos to serve these purposes it is important to maintain self-sustaining populations well into the future, which until recently has not been a main focus of captive elephant management (**Faust et al 2006; Wiese & Willis, 2006**). Little effort was invested in breeding the African elephant in captivity because the numbers of wild elephants in Africa were high. In the 1970s and 1980s large scale culling programmes were even performed in an attempt to manage the overpopulation of elephants throughout the continent and the calves were exported to zoological institutions. This constant supply of exhibit animals meant the need to invest in and develop self-sustaining populations was not recognised (**Olsen & Wiese, 2000; Wiese & Willis, 2006**) and the priority of what limited resources and effort, has and still is, designated for the more endangered Asian elephant (*Elephas maximus*) whose population totals one tenth of the African elephant (**Olsen & Wiese, 2000**). By the late 1980s the culling programmes were discontinued as it was no longer viewed as a viable population management technique. This species was also listed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix 1 after it was recognised that elephant populations were in decline and needed legal protection. This meant greater controls were put on elephant trade and there were fewer opportunities for zoological institutions to import wild caught elephants making the need for self-sustaining populations even more crucial (**Clubb & Mason, 2002**).

Zoos now coordinate breeding programmes for hundreds of species to ensure they have access to animals into the foreseeable future and potentially for reintroduction back into the wild. To assist in managing the genetic and demographic structure of captive animal populations zoo associations have developed programmes; for example: the European Association of Zoos and Aquaria (EAZA) European Endangered species Programme (EEP), the American Zoo and Aquarium Association (AZA) Species Survival Plan (SSP) and the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) Australasian Species Management Program (ASMP) (**Wiese & Willis, 2006**).

The African elephant EEP was established in 1993, with the initial purpose of collating information about the population (**Terkel, 2004**). This has since been revised and now follows the same guidelines as other EEP programmes i.e. the captive population is managed to maintain a level of genetic diversity and size commensurate with that required to sustain a captive population for a minimum period of 100 years (**Walter, 2010**). The most important component of any captive breeding programme is compiling reliable and accurate population data required for population analysis and management. A studbook is the best source of compiled data, which is a chronology of a captive population containing detailed records of individual animals, including sex, parentage, location and date of birth, date of death, age, and details of transfers between facilities (**Ballou & Foose, 1996; Glatston, 1986; Hutchins & Wiese, 1991**). A well managed studbook is imperative for the establishment and long-term management of captive populations so they can fulfil their specific conservation goals. Analysing studbook data provides an insight into the genetic diversity and demographic stability of a population. It also yields invaluable data on patterns of fertility and mortality occurring under the prevalent management conditions. This information is equally relevant to conservation research and to captive management (**Glatston, 2001**).

Studies to date have performed demographic analyses on North American Asian and African elephant studbooks and European Asian elephant studbooks and have concluded that these captive populations are currently not reproducing at sustainable levels (**Clubb & Mason, 2002; Olson & Wiese, 2000; Wiese, 2000**). The results indicate that the EEP's are failing to establish self sustaining populations and without further importations from the wild and/or dramatic improvements in mortality and fecundity rates, they are likely to become extinct in captivity within the next 50 years (**Olson & Wiese, 2000; Wiese, 2000**). This analysis has not yet been performed on the European African elephant studbook.

There is an ongoing debate whether changes in management programmes would be desirable or even feasible. Many now argue that the self sustaining population goal is not achievable and that elephants should no longer be held in captivity (**Clubb and Mason, 2002; Cohn, 2006; Faust *et al.*, 2006; Rees, 2003; Schmid, 1998; Sukumar, 2003**). One study in particular "*Live Hard, Die Young*" which was commissioned by the Royal Society for the Prevention of Cruelty to Animals (RSPCA) concluded that elephants should be phased out in captivity with the immediate end to imports and breeding (**Clubb & Mason, 2002**).

Captive elephants have an uncertain future, particularly for the African elephant. The purpose of this paper is to evaluate the current status of African elephants in European zoos and to make predictions for the future based on current rates of fecundity and mortality. This will provide valuable information for assessing whether the European African elephant population is self sustaining, whether it has the potential to be self-sustaining and what management goals must be met for it to become self sustaining.

Methods and Materials

The study used data from the 2012 African elephant studbook (**Schwammer & Fruehwirth, 2012**), compiled by the Endangered Species Programme (EEP), which covers the periods 1861 to 31st May 2012. However, only data from 1st January 1960 through to 31st May 2012 were used for the analyses in order to facilitate comparisons with similar studies and wild population data. Furthermore, it was not mandatory for zoological institutions to keep records prior to this so it is likely that the data before this time are incomplete. The studbook contains detailed records (includes date of birth, sex, location, parentage, date of death and details of transfers between facilities) for a total of 430 (111.314.5: male.female.unknown) African elephants. This includes a living population of 206 (52.154) as of 31st May 2012.

Age-specific mortality and fecundity values were calculated following the methodology of **Wiese (2000)**, **Olsen and Wiese (2000)** and **Clubb & Mason (2002)**. Data were available for a total of 140 (35.105) elephants that died at a known age. Wild-caught elephants have estimated ages but since elephants were historically caught as juveniles, age estimates are generally correct to within 1 year so estimation errors should not alter predictions greatly in these analyses. These data were used to calculate age-specific mortality (Qx) which uses the age of the current population to estimate the proportion of animals that die during age X. A similar procedure was used to calculate age-specific fecundity (Mx) which is half the average number of young produced by parents of age X. Mortality and fecundity values were calculated for males and females separately.

The age-specific mortality and fecundity values were applied to the living population on 31st May 2012 to predict population growth 50 years into the future. This was done for the female population only since females are typically the limiting gender in the demographics of most mammal populations (**Ricklefs, 1979**) and there have been few males in the European population that sample sizes are relatively small and would give less reliable results. It was presumed that all animals were dead at the age of 52. Although elephants are known to live beyond this age, no data on African elephants living beyond this age in European zoos exists so any estimates would be guesses. It is possible that some elephants will live longer than 52 years in the future but numbers are likely to be low and will not dramatically affect the total population size. Furthermore, elephants at this age are reproductively senescent according to current data so will have no effect on the population's growth potential. The projection groups the age classes into three life stages; pre-reproductive (age classes 0-10), reproductive (age classes 11-35) and non-reproductive (age classes 36-50) (**Olsen & Wiese, 2000; Wiese, 2000**).

To determine what mortality and fecundity values are required to establish a self-sustaining captive population, mortality was reduced to a balanced low, based on data available (**Wiese, 2000; Olsen & Wiese, 2000**). Fecundity values were then gradually increased over an optimistic, but possible, range of age classes until the life table yielded a self-sustaining rate of growth (lambda=1.0).

Results

The European African Elephant Studbook reported 206 (52.154) African elephants living in European zoos as of 31st May 2013, of which 66% were wild caught (17.119) and 33% were captive born (35.35). The current age structure shows that the population is relatively young. The oldest living African female at this time was 51 years whilst the oldest male was just 38 years. 36% of all the females are aged between 25 and 34. Males constitute a small proportion of the population (25%) of which 52% are 15 years or below and are therefore not yet reproductively viable (**Sukumar, 1989**) (**Fig.1**).

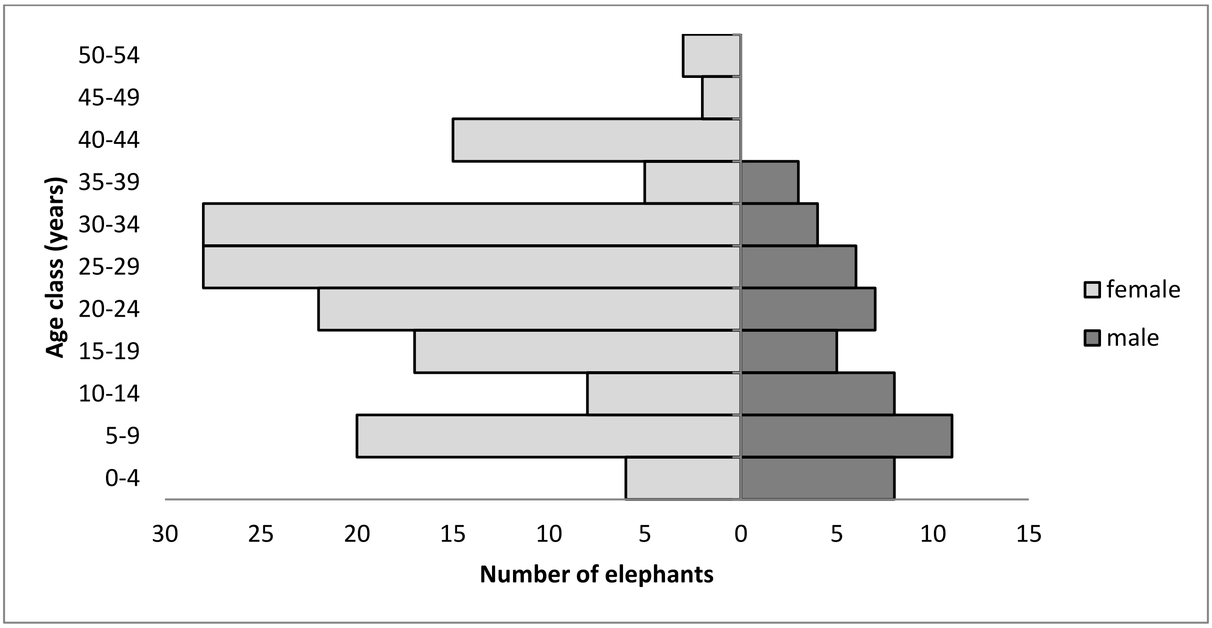

Fig.1: Population pyramid illustrating the skewed age distribution of male ( ) and female ( ) African elephants in the European studbook population as of the 31st May 2012.

144 (35.105.4) elephants with known ages at death have died in European zoos since 1960, 72% of which were wild born animals. The mean life expectancy (i.e. mean age at death) was 19 and 14 years for females and males respectively. Recalculating this figure to exclude calves 5 years old and under (because of the possibility that deaths have very different causes e.g. stillbirths, infanticide and rejection) increased the mean life expectancy slightly to 23 and 18 years for females and males respectively.

Age-specific mortality was found to peak in infants less than 1 year of age (10% of males, 12% of females) and then remains under 3% until 17 years of age when it peaks again in the female population. After 19 years it drops again and remains under 3% until 30 years when it rises in a series of peaks. Males have a higher mortality than females remaining below 5% until around 16 years of age when several large peaks and troughs appear (**Fig.2**).

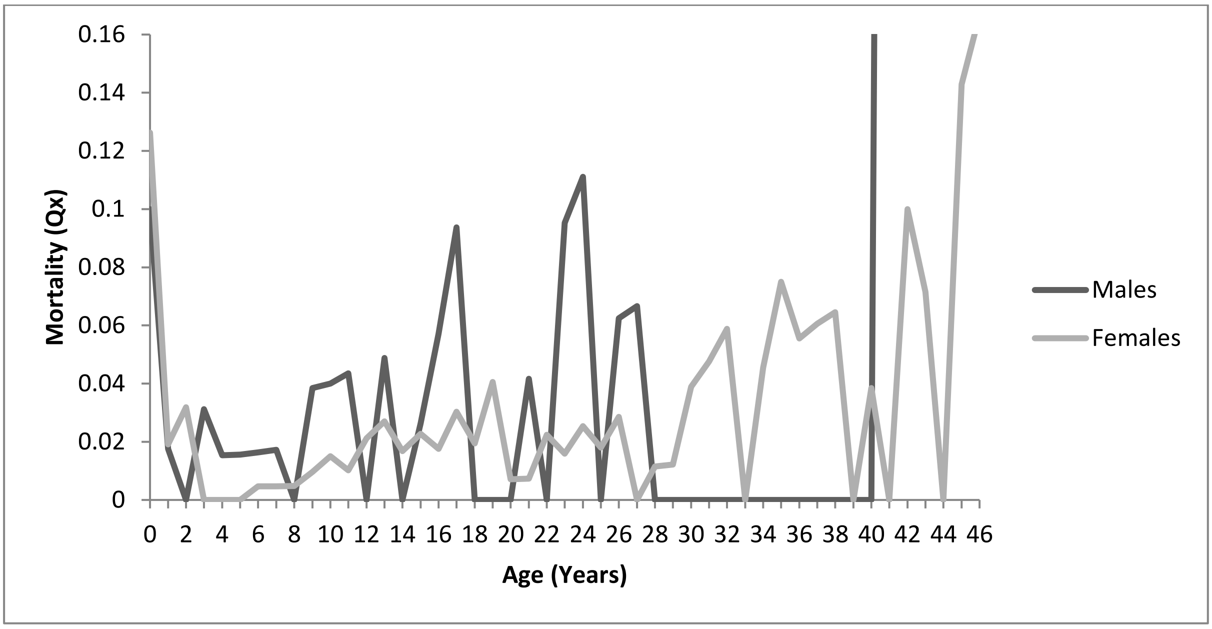

Fig.2: Age-specific mortality (Qx) of African male ( ) and female ( ) elephants in European zoos.

A total of 112 African elephants have been born into European zoos between 1960 and 31st May 2012. After the first birth occurred in 1965, there was a significant increase in the absolute number of captive births ($r=0.749$, $n=52$, $P<0.001$) with a peak of 10 births in 2005 (This includes all births and does not account for infant mortality) (**Fig.3**). All African elephant reproduction in European zoos has been attributed to 56 females and 18 males. Few elephants produce calves until around 13 years of age, yet females have given birth as young as 3 years old and males as young as 6 years old have sired calves.

For the female population, fecundity fluctuates between 0.01 and 0.02 until the age of 27 when reproduction largely ceases. However there is a secondary peak at 41 years. In male elephants, fecundity fluctuates between 0.02 and 0.06 until the age of 34 when reproduction ceases (**Fig.4**). The average age at which females and males produce calves was 19.1 and 21.3 respectively and the average age at first calving was 15.2 years (range 4-28) and 15.5 (range 6-24) respectively.

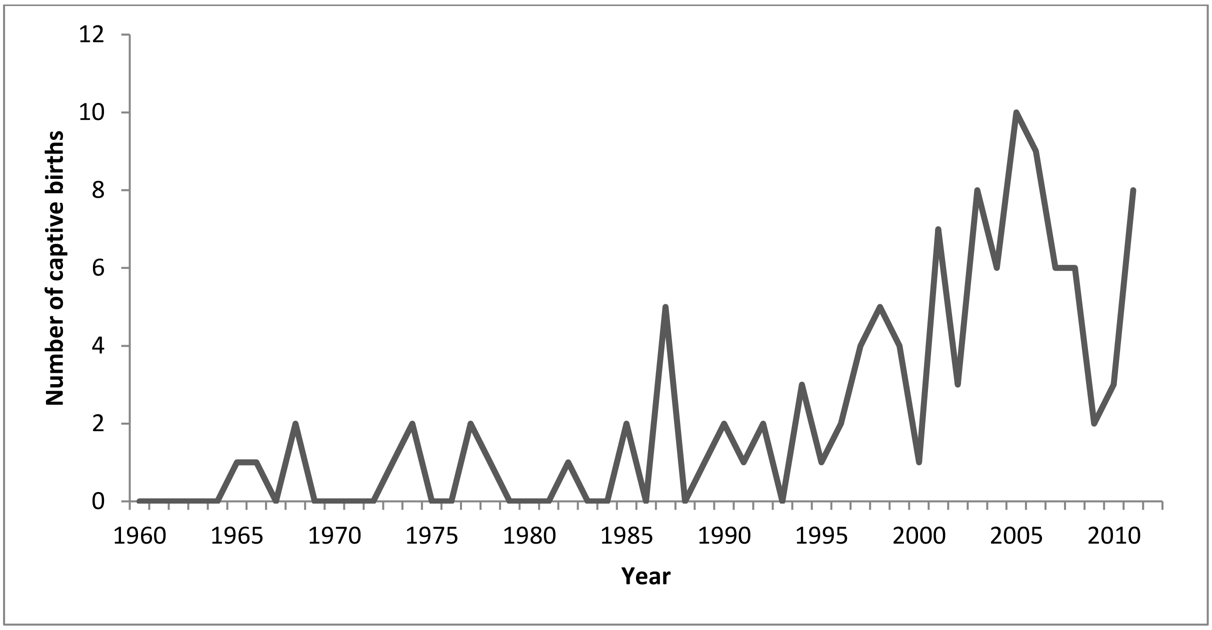

Fig.3: Absolute number of captive births in European zoos between 1960 and 2012.

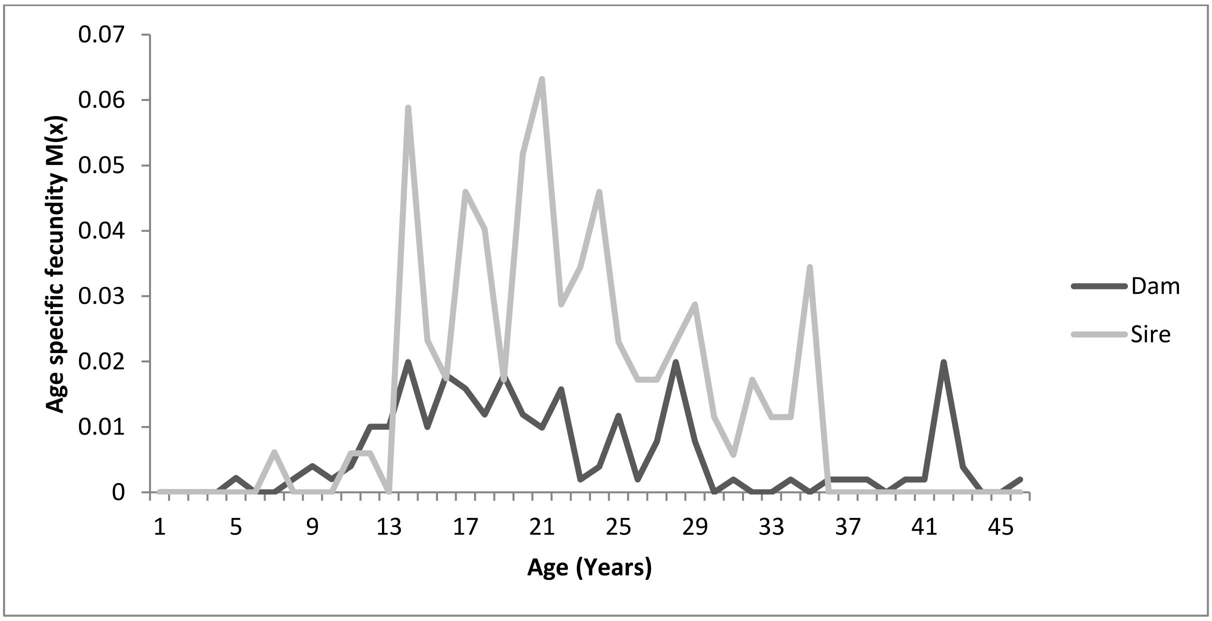

Fig.4: Age-specific fecundity (Mx) in male (☐) and female (■) African elephants in European zoos.

Applying the current age structure to the mortality and fecundity values, it is predicted that the captive population will decline in the future if we rely on births rather than importation to sustain the population and assuming that the same management success as in the past 50 years. The current population (2012) consists of 154 female elephants. In 50 years (2062), the projected population without imports or improved mortality and fecundity will consist of just 7 female elephants 4 of which will be post-reproductive (**Fig.5**).

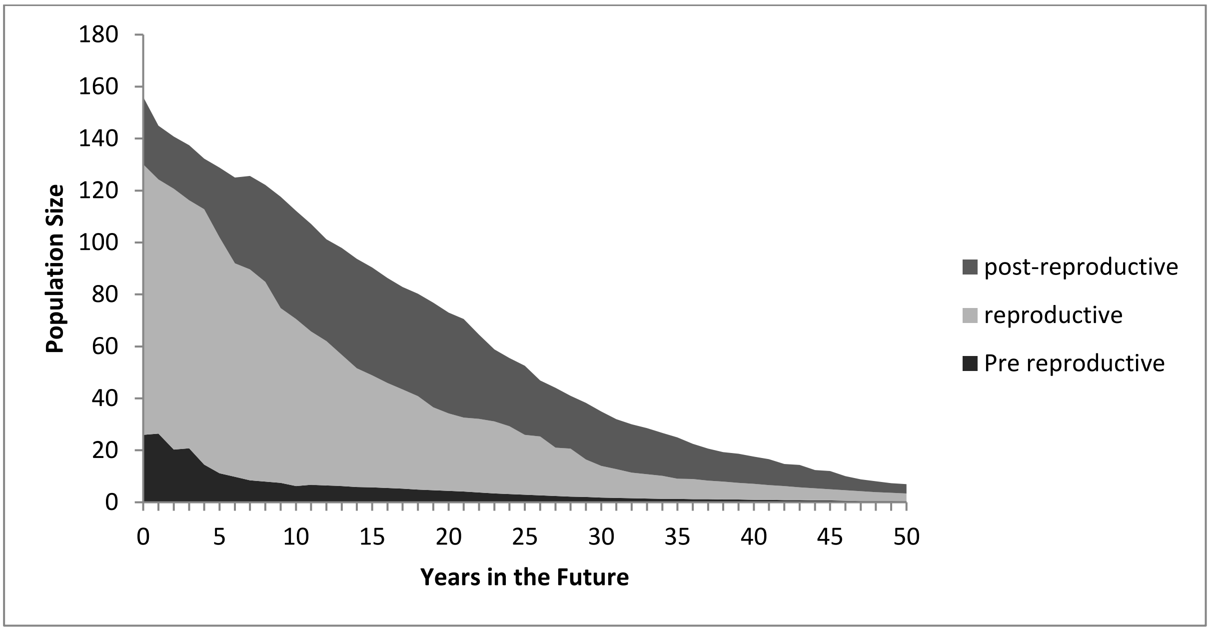

Fig.5: The population projection for the captive African elephant population in European zoos based on the current mortality and fecundity rates. The projection groups the age classes into three life stages defined by Wiese, 2000 and Olsen & Wiese, 2000; Pre-reproductive (age classes 0-10), reproductive (11-35) and non-reproductive (36-50).

To determine what is required to create a self sustaining captive population, model mortality and fecundity curves (**Fig.6**) were created using optimistic, but reasonable, values. For this model, first year mortality was lowered to $Q_0 = 0.10$. Model mortality remains at $Q_{3\text{-}32} = 0.01$ for ages 3 to 32, then rises as the population ages through the late 30s and 40s. All animals are assumed dead after the age of 52 ($Q_{52} = 1.0$). Like the North American elephant populations (**Olson & Wiese, 2000; Wiese, 2000**), increased fecundity must be the focus to attain a self sustaining population. The model fecundity curve increases rapidly from the age of 8 and remains at $M_{12\text{-}35} = 0.06$. Elephants in the model reproduce until the age of 37, which is optimistic but not biologically impossible.

The model yields a population growth rate of lambda=1.32. Initially, the population rises slightly as the number of pre-reproductive individual's increases. In 20 years the population falls due to the large proportion of individuals entering the post-reproductive age classes. However, after 28 years there is a sudden population growth as the number of reproductive-age animal's increases and the population rises above current numbers (156 females) to 208 females with the majority of animals in the reproductive and pre-reproductive age groups (**Fig.7**).

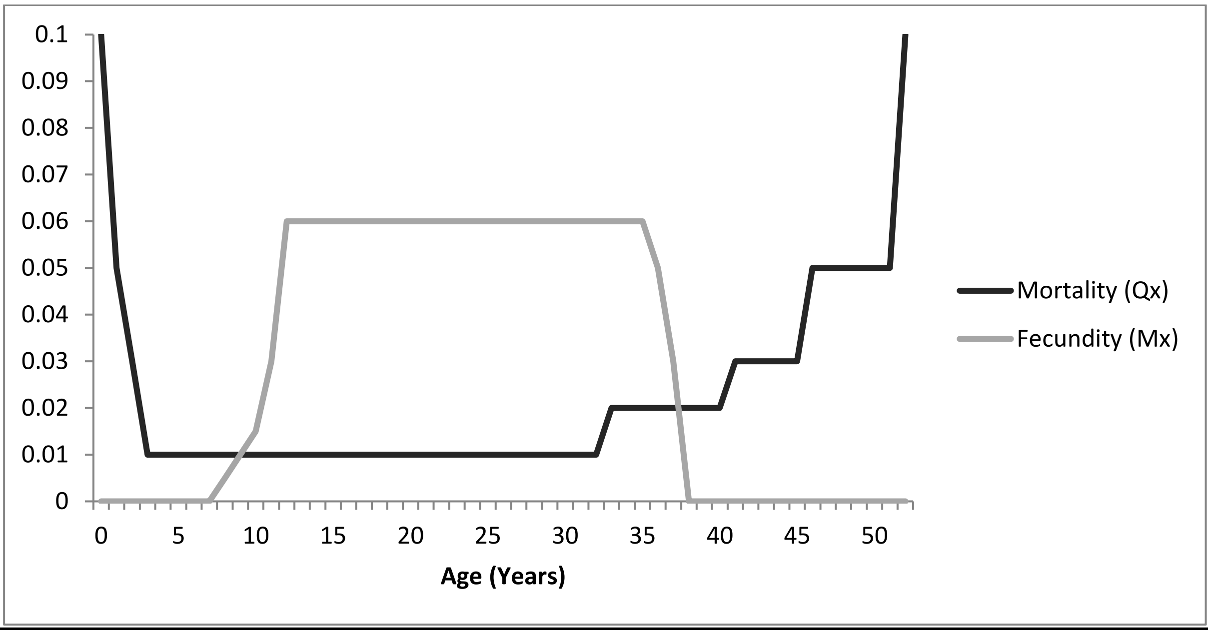

Fig.6.: Model mortality (Qx) and fecundity (Mx) values necessary to support a self-sustaining population of female African elephants in European zoos.

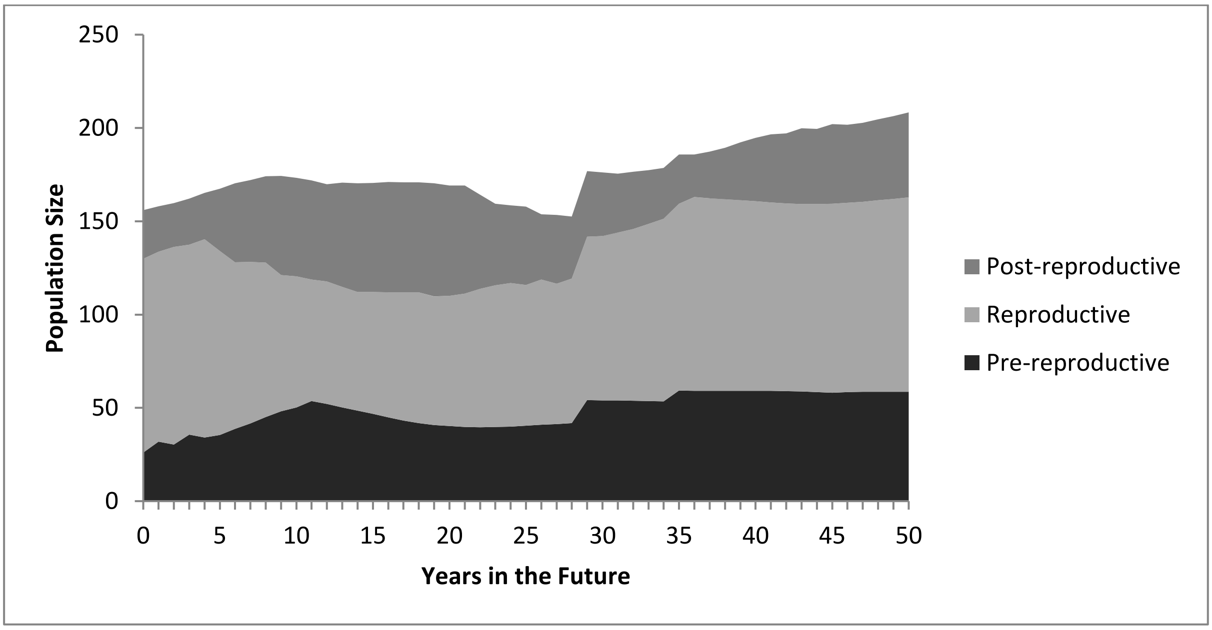

Fig.7: The model mortality and fecundity curves applied to the European African elephant population as of 31st May 2012.

Discussion

The population of African elephants in European zoos is not self sustaining. On the 31st May 2012 the population was heavily skewed towards females in their late twenties and early thirties (**Fig.1**), due to the selective importation from the wild in the 1980's. Females were the preferred sex largely due to the practical problems and financial constraints of housing adult males which are notorious for becoming unmanageable and aggressive (**Schulte, 2000**). Consequently, females are the most common sex in zoos (ratio 1.3). In the younger age groups, however, the number of males and females is almost equal because the majority of the younger generation are captive born animals that have a sex ratio of 1:1 (**Fig.1**).

Most species have a greater life expectancy in captivity compared to their wild counterparts, due to the reduced risks of disease, predation, starvation and competition (e.g. **Conway, 1986; Mallinson & Barker, 1998**). However, it appears that African elephants live far longer in the wild than in European zoos. For instance, **Moss, 2001**, concluded that female and male elephants in Kenya have life expectancies of 41 and 24 years respectively and they had a maximum lifespan of over 65 years. In contrast, African elephants in European zoos have life expectancies of 19 and 14 years for females and males respectively and a maximum lifespan of 51 years. Male elephants have an even shorter lifespan with the oldest recorded just 38.

There has already been much discussion in recent literature as to why elephants are dying so prematurely (**Clubb et al., 2008; Club & Mason, 2002; Mason *et al.,* 2009; Saragusty *et al.,* 2009**). Obesity, stress, health and reproductive problems, aggression-related incidences, accidents often relating to enclosure design and malnutrition are all contributing factors to the lowered life expectancy in zoo elephants. **Clubb & Mason, (2002)** found illnesses and diseases such as circulatory problems, heart failure, arthritis, cancer, tumours and salmonellosis were the most common cause of death.

Age specific mortality curves showed a peak in infant mortality (<1 year) which is not surprising due to their vulnerability. Infant mortality was 10% for males and 12% for females which is slightly higher compared to their wild counterparts (**Fig.2**). For instance, **Whitehouse & Hall-Martin (2000)** calculated infant mortality at 6.2% for a population in Addo Elephant National Park. Nevertheless, for most species, 10% juvenile mortality is extremely low and may be near the elephant's biological minimum (**Taylor & Poole, 1998**). Unlike American Asian elephants that have an infant mortality of 40% (**Wiese, 2000**), improving infant mortality is not a fundamental requirement to achieving a self-sustaining African elephant population in European zoos. Mortality peaked again when elephants were in their late teens and continued to fluctuate in a series of peaks and troughs thereafter (**Fig.2**). It is likely that the uneven nature of the mortality curve is due to the relatively small sample size for this species, especially in the older age groups so interpretation should be subject to caution. But there is no denying that captive elephants are dying prematurely.

Breeding African elephants in European zoos is a relatively new phenomenon with the first elephant born in 1965. But it wasn't until the late 1980's when captive breeding began to accelerate. This coincides with the time period when African elephants were awarded CITES Appendix 1 protection and when the large scale culling programs were discontinued as a population management option. Subsequently, importation of wild elephants which until this time had been the primary source for zoos became challenging (**Wiese & Willis, 2006**). As a result, a concerted effort was made to improve breeding rates in zoos. A significant increase in the number of captive births was found between 1965 and 2012 with a peak of 10 births in 2005. The series of peaks and troughs evident in figure 3 is likely a result of the small number of births and the sporadic nature of breeding success.

Asian and African elephants in North American zoos and Asian elephants in European zoos are breeding at younger ages than their wild counterparts (**Olson & Wiese, 2000; Schmid, 1998; Wiese, 2000**). This is, in part, also true for African elephants in European zoos. Females as young as 3 years old have given birth and males as young as 6 have sired calves **(Fig.4**). These findings have not been observed in wild populations. For example, **Moss, (2001)** and **Owens & Owens, (2009)** report the youngest female to give birth in wild populations to be 8.5 and 8.9 years respectively. There are several reasons that could explain why elephants in captivity are sexually precocious. **Mar (2001)** suggests this may be due to the greater level of nutrition received in captivity compared to the wild. Most zoo elephants are considered obese, and are therefore likely to raise their fat reserves above the threshold required for ovulation at an earlier age (**Barnes, 1982; Kurt, 1995**). The rearing environment has also been attributed to premature reproduction as captive born females give birth significantly earlier than wild caught ones (**Clubb & Mason, 2002**). In male elephants, the lack of competition in captivity between males for estrous females causes elephants to produce active sperm earlier in life (**Olsen & Wiese, 2000**).

Despite elephants breeding younger in captivity, the mean age at first calving was 15 years for both males and females. Due to the almost 2 year gestation period of elephants (**Kurt & Mar, 1996**), the average age at conception was 13 years. For comparison, the average age at sexual maturity in wild female African elephants taken from 14 studies summarised by **Croze *et al.*, (1981)** was 12.2 years (range 7.5-23). Thus for African females, the average age at first calving in European zoos and the wild is very similar.

Reproduction in female elephants generally begins at the age of 13 when fecundity fluctuates between 0.01 and 0.02 until the age of 27 when reproduction largely ceases. Males have a higher fecundity than females fluctuating between 0.02 and 0.06 until the age of 34 when reproduction ceases (**Fig.4**). These birth rates are considerably low compared to wild data. For example, **Whitehouse & Hall-Martin (2000)** calculated fecundity rates between 0.20 and 0.25 for a wild African elephant population and only after the age of 40 did fecundity begin to decline slightly. The shortened reproductive lifespan of captive elephants is likely due to the small number of individuals surviving in the older age groups. However, it is not currently possible to isolate whether low birth rates is a result of biological factors or management practices that restrict female access to males. The recent increase in birth rate since the development of the 'Forward Planning and EEP Management for Elephants in EAZA Institutions' in 1998 (**Fig.3**) would suggest that the low birth rate observed before this initiative was the result of management practices and not biological factors. This would indicate that focused efforts and adequate availability of reproductive-age animals would enable population to become self-sustaining (**Wiese & Willis, 2006**).

Applying the current age structure to the mortality and fecundity curves predicts a similar population decline to the Asian and African elephant populations in North American zoos (**Olsen & Wiese, 2000; Wiese, 2000**). The projected population in 50 years without imports or improved mortality and fecundity will decline from 154 females to 7 (**Fig.5**). The model predictions indicate that to establish and maintain a self-sustaining population given the current age structure and assuming mortality rates are reduced, would require a fecundity rate of M_x=0.06 (**Fig.6**). This would achieve the same goal as North American African and Asian populations would achieve with a fecundity rate of M_x=0.05 and M_x=0.08 respectively (**Olsen & Wiese, 2000; Wiese, 2000**). It appears that the African elephant is faring better in captivity than their Asian cousins. Even with dramatic increases in births it is likely that the Asian population will require importations into the future (**Olsen & Wiese, 2000**). But importation is not nearly as crucial for the African populations since the current excess of females in the reproductive age class will increase the population quickly if improvements can be made within the next 5-10 years (**Fig.7**).

The model curves (**Fig.6**) indicate that a population with low mortality would still require a substantial increase in fecundity (i.e. M_x=0.01-0.02 to M_x=0.06) to be self sustaining. This highlights the need for elephant management plans to develop and focus on captive breeding to achieve the goal of maintaining a self-sustaining population. Since the sex ratio of captive births is 1:1, the total number of births must be doubled to account for male offspring. Therefore, under the model conditions, the studbook population would require 12 births annually. Given the significant increase in births over the last 50 years (**Fig.3**), this fecundity rate is achievable. However, the limited number of males in European zoos will hinder increased reproduction without numerous moves to bring reproductive females to breeding institutions. Currently efforts are underway to examine acyclicity in elephants (**Dow *et al.,* 2011; Freeman *et al.,* 2009**) and the recent success in artificial insemination will aid breeding by allowing females that do not have physical access to a bull to reproduce (**Brown *et al.,* 2004; Thorngtip et al., 2009**).

An effort to increase captive breeding in order to maintain a self-sustaining African elephant population in Europe will inevitably increase the number of male offspring to be managed. This will require a significant change in elephant-management practices since males are notorious for being unmanageable and aggressive (**Kurt, 1974; Poole, 1987; 1989; Sukumar, 1989**). This represents a considerable management problem in that it poses a degree of risk and requires highly specialised husbandry and expensive housing which has been a major factor in institutions deciding not to breed reproductive-aged females. Relatively few zoos are willing or able to invest in facilities suitable for keeping adult males (**Ganswindt *et al.,* 2005**). Nevertheless, holding institutions for elephants will need to develop facilities for excess bulls that can be rotated through the breeding facilities for access to cows if the self-sustaining goal is to be achieved. Sperm sorting and other gender selection research techniques are being developed and these may relieve the excess male situation in the long term. However, these techniques will take decades to affect the population significantly (**Wiese & Willis, 2006**).

It should be emphasised that the model presented here is as optimistic as possible and assumes that mortality and fecundity will change to the model values immediately. In reality, it is likely that these values are not met for a number of years but the longer it takes, the higher fecundity will have to rise to bring the population back to a self-sustaining level. It also assumes that all females of a given age have the same probability of giving birth regardless of whether they are pregnant or non-cycling. It is recommended that the reproductive status of all individuals in the population is evaluated in order to uncover any fertility problems that may make the model values unreachable for the current population. Further investigation into social and breeding behaviour is also recommended to determine whether husbandry and management techniques should be modified to improve natural reproduction and survival rates (**Olsen & Wiese, 2000**).

Individual-based models can be more reliable as they incorporate individual behaviour, animal location, genetic background, reproductive status and other species specific variables. Individual-based models are also stochastic and can be used to predict the variability around an outcome, which is rarely the case for deterministic models (**Wiese & Willis, 2006**). Even so, recent stochastic simulations using individual-based models predict a situation for the American elephant population that is only a slight improvement on the previous deterministic projections (**Wiese, 2000**).

In conclusion, captive elephants have an uncertain future. The European African elephant population is not self-sustaining and will decline quickly over the next 50 years without improved mortality and fecundity. In order to become self-sustaining, the primary goal for zoo managers is to increase birth rates in the population, with a secondary goal of reducing mortality rates. With this increased reproduction, however, institutions must also plan for an increase in bull elephants and demonstrate their commitment to breeding by developing adequate holding facilities promptly. Artificial insemination can assist with captive elephant breeding but this and other technologies need further investigation as potential aids to increasing the probability of self-sustaining captive populations. Furthermore, resources and efforts must be committed towards further understanding the reproductive biology of African elephants to increase reproductive success.

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