Fecundity and population viability in female zoo elephants: problems and possible solutions

R Clubb[†], M Rowcliffe[‡], P Lee[§#], KU Mar[¶], C Moss[#] and GJ Mason*[¥]

[†] Wildlife Department, RSPCA, Wilberforce Way, Southwater, West Sussex RH13 9RS, UK
[‡] Institute of Zoology, Zoological Society of London, London NW1 4RY, UK
[§] Department of Psychology, University of Stirling, Stirling FK9 4LA, UK
[#] Amboseli Trust for Elephants, PO Box 15135, 00509 Langata, Nairobi, Kenya
[¶] Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
[¥] Animal Sciences Dept, University of Guelph, Guelph N1G 2M7, Canada
* Contact for correspondence and requests for reprints: gmason@uoguelph.ca

Abstract

*We previously reported that African (*Loxodonta africana*) and Asian (*Elephas maximus*) female elephants in European zoos have shorter adult lifespans than protected conspecifics in range countries. This effect was the cause of greatest concern in Asian elephants, and risk factors within this species included being zoo-born, transferred between zoos, and possibly removed early from the mother. Here, we investigate these risk factors further; assess fecundity and sustainability in European zoos; and propose testable hypotheses as to the causes of these animals' problems. Although imported wild-born Asian elephants live longer than zoo-born conspecifics, being imported when juvenile or adult appears no more protective than being imported in infancy, suggesting that the benefits of being wild- rather than zoo-born are conferred early in life. Zoo-born Asian neonates are significantly heavier than those born to working animals in range countries, with a possible tendency to be fatter. In zoos, African elephants have tended to be removed from their mothers at older ages than young Asians, and were also transferred between zoos significantly less often: factors that could possibly underlie this species' lower calf losses and improving adult survivorship in Europe. Both species have low fecundity in European zoos compared to in situ populations, and are not self-sustaining, declining at approximately 10% per annum if reliant on captive-bred females under historically prevailing conditions. Data from other species suggest that stress and/or obesity are parsimonious explanations for the suite of problems seen. We recommend specific screens for testing these hypotheses, and for potentially identifying vulnerable individuals within the extant zoo populations.*

Keywords: *African elephant, animal welfare, Asian elephant, fecundity, population viability, survivorship*

Introduction

Zoo elephants experience a range of problems suggestive of compromised welfare, such as elevated mortality and reproductive failure (eg Kurt & Mar 1996; Taylor & Poole 1998; Clubb & Mason 2002; Clubb *et al* 2008). Here, we use data analysis to explore the reasons for this. There are at least 2,114 elephants worldwide, currently living in zoos, safari parks, sanctuaries, circuses and with private keepers (Koehl 2008). European zoos and circuses house approximately 300 African elephants (EEG 2008) while North American zoos house approximately 220 (Olson 2008). In contrast, about 500,000 African elephants (*Loxodonta africana*) live in the wild; these recently came off the IUCN 'Endangered' list (AfESG 2004), having shown an annual increase of 4% since 2002 (Blanc *et al* 2007). European zoos and circuses house approximately 450 (EEG 2008), and North American zoos, approximately 260 (Keele *et al* 2007) Asian elephants (*Elephas maximus*). This species

is still 'Endangered' (AsESG 1996), with around 60,000 living in range countries (Sukumar 2006; Hedges 2007). In North American zoos, neither species is self-sustaining, requiring importation from range countries in order to prevent population decline (Hutchins & Keele 2006; Wiese & Willis 2006): a practice criticised by the IUCN and others (Waithaka *et al* 1998; AfESG 2003; Hedges *et al* 2006). Despite considerable financial outlay — elephants' *ex situ* captive costs are an estimated ten times higher per capita per year than *in situ* conservation costs (Balmford *et al* 1995, 1996) — zoo elephants have apparently high mortality and low breeding rates. This has led to concerns over their health and welfare, with long-reported contributory problems (eg Taylor & Poole 1998; Richman *et al* 1999; Brown *et al* 2004) including *Herpes* virus, infertility and infanticide. Recently, we have shown that adult females of both species also have shorter lives in European zoos than in protected *in situ* populations (Clubb *et al* 2008).

This effect was the cause of greatest concern in Asian elephants: unlike Africans, overall lifespan in this species did not appear to have improved in recent years, and infant mortality was high. Risk factors included being born in a zoo rather than in the wild, being moved between zoos, and possibly being removed from the mother at a young age. These findings are presented briefly elsewhere (Clubb *et al* 2008). Here, we take the opportunity to provide specifics on the datasets used, expand on these findings, and discuss the potential causes of — and, hence, potential solutions to — these problems. First, we investigate the benefits to Asian elephants of being wild-born by: i) investigating whether a longer infancy spent in the wild prior to importation is associated with a longer lifespan, and ii) testing the hypothesis that zoo-born infants are abnormally heavy (cf Kurt & Mar 1996; Dale 2009), since large birth weights can have lasting adverse effects on health (see *Discussion*). Second, we investigate whether species differences in: i) age at separation from the mother, and ii) transfers between zoos, potentially explain the more worrying mortality patterns of Asian elephants. Third, we assess fecundity and long-term equilibrium population growth, to determine whether zoo populations are self-sustaining.

Materials and methods

Datasets for elephants in zoos and reference populations

Zoo data came from European Endangered Species Programme 'studbooks'. These were accurate to 15 July 2005 (African elephants) and 12 June 2005 (Asian elephants). Data were checked for internal consistency using 'Clean Up' and 'Data Validation' functions in SPARKS (Single Population Analysis and Records Keeping System, Version 1 52); all errors found were corrected. Supplemental information was added from the European Elephant Group report (EEG 2002); this contained data for additional elephants (108 African, 96 Asian) plus some key missing dates. The African studbook contained few errors, and was largely corroborated by EEG data (EEG 2002). The Asian studbook initially contained numerous errors (eg missing birth types, dams listed in different locations to their calves at birth, etc), but most could be corrected via internal checks and comparison with EEG data.

Zoo records cover many decades, but we used only data from animals living in the population from 1st January 1960. Birth-dates for wild-born females were estimated to the nearest year (cf Wiese 2000), and those imported when under one-year old were assigned the maximum age at import (one year) to avoid estimated lifespan of zero. We excluded the few African forest elephants (*Loxodonta africana cyclotis*), plus any individual with unknown ages/dates of entry to (or exit from) the zoo population, or ambiguous birth origins (eg unknown, or recorded as 'timber camp'). This resulted in a dataset comprising information on import/birth and death dates (where applicable) for 1,055 elephants (402 African, 653 Asian). These came from 236 zoos across Europe, Israel and the former Soviet Union (which we call 'European' for brevity). Our analyses focus on females (n = 786: 302 African, 484 Asian), since the small population sizes for males and their relative recency (few wild-caught elephants are male) means that too few animals have died in each age class to allow valid survivorship analyses (cf Wiese 2000).

To act as reference populations, we used two well-documented *in situ* populations judged to yield demographic benchmarks that zoos should reasonably meet or exceed (Clubb *et al* 2008). For African elephants, we used a population continuously monitored in and around Amboseli National Park, Kenya, from 1972 to the present (see Moss 2001). Data came from 2,173 individually-recognised elephants of both sexes. Analyses here were based on births up to the end of 2004, for a total of 1,093 females. Ages were known with a maximum error ± 6 months for most females under the age of 35 (n = 799). Ages were estimated either to the nearest year or ± 2.5 years for females aged between 35 and 45 (n = 125), and estimated to a maximum of ± 5 years for animals over 45 years (n = 179). Animals whose ages were estimated at first sighting were reassessed at death (from tooth ages), or by changes in size and shape during maturation compared to known-age reference animals (Moss 2001). Human-caused deaths (for details, see Clubb *et al* 2008) were treated as right-censored in survivorship analyses to create 'Natural mortality' datasets conforming more closely to fully protected populations.

Compared to similar protected *in situ* populations, our African reference population seems representative, even conservative. The Amboseli population has a long-term average growth of 3.75% (Moss 2001), and rates in other African reserves are similar or greater, eg 4.6% per annum in Samburu, Kenya (Wittemeyer *et al* 2005), 6% in Addo, South Africa (Whitehouse & Kerley 2002), and over 8% elsewhere in South African (Slotow *et al* 2005; van Aarde & Jackson 2007). Furthermore, calf mortality in other reserves is similar to or lower than Amboseli, eg just 10.5% over five years in Samburu, Kenya (Wittemeyer *et al* 2005) compared to 10% in the first year for Amboseli (Clubb *et al* 2008; Moss & Lee, in press). Finally, deaths caused by humans were almost certainly random with respect to elephant quality (ie weak animals were not targeted): thus treating them as right-censored should not increase the apparent fitness of this population.

For Asian elephants, our reference was captive elephants working for the Government-run Myanma Timber Enterprise ([MTE]; Mar & Win 1997; Sukumar 2003; Mar 2007; Saragusty *et al* 2008). MTE studbooks document animals' histories to inform company veterinarians, forest officials and mahouts, recording over 8,000 elephants living in approximately 260 timber camps throughout Burma's forested regions since the early 20th century. For analysis, we excluded males and animals with unknown ages, sexes, birth origins or dates of entry to (or exit from) the population, and records with obvious errors (eg birth dates later than death dates). At the time of this analysis, valid data were available on 5,213 animals of both sexes, 2,905 of them female. The earliest useable captive birth record was in 1925, the earliest useable wild-capture record was in

1951, and the last year of follow-up was 2000. It is worth noting that the data have been subject to a long and continuing process of checking and validation over which the number of useable records has fluctuated to a small degree; the total number of individuals used here may therefore differ slightly from that reported in earlier or subsequent publications based on the same data set. For captive-born animals, ages were known precisely. For wild-born animals (largely from before a capture-ban in 1994), age at capture was estimated by experienced elephant handlers, based on shoulder height and other indicators, such as skin characteristics (Kurt & Kumarasinghe 1998; Sukumar 2003) and folding patterns of the dorsal aspect of the ear flap (Goswami *et al* 2007). The error in these estimates is likely to be within one year for young animals (under 20), which form the majority (68%) of those captured from the wild (n = 1,344). Again, human-caused deaths (see Clubb *et al* 2008) were treated as right-censored in analyses to create 'Natural mortality' datasets.

Just as for the Amboseli population, human-caused deaths were almost certainly random with respect to elephant age/health — thus, again, treating them as right-censored should not bias increase this population's apparent fitness. While there have been suggestions that MTE records under-report infant mortality, this was not a serious problem for our analyses (see also Saragusty *et al* 2008). For MTE infant mortality to be as high as that seen in European zoos (Clubb *et al* 2008), some 161 deaths of live-born female calves (thus approximately 320 calves in total, assuming similar male losses) would need to be unreported: this would represent approximately 20% of overall calf production, and experience of MTE recording procedures suggests this is implausible. Furthermore, the MTE population is potentially self-sustaining (based on modelling equilibrium growth rate using the demographic rates of captive-born elephants; Mar 2007), and comparisons with other populations further validate this dataset. Other, well-managed, self-sustaining captive populations in southern India and Sri Lanka resemble MTE (see Mar 2007; Clubb *et al* 2008) in having infant mortality rates under 15%, median complete female lifespan of approximately 45 years, and annual fecundities of over 0.05 (Sukumar *et al* 1997; Taylor & Poole 1998). We used captive working animals, rather than wild individuals as our reference because good, valid data were readily available. However, conditions for working elephants in range countries are not necessarily ideal (eg Lair 1997; Hedges *et al* 2006, Ramanthan & Mallapur 2008; Saragusty *et al* 2008) particularly if wild-caught (see Mar 2007; Clubb *et al* 2008). The MTE population thus probably underestimates how well Asian elephants fare if optimally protected; for instance, data from wild Asian elephants suggest even better calf survivorship, with just 5% infant mortality per annum between 0 and 5 years (Sukumar 1989).

Age at import

We focused on wild-born, zoo Asian elephants because 'birth origin' affected this species (see *Introduction*), and because sample sizes were too small for African elephants. The age at which each elephant entered captivity ('Import age') was included as covariate in an adult survivorship analysis (see below).

Birth weight

Birth weight data for zoo and *in situ* elephants were gleaned from a data and literature search. Again, this focused on Asian elephants due to their birth origin effect plus the paucity of data for African elephants. Information came from European zoo studbooks, along with *Asdell's Patterns of Mammalian Reproduction* (Hayssen *et al* 1993), Kurt and Mar (1996), and the *International Species Inventory System* accessed via the Elephant Care International website (http://www.elephantcare.org). Where possible, data were used to calculate two estimates of body fat: Body Mass Index (BMI: weight/frame size^2) and Ponderal Index (PI: weight/frame size^3).

Age at separation from mother

The age at which zoo-born, female calves were separated from their mothers, defined as calf transfer to another zoo, was extracted from studbooks. One calf was separated by the dam moving zoo; this data point was excluded.

Transfer rates

For each individual, the number of times she was transferred between zoos was totalled, excluding initial importation for wild-born animals, as was the total number of years she spent in captive facilities over her entire life. The ratio of these two figures was our index of transfer rate.

Fecundity and population growth rates

Age-specific fecundity, the number of live-born, female offspring born, B_x, per female alive, f_x, between the ages of x and $x + 1$: B_x/f_x (Caughley 1977), was calculated for zoo and reference populations. Results were plotted for visual comparison. The future population viability (long-term equilibrium growth rate) of zoo elephants was also modelled to identify whether European populations are expected to be self-sustaining. Parameter values were taken from fecundities calculated here, and previous survivorship analyses (Clubb *et al* 2008). We used captive-born animals' characteristics where they differed from wild-born, to model the situation without further importation to zoos.

We then re-ran all matrices using the demographic parameters of our reference populations in order to model better possible future scenarios for European zoo elephants and identify the respective benefits of improved fecundity and improved survivorship. Using their age-specific fecundities represents scenarios in which all zoo females have ready access to males, high conception rates, and low stillbirth rates. Using the 'natural mortality' survivorship of our reference populations (Clubb *et al* 2008), instead provides scenarios in which zoo elephant mortality rates are reduced to the low levels experienced in the wild, thus assessing whether improving survival alone would render zoo populations self-sustaining.

Statistical analyses

All statistical tests are two-tailed, with an alpha of 0.05. Cox Proportional Hazards Regressions were used to investigate the effects of import age on elephant survivorship since these can assess the impact of both categorical and contin-

uous independent variables on age-specific survivorship (cf, Raggi *et al* 2004; Del Giudice *et al* 2006; Anthony *et al* 2007; Clubb *et al* 2008). Animals were included in survival analyses from the point they entered the population (eg through importation, capture or birth) and an 'event' (eg death from natural causes, or censorship through loss to follow-up or being alive at the end of the dataset). Premature and stillborn calves were excluded. Survivorship analyses were also used to explore species differences in the age at separation from the dam, this being treated as an 'event'. The proportionality assumption of the Cox model was always tested using scaled Schoenfeld residuals (Grambsch & Therneau 1994); all reported results met this assumption. Analyses were all run using 'R' (version 1 9 1).

Body Mass and Ponderal Indices for zoo elephants and *in situ* conspecifics were compared where possible using Mann-Whitney *U*- or *t*-tests. Transfer rates for African and Asian elephants were compared using a *t*-test (Minitab v 13).

Population growth rate analyses used a female-only Leslie matrix formulation (Caswell 2000) with 70 annual age classes, and a transition matrix of the form:

$$\begin{matrix} s_0.m_1 & s_0.m_2 & \ldots & s_0.m_{69} & s_0.m_{70} \\ s_1 & 0 & \ldots & 0 & 0 \\ 0 & s_2 & & 0 & 0 \\ \vdots & & \ddots & & \\ 0 & 0 & & s_{69} & s_{70} \end{matrix}$$

where survival s_x is the probability that an individual aged x survives to age $x + 1$, and m_x is the per capita production of female calves by females in the year group to age x. The rate of population change of this matrix at stable structure, λ, gives the equilibrium population multiplication rate. Raw age-specific fecundity estimates were used in the matrix up to year group z, in which there were at least 20 potential mothers in the population ($z = 49$ in Asian elephants, $z = 53$ in African); in older females, fecundity was assumed to be constant at the average for this age group: $m > z = B > z/f > z$. Survivorship values, σ, from Kaplan-Meier curves were smoothed using Siler's (1979) model of mortality under competing risks:

$$\sigma_x = e^{(-a/b)(1-e^{-bx})}e^{-cx}e^{(f/g)(1-e^{gx})}$$

where a, b, c, f and g are parameters to be estimated. From this, survival probability for age class x is given by:

$$s_x = \frac{\sigma_{x+1}}{\sigma_x}$$

Curve parameters were estimated using a Gauss-Newton non-linear fitting procedure, again implemented in R.

Results

Exploring the effects of being zoo-born

Import ages for wild-born, Asian females were extremely wide-ranging: from 7 months to 54 years. However, import age had no significant effect on adult survivorship ($z = -0.88$, $P = $ ns). Calf birthweight data did, in contrast, yield effects: Asian calves born in zoos were significantly heavier than those born in timber camps (Table 1); they also tended to

have greater Ponderal Indices — a trend we suggest needs verifying and investigating in future work (see *Discussion*).

Exploring how husbandry differs between the species

Median ages of separation from the dam were 8.3 years for zoo-born Asian females, and 16.3 years for zoo-born African females: this showed a trend towards significance ($z = 1.65$, $P < 0.10$). Inter-zoo transfer rates averaged 0.140 transfers per year for Asian females (n = 386 individuals), and 0.026 transfers per year for African females (n = 216 individuals) ($t = 3.91$, $P < 0.0001$, df = 393).

Fecundity and population growth rates of both species

Fecundity is much lower in zoos than reference populations, and breeding ceases at least a decade earlier (Figure 1). Note that sample sizes for Amboseli females over 50 were small (fewer than 10 females per age class), and this probably accounts for the apparent increases in fecundity towards the end of life. Some females carry on giving birth into their 60s (see Moss 2001), which is why the plot fails to return to zero even at these older ages. Small sample sizes precluded investigating birth origin effects on reproductive rates in zoos.

Both species are projected to decline at a rate of approximately 10% per year, if reliant on captive-bred animals and kept under historically-prevailing conditions (Figure 2). Improving fecundity to reference population levels would have a much greater effect than would improving survival (Figure 2); indeed, predicted population growth rates approach stability for African elephants if just fecundity alone is improved. However, for both species it is still necessary to improve survival too, this being especially crucial for Asian elephants.

Discussion

Here, we summarise our analyses of fecundity and population viability in European zoos, and compare these results, alongside our previous survivorship findings, with North American zoo populations. We look in detail at risk factors for Asian elephant survivorship, and potential species differences in husbandry. Finally, we identify potential causes of zoo elephants' problems, and suggest how to test these hypotheses.

The fecundity and population viability of female elephants in European zoos

For both species, fecundity is much lower in European zoos than in reference populations. To some extent, this is simply caused by logistics, particularly restricted breeding opportunities: zoo females, unlike Amboseli and MTE females, have limited male access. However, there are clearly zoo-specific physiological problems too: while their *in situ* conspecifics breed well at least into their late 40s, zoo females show minimal breeding after their 30s. This combines with prevalent acyclity (see Brown *et al* 2004; Freeman *et al* 2004; Hermes *et al* 2004), and, in Asian females, high still-birth rates (Clubb *et al* 2008). One potential explanation for reproductive senescence involves not breeding while young (eg Hermes *et al* 2004), but cause and effect have yet to be

Table 1   Asian elephant neonatal bodyweights and body fat estimates.

Group/measure	Population		Population difference	Data source/notes
	In situ	**Zoo**		
Birth weight	89.5 (± 6.3) kg (n = 5)	102.1 (± 9.6) kg (n = 63)	$F_{1,66}$ = 8.32, P = 0.005	Hayssen *et al* 1993
	74.0 kg (n = 6)	105.6 kg (n = 40)	Reported in paper as significant	Kurt & Mar 1996 (sexes pooled)
	–	118.8 kg (n = 7)	n/a	ISIS 2002 (females only)
	–	Females, including one stillbirth: 112.9 kg (n = 14) Males, including 4 stillbirths: 117.2 kg (n = 14)	n/a	EEP studbook for Asian elephants 2005
PI	Median: 0.114 (n = 5)	Median: 0.150 (n = 19)	Mann-Whitney W = 262.5, P < 0.10	Kurt & Mar 1996 (sexes pooled)
BMI	Median: 11.16 (n = 5)	Median: 13.00 (n = 19)	Mann-Whitney W = 39, P = 0.10	Kurt & Mar 1996 (sexes pooled

Bodyweight (kg) and height (cm) used to calculate Ponderal Index (1000 × [kg/cm³]) and Body Mass Index (1000 × [kg/cm²]).

demonstrated here (Mason & Veasey 2009, in press), and there are alternative explanations for both this phenomenon and poor cyclity/high stillbirths (see below).

We project population declines in European zoos, if kept under historically prevailing conditions with no imports, of 11% a year for African elephants and 10% a year for Asian elephants. With no improvement, and assuming stable age structures and no imports, European African elephant populations would be expected to fall to 10 females within around 29 years, and Asian elephants to fall to 10 in around 37 years. For African zoo elephants, solely improving fecundity to Amboseli levels would almost achieve a self-sustaining population. For Asian elephants, in contrast, both fecundity and survivorship need improving to at least MTE levels if the European zoo population is to become self-sustaining. This apparent species difference could reflect differences between the two zoo populations (eg higher calf losses in zoo Asians), and/or differences between reference populations. MTE fecundity is lower than Amboseli, suggesting that MTE values are not optimal (see *Materials and methods*); thus, if data from well-protected wild, Asian populations became available, it would be advisable to re-analyse the relative importance of achieving reference levels of fecundity versus survivorship.

Comparisons with North American zoos

African elephants in North American zoos are not self-sustaining, and have infant mortality rates, including stillbirths, of approximately 40% (Olson & Wiese 2000; Faust 2005) — more than double female calf loss rates in Europe (Clubb *et al* 2008). Population declines are similarly projected for North American Asian elephants, even in analyses combining zoo-born with wild-born

individuals (eg Wiese 2000; Faust *et al* 2006). Infant mortality rates — at least prior to 2005 — were similar in both continents for this species, with total first year mortalities of approximately 40% (Clubb *et al* 2008; Saragusty *et al* 2008). Analyses of more up-to-date datasets, however, suggest an improvement in Europe in recent years, but no similar upturn in North America (Saragusty *et al* 2008). Furthermore, after infancy, the median lifespan of those Asian female elephants which survive their first year seems slightly longer in Europe, at 47.6 compared to 44.8 in North America (Wiese & Willis 2004). Thus, overall, the female African and Asian elephants of Europe seem to be faring similarly to, or even better than, those in North America. The problems reported here are therefore not particular to Europe. Indeed, since North American and European populations combined represent the vast majority of *ex situ* zoo elephants, these problems (and the potential solutions we identify) probably apply globally to all zoo elephants.

Risk factors for Asian elephants in European zoos

Our previous investigations (see *Introduction*) revealed that one risk factor affecting adult Asian elephant survivorship in European zoos was being born into a zoo rather than imported from the wild. Demographically, this birth origin effect is likely to become increasingly important; the captive-born proportion of the Asian, female zoo population has already increased from 6.7% in 1960 to 18.6% in 2004. Analyses here yielded more information. First, for wild-caught animals, longer periods in (and/or perhaps en route from) the wild before transfer to a zoo did not confer significant additional benefits. This suggests that the benefits of being wild-born are conferred early in life (via potential mechanisms discussed below). Second, building on previous

Figure 1

(a)

(b)
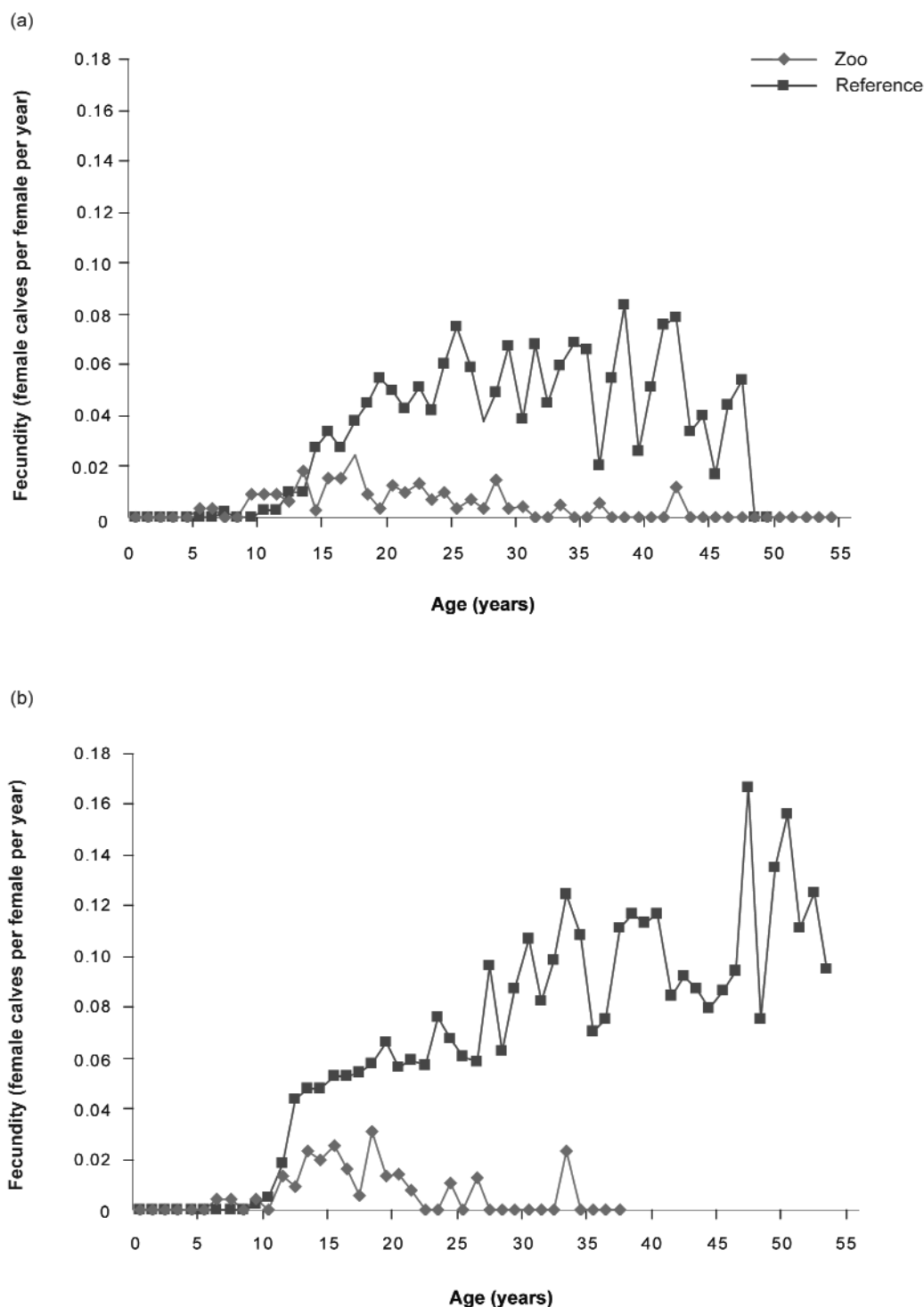
Fecundity curves for female (a) Asian and b) African elephants, expressed as female calves per female per year. Note that sample sizes for the reference African population in (b) are small after 50 years of age (10 females or fewer per age class).

analyses (Kurt & Mar 1996, reviewed by Dale 2009), we found that one consequence of being zoo-born is being heavy at birth, possibly also with a higher Ponderal Index. Our analyses probably underestimate the magnitude of this effect since more recent work puts the mean zoo Asian calf weight

at approximately 118 kg: heavier than the zoo values we used, and perhaps reflecting a recent increase in Asian zoo neonate weight (Dale 2009). This is informative because in other species, excess peri-natal weight has harmful long-term effects (reviewed below).

Figure 2
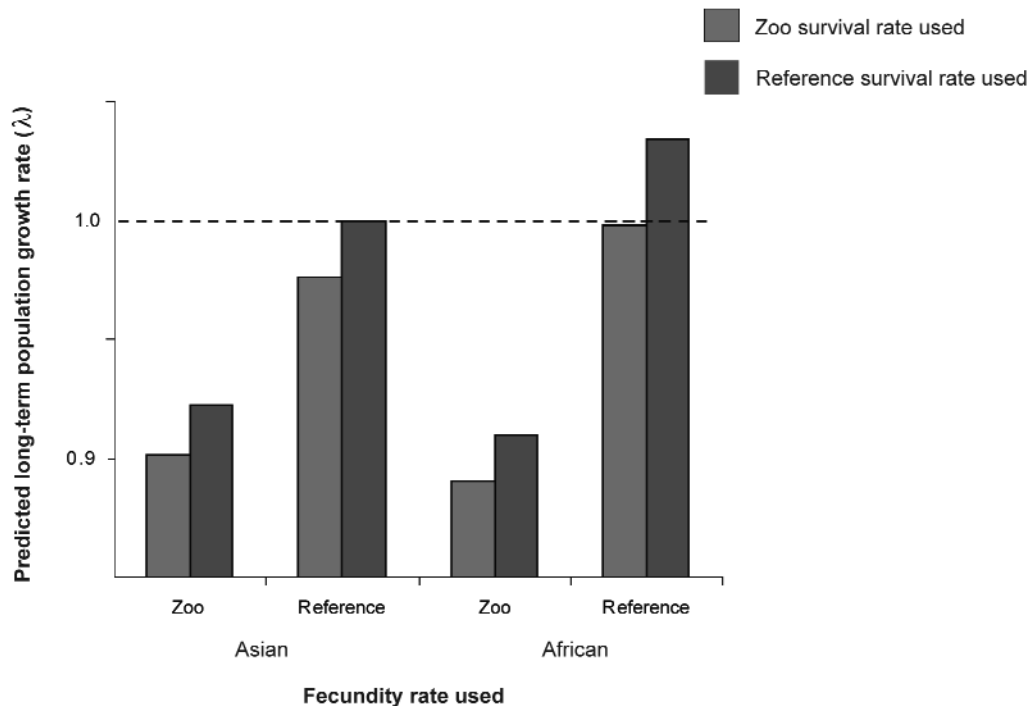
Predicted long-term population growth rate, λ, given by the rate of change at stable age structure of a Leslie matrix model, under various scenarios. A self-sustaining population is reached when λ = 1, as marked by the dashed line. Survival and fecundity rates are assumed to be either as measured in zoo-born elephants, or, to model improved future scenarios, as measured in the captive-born Asian MTE reference population and the 'natural mortality' African reference population (Amboseli). Models that used the rates of fecundity found in either the Zoo or Reference populations are indicated by their location on the x-axis. Red bars indicate scenarios where Zoo survival rates were used, and blue bars, where Reference survival rates were used. The combination of x-axis location and colour of bar thus indicates which fecundity and survival values were used, respectively, in each analysis yielding a given λ.

Other risk factors for Asian female survivorship in European zoos are inter-zoo transfer, and possibly also early maternal separation (see *Introduction*). Here, we show that compared to female African elephants in European zoos, their Asian counterparts are transferred around five times more frequently. Asian females were also separated from their mothers at half the median age seen in African females (although this difference was just a trend). These husbandry differences could explain why Asian elephants in European zoos have more marked survivorship problems than African elephants, and with no significant improvement in recent years.

What are the potential causes of zoo elephants' problems? Two hypotheses and how to investigate them in extant zoo elephant populations

Current knowledge (eg reviewed Clubb & Mason 2002; Mason & Veasey 2008) suggests that the main causes of zoo elephant infant mortality are dystocia, infanticide, maternal neglect and, especially for Asian elephants, *Herpes* virus; while adult deaths in zoos often reportedly stem from cardio-vascular disease, but are frequently for reasons unknown. Poor conception rates stem from acyclicity and premature senescence, ovarian cysts, male fertility problems, and low libido. There are numerous possible explanations for why these problems are more serious or prevalent in zoos than *in situ* populations, but here we propose two broad candidates: obesity and stress (not mutually exclusive, since chronic stress can facilitate fat deposition: eg Chrousos 2000; Tiley *et al* 2007). As we review below, these two hypotheses are parsimonious, having the potential to explain all observed effects; plausible given what is known about elephant health and husbandry; testable (ie open to falsification); and, we hope, useful: they could potentially enable the identification of at-risk individuals before they die (allowing intervention), and the objective evaluation of changes in zoo husbandry and management.

In many species, including humans, obesity increases morbidity, for example from cardiovascular disease, diabetes, cancer and asthma, and shortens adult lifespan (Bennett 1999; British Nutrition Foundation 1999; Kealy *et al* 2002; Rodrigues-Artalejo *et al* 2002; Royal College of Physicians 2004). It also reduces fertility and increases the risk of stillbirths (Clark *et al* 1998; British Nutrition Foundation 1999; Kristensen *et al* 2005; Baur *et al* 2006). There have long been suggestions that adult elephants in zoos are overweight (Kurt & Mar 1996; Ange *et al* 2001;

Hatt & Clauss 2006). Kurt and Mar (1996) also report that overweight zoo dams have more stillbirths, while Dale (2009) shows that stillborn Asian calves weigh more than liveborn (see also Kurt & Mar 1996). Excess body fat could thus explain the high stillbirth rates of Asian elephants, large calf sizes, and low fecundities and shortened adult lifespans of both species. Furthermore, in humans, overweight babies have elevated risks of obesity, cancer, cardiovascular disease and Type II diabetes in adulthood (McCance *et al* 1994; Rasmussen & Johanssen 1998; Bennett 1999; Samaras *et al* 2003; Singhal & Lucas 2004; Jiminez-Challaron & Patti 2007). Excess neonatal or infant body fat could also thus potentially explain why zoo-born Asian elephants have premature adult deaths.

To investigate whether peri-natal and/or adult obesity does indeed cause poor fecundity or survivorship in zoo elephants, useful screens of the extant population include: scores for overall body fat and deposition patterns, and kidney fat deposit size post mortem; serum triglyceride and cholesterol levels; and indices of insulin resistance such as decreased glucose tolerance and fasting hyperglycaemia (Albl 1971; British Nutrition Foundation 1999; Samaras *et al* 2003; Kronfeld *et al* 2005). Leptin, which correlates with adiposity in many species (eg Fors *et al* 1999; Banks *et al* 2001; Buff *et al* 2002), should also be assessed.

Our second hypothesised cause of problems is stress. Chronic and acute stress both reduce adult lifespan in humans and other species (eg Kiecolt-Glaser *et al* 2002; Cavigelli & McClintock 2003; Donaldson 2003; Vitetta *et al* 2005); indeed, the post-capture deaths of wild-born Burmese elephants caught for logging are likely examples (Mar 2007; Clubb *et al* 2008). In addition, in a range of species, chronic stress reduces fertility and elevates still-birth rates (eg Janczak *et al* 2003; Wingfield & Sapolsky 2003), impairs maternal care and infant survivorship (eg Bahr *et al* 1998; Clubb & Mason 2003, 2007; Janczak *et al* 2003), and even induces reproductive senescence (Kaplan & Manuck 2004; Cavigelli *et al* 2006). Zoo elephants are often subject to treatments known or likely to elevate stress, such as chaining and translocation (reviewed eg Clubb & Mason 2002; Mason & Veasey 2008; see also Harris *et al* 2008). We strongly suspect that stress underlies the harmful effects of repeated transfers on survivorship, and possibly early separation from mothers (for effects of breaking social bonds in other species, see eg Moore *et al* 1994; Capitanio *et al* 1998; Ha *et al* 1999). Furthermore, stress early in life can have lasting deleterious effects: exposure to elevated stress hormones *in utero* and/or inadequate parental care in infancy may disrupt stress responses throughout life (eg Francis *et al* 1999; Otten *et al* 2001; Cronje 2003; Pryce *et al* 2005), elevate stress-related disease (Danese *et al* 2007) and shorten lifespan (Lewis *et al* 2000). If zoo-born calves experience more early stress than wild-born calves (perhaps because their own dams are stressed, or a lack of competent allomothering), this provides an alternative explanation for zoo Asian elephants' birth origin effect.

To test the stress hypothesis, useful screens would include: measures of corticosteroid, ACTH and catecholamine outputs; assessments of immune (eg IL-6) and inflammatory responses (and related diseases); wound-healing rates; and adrenal and thymus weights, post mortem (eg Broom & Johnson 1993; Kiecolt-Glaser *et al* 2002; Cronje 2003; Kielcolt-Glaser *et al* 2003; Terio *et al* 2004; Danese *et al* 2007; Mason & Veasey 2009, in press).

Additional questions that could be addressed from zoo records

We also recommend further analyses of zoo records. Re-running analyses with pooled European and North American studbook data could elucidate whether the lack of significant findings in African cf Asian elephants was simply the result of low power; identify further aspects of husbandry with an effect on survivorship and fecundity; test whether our two weaning age trends (the possible earlier separation of young Asian elephants than young African elephants; and the possible link in the former between early 'weaning' and reduced survivorship) can be replicated; and also enable studies of male survivorship. Analyses of more up-to-date datasets than our own could also show whether apparent recent improvements in calf survival in Europe (Saragusty *et al* 2008), are statistically significant. We suggest analysing historical data on infant birth-weights, to see if these predict later health and lifespan in adulthood. If Ponderal Indices can be calculated from such records, such data would also test the robustness of our trend finding that zoo neonates have higher Ponderal Indices than timber camp neonates. Analysing health records could also reveal whether zoo-born and wild-born elephants die for different reasons, and identify what causes Asian elephant deaths in the years after each inter-zoo transfer, to help test the hypotheses outlined above. Lastly, it would be valuable to analyse records of changes in zoo housing or husbandry to investigate why survivorship in African, but not Asian, elephants has improved in recent years in Europe; compare the enclosure sizes, group sizes and group structures of Asian and African elephants in European zoos; and compare European and North American husbandry, to find reasons for the apparently lower infant losses seen in European African elephants and more recently also perhaps Asian elephants.

Animal welfare implications

The high mortality and low fecundity seen in Asian elephants, and to a lesser extent in African elephants, raises questions regarding their health and welfare. To date, many zoos have responded to their declining elephant populations by advocating importation from successful *in situ* populations (Hutchins & Keele 2006; Wiese & Willis 2006). Substantial sums have also been invested in new enclosures — but research is still needed into what housing or husbandry methods are most beneficial (Mason & Veasey 2008) and truly provide 'an environment well-adapted to meet the physical, psychological and social needs of the species' as stated in the 2002 EC 'Zoo' Directive 1999/22/EC; Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations. We recommend that new tests sensitive to altered stress physiology and morbid obesity are incorporated into zoo elephant health screen-

ings. This would enable testing of the hypotheses that stress and/or obesity underlie the observed effects, and potentially allow at-risk individuals to be identified, allowing timely intervention. Even in the absence of such data, however, the effect of inter-zoo transfer, and possible effect of early separation from mothers, on the survivorship of Asian female elephants seem very likely to be stress-related. We suggest therefore that avoiding inter-zoo transfer and early separation should be a welfare priority, until it is understood how to mitigate their harmful effects.

Acknowledgements

References

African Elephant Specialist Group 2003 *Statement from the African Elephant Specialist Group of the IUCN Species Survival Commission on the removal of African Elephants for Captive Use.* IUCN/SSC African Elephant Specialist Group: Mokuti Lodge, Namibia, Africa

African Elephant Specialist Group 2004 Loxodonta africana. *2007 IUCN Red List of Threatened Species.* www.iucnredlist.org. (Accessed 8 July 2008)

Albl P 1971 Studies on assessment of physical condition in African elephants. *Biological Conservation 3*: 134-140

Ange K, Crissey SD, Doyle C, Lance K and Hintz H 2001 A survey of African (*Loxodonta africana*) and Asian (*Elephas maximus*) Elephant diets and measured body dimensions compared to their estimated nutrient requirements. *Proceedings of the Nutrition Advisory Group Conference 4*: 5-14

Anthony KRN, Connolly SR and Hoegh-Guldberg O 2007 Bleaching, energetics, and coral mortality risk: Effects of temperature, light, and sediment regime. *Limnology and Oceanography 52*: 716-726

Asian Elephant Specialist Group 1996 Elephas maximus. *2007 IUCN Red List of Threatened Species.* www.iucnredlist.org. (Accessed 8 July 2008)

Bahr NI, Pryce CR, Dobeli M and Martin RD 1998 Evidence from urinary cortisol that maternal behaviour is related to stress in gorillas. *Physiology and Behavior 64*: 439-437

Balmford A, Leader-Williams N and Green MJB 1995 Parks or arks — where to conserve threatened mammals? *Biodiversity and Conservation 4*: 595-607

Balmford A, Mace G and Leader-Williams N 1996 Designing the ark: Setting priorities for captive breeding. *Conservation Biology 10*: 719-727

Banks WA, Phillips-Conroy JE, Jolly CE and Morley JE 2001 Serum leptin levels in wild and captive populations of baboons (*Papio* spp): Implications for the ancestral role of leptin. *Journal of Clinical Endocrinology & Metabolism 86*: 4315-4320

Baur JA, Pearson KJ, Price NL, Jamieson HA, Lerin C, Kalra A, Prabhu W, Allard JS, Lopez-Lluch G, Lewis K, Pistell PJ, Poosala S, Becker KG, Boss O, Gwinn D, Wang M, Ramaswamy S, Fishbein KW, Spencer RG, Lakatta EG, Le Couteur D, Shaw RJ, Navas P, Puigserver P, Ingram DK, de Cabo R and Sinclair DA 2006 Resveratrol improves health and survival of mice on a high-calorie diet. *Nature 444*: 337-342

Bennett PH 1999 Type 2 diabetes among the Pima Indians of Arizona: An epidemic attributable to environmental change? *Nutrition Reviews 57*: S51-S54

Blanc JJ, Barnes RFW, Craig GC, Dublin HT, Thouless CR, Douglas-Hamilton I and Hart JA 2007 *African Elephant Status Report 2007: An Update from the African Elephant Database. Occasional Paper of the IUCN Species Survival Commission No. 33.* IUCN: Gland, Switzerland

British Nutrition Foundation 1999 *Obesity — the Report of the British Nutrition Foundation Task Force.* Blackwell Science: Oxford, UK

Broom DM and Johnson KG 1993 *Stress and Animal Welfare.* Chapman & Hall: London, UK

Brown JL, Olson D, Keele M and Freeman EW 2004 Survey of the reproductive cyclicity status of Asian and African elephants in North America. *Zoo Biology 23*: 309-321

Buff PR, Dodds AC, Morrison CD, Whitley NC, McFadin EL, Daniel JA, Djiane J and Keisler DH 2002 Leptin in horses: Tissue localization and relationship between peripheral concentrations of leptin and body composition. *Journal of Animal Science 80*: 2942-2948

Capitanio JP, Mendoza SP, Lerche NW and Mason AW 1998 Social stress results in altered glucocorticoid regulation and shorter survival in simian acquired immune deficiency syndrome. *Proceedings of the National Academy of Sciences, USA 95*: 4714-4719

Caswell H 2000 *Matrix Population Models: Construction, Analysis and Interpretation, 2nd Edition.* Sinauer Associates: Sunderland, MA, USA

Caughley G 1977 *Analysis of Vertebrate Populations.* Wiley: New York, USA

Cavigelli SA and McClintock MK 2003 Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. *Proceedings of the National Academy of Science 100*: 16131-16136

Cavigelli SA, Yee JR and McClintock MK 2006 Infant temperament predicts life span in female rats that develop spontaneous tumors. *Hormones and Behavior 50*: 454-462

Chrousos GP 2000 The role of stress and the hypothalamic-pituitary-adrenal axis in the pathogenesis of the metabolic syndrome: neuron-endocrine and target tissue-related causes. *International Journal of Obesity 24*: S50-S55

Clark AM, Thornley B, Tomlinson L, Galletley C and Norman RJ 1998 Weight loss in obese infertile women results in improvement in reproductive outcome for all forms of fertility treatment. *Human Reproduction 13*: 1502-1505

Clubb R and Mason G 2002 *A Review of the Welfare of Elephants in European Zoos.* RSPCA: Horsham, UK

Clubb R and Mason G 2003 Captivity effects on wide-ranging carnivores. *Nature 410*: 35-36

Clubb R and Mason G 2007 Natural behavioural biology as a risk factor in carnivore welfare: how understanding species differences could help zoos redesign enclosures. *Applied Animal Behaviour Science 102*: 303-328

Clubb R, Lee P, Mar KU, Moss C, Rowcliffe M and Mason GJ 2008 Compromised survivorship in zoo elephants. *Science 322*: 1649

Cronje PB 2003 Foetal programming of immune competence. *Australian Journal of Experimental Agriculture 43*: 1427-1430

Dale RHI 2009 Birth statistics for African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in human care: history and implications for elephant welfare. *Zoo Biology*, doi: 10.1002/zoo.20234

Danese A, Pariante CM, Caspi A, Taylor A and Poulton R 2007 Childhood maltreatment predicts adult inflammation in a life course study. *Proceedings of the National Academy of Sciences 104*: 1319-1324

Del Giudice GD, Fieberg J, Riggs MR, Carstensen Powell M and Pan W 2006 A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management 70*: 1556-1568

Donaldson R 2003 *Experiences of Older Burglary Victims. Home Office Findings No 198*. Home Office: London, UK

European Commission 2002 *EC Zoo Directive 1999/22/EC. Zoo Licensing Act Amendment Regulations* European Commission: Brussels, Belgium

European Elephant Group (EEG) 2002 *Elefanten in zoos und safariparks Europa*. Schling Verlag: Munster, Germany

European Elephant Group 2008 http://www.elefanten-schutz-europa.de/index.html

Faust L 2005 *Technical Report on Demographic Analyses and Modeling of the North American African Elephant Population. African Elephant Modelling Technical Report, AZA*. Association of Zoos and Aquariums: Silver Springs, Maryland, USA

Faust LJ, Thompson SD and Earnhardt JM 2006 Is reversing the decline of Asian elephants in North American zoos possible? An individual-based modeling approach. *Zoo Biology 25*: 201-218

Fors H, Matsuoka H, Bosaeus I, Rosberg S, Wikland KA and Bjarnson R 1999 Serum leptin levels correlate with growth hormone secretion and body fat in children. *Journal of Clinical Endocrinology & Metabolism 84*: 3586-3590

Francis D, Diorio J, Liu D and Meaney J 1999 Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science 286*: 1155-1158

Freeman EW, Weiss E and Brown JL 2004 Examination of the interrelationships of behavior, dominance status, and ovarian activity in captive Asian and African elephants. *Zoo Biology 23*: 431-448

Goswami VR, Madhusudan MD and Karanth KU 2007 Application of photographic capture-recapture modelling to estimate demographic parameters for male Asian elephants. *Animal Conservation 10*: 391-399

Grambsch PM and Therneau TM 1994 Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika 81*: 515-526

Ha J, Robinette RL and Sackett GP 1999 Social housing and pregnancy outcome in captive pigtailed Macaques. *American Journal of Primatology 47*: 153-163

Harris M, Sherwin S and Harris S 2008 *The welfare, housing and husbandry of elephants in UK zoos: final report*. University of Bristol, DEFRA Science and Research Project WC05007, Bristol, UK

Hatt JM and Clauss M 2006 Feeding Asian and African elephants (*Elephas maximus* and *Loxodonta africana*) in captivity. *International Zoology Yearbook 40*: 88-95

Hayssen V, van Tienhoven A and van Tienhoven A 1993 *Asdell's Patterns of Mammalian Reproduction*. Cornell University Press: Ithaca, USA

Hedges S, Tyson MJ, Sitompul AF and Hammatt H 2006 Why inter-country loans will not help Sumatra's elephants. *Zoo Biology 25*: 235-246

Hedges S 2007 Conservation. In: Fowler ME and Mikota SK (eds) *Biology, Medicine, and Surgery of Elephants* pp 475-490. Blackwell Publishing: UK

Hermes R, Hildebrandt TB and Göritz F 2004 Reproductive problems directly attributable to long-term captivity: asymmetric reproductive aging. *Animal Reproduction Science 82-83*: 49-60

Hutchins M and Keele M 2006 Elephants importation from range countries: Ethical and practical considerations for accredited zoos. *Zoo Biology 25*: 219-233

International Species Inventory System (ISIS) 2002 *Elephas maximus, Asian Elephant. Reference Ranges for Physiological Data Values (average values calculated for: females only)*. http://www.elephantcare.org/protodoc_files/Isis/isis2.htm (accessed May 2009)

Janczak AM, Pedersen LJ, Rydhmer L and Bakken M 2003 Relation between early fear and anxiety-related behaviour and maternal ability in sows. *Applied Animal Behavior Science 82*: 121-135

Jimenez-Chillaron JC and Patti ME 2007 To catch up or not to catch up: is this the question? Lessons from animal models. *Current Opinions in Endocrinology, Diabetes and Obesity 14*: 23-29

Kaplan JR and Manuck SB 2004 Ovarian dysfunction, stress and disease: A primate continuum. *ILAR Journal 45*: 89-115

Kealy RD, Lawler BF, Ballam JM, Mantz SL, Biery DN, Greeley EH, Lust G, Segre M, Smith GK and Stowe HD 2002 Effects of diet restriction on life span and age-related changes in dogs. *Journal of American Veterinary Medical Association 220*: 1315-1320

Keele M, Lewis K and Owens T 2007 *Asian Elephant (*Elephus maximus*) North American Regional Studbook Update 1 May 2005-16 July 2007*. Association of Zoos and Aquariums: Silver Springs, Maryland, USA

Kiecolt-Glaser JK, McGuire L, Robles TF and Glaser R 2002 Emotions, morbidity, and mortality: new perspectives from psychoneuroimmunology. *Annual Review of Psychology 53*: 83-107

Kiecolt-Glaser JK, Preacher KJ, MacCallum RC, Atkinson C, Malarkey WB and Glaser R 2003 Chronic stress and age-related increases in the proinflammatory cytokine IL-6. *Proceedings of the National Academy of Science 100*: 9090-9095

Koehl D 2008 *Elephant Database* http://www.elephant.se/elephant_database.php?open=Elephant%20database

Kristensen J, Vestergaard M, Wisborg K, Kesmodel U, and Jørgen Secher N 2005 Pre-pregnancy weight and the risk of still birth and neonatal death. *BJOG: an International Journal of Obstetrics and Gynaecology 112*: 403-408

Kronfeld DS, Treiber KH and Geor RJ 2005 Comparison of nonspecific indications and quantitative methods for the assessment of insulin resistance in horses and ponies. *Journal of American Veterinary Medical Association 226*: 712-719

Kurt F and Mar DK 1996 Neonate mortality in captive Asian elephants (*Elephas maximus*). *Zeitschrift für Säugetierkunde 61*: 155-164

Kurt F and Kumarasinghe JC 1998 Remarks on body growth and phenotypes in Asian elephant *Elephas maximus*. *Acta Theriologica Supplement 5*: 135-153

Lair RC 1997 *Gone Astray: The Care and Management of the Asian Elephant in Domesticity. FAO/RAP Publication 1997/16*. FAO Regional Office for Asia and the Pacific: Thailand

Lewis MH, Gluck JP, Petitto JM, Hensley LL and Ozerd H 2000 Early social deprivation in nonhuman primates: Long-term effects on survival and cell-mediated immunity. *Biological Pshychiatry 47*: 119-126

Mar KU and Win S 1997 Working elephants for the timber industry. *Draught Animal News 26*: 6-13

Mar KU 2007 *The demography and life history strategy of timber elephants in Myanmar*. PhD Thesis, University College London, London, UK. http://www.zoo.cam.ac.uk.theses.htm

Mason G and Veasey J 2008 How should the psychological welfare of zoo elephants be investigated? In: Forthman DL, Kane LF and Waldau PF (eds) *An Elephant in the Room: the Science and Well Being of Elephants in Captivity* pp 154-174. Tufts University Cummings School of Veterinary Medicine's Center for Animals and Public Policy: North Grafton, MA, USA

Mason G and Veasey J 2009 How should the psychological well-being of zoo elephants be objectively investigated? *Zoo Biology*, in press

McCance DR, Pettitt DJ, Hanson RL, Jacobsson LTH, Knowler WC and Bennett PH 1994 Birth-weight and non-insulin-dependent diabetes – thrifty genotype, thrifty phenotype or surviving small baby genotype. *British Medical Journal 308*: 942-945

Moore AS, Gonyou HW, Stookey JM and McLaren DG 1994 Effect of group composition and pen size on behavior, productivity and immune response of growing pigs. *Applied Animal Behaviour Science 40*: 13-30

Moss CJ 2001 The demography of an Africa elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology 255*: 145-156

Moss CJ and Lee PC Female reproductive strategies: individual life histories. In: Moss CJ and Croze H (eds) *The Amboseli Elephant: a Long-term Perspective on a Long-lived Species.* University of Chicago Press: Chicago, IL, USA, in press

Olson D and Wiese RJ 2000 State of the North American African elephant population and projections for the future. *Zoo Biology 19*: 311-320

Olson D 2008 *North American Regional Studbook for the African Elephant (*Loxodonta africana*).* Association of Zoos and Aquariums: Silver Springs, Maryland, USA

Otten W, Kanitz M, Tuchscherer M and Numberg G 2001 Effects of prenatal restraint stress on hypothalamic-pituitary-adrenocortical and sympatho-adrenomedullary axis in neonatal pigs. *Animal Science 73*: 279-287

Pryce CR, Ruedi-Bettschen D, Dettling AC, Weston A, Russig H, Ferger B and Feldon J 2005 Long-term effects of early-life environmental manipulations in rodents and primates: Potential animal models in depression research. *Neuroscience and Biobehavioral Reviews 29*: 649-674

Raggi P, Shaw LJ, Berman DS and Callister TQ 2004 Prognostic value of coronary artery calcium screening in subjects with and without diabetes. *Journal of the American College of Cardiology 43*: 1663-1669

Ramanthan A and Mallapur A 2008 A visual health assessment of captive Asian elephants (*Elephas maximus*) housed in India. *Journal of Zoo & Wildlife Medicine 39*: 148-154

Rasmussen F and Johanssen M 1998 The relation of weight, length and Ponderal index at birth to body mass index and overweight among 18-year-old males in Sweden. *European Journal of Epidemiology 14*: 373-380

Richman LK, Montali RJ, Garber RL, Kennedy MA, Lehnhardt J, Hildebrandt T, Schmitt D, Hardy D, Alcendor DJ and Hayward GS 1999 Novel endotheliotropic herpesviruses fatal for Asian and African elephants. *Science 283*: 1171-1176

Rodríguez-Artalejo F, Garcés C, Gorgojo L, López García E, Martín-Moreno JM, Benavente M, del Barrio JL, Rubio R, Oretga H, Fernandez O and de Oya M 2002 Dietary patterns among children aged 6-7 in four Spanish cities with widely differing cardiovascular mortality. *European Journal of Clinical Nutrition 56*: 141-148

Royal College of Physicians 2004 *Storing Up Problems: The Medical Case for a Slimmer Nation.* Royal College of Physicians: London, UK

Samaras TT, Eirick H and Storms LH 2003 Birthweight, rapid growth cancer and longevity: a review. *Journal of the National Medical Association 95*: 1170-1183

Saragusty J, Hermes R, Göritz F, Schmitt DL and Hildebrandt TB 2008 Skewed birth sex ratio and premature mortality in elephants. *Animal Reproduction Science.* Oct 31 doi:10.1016/j.anireprosci.2008.10.019

Siler W 1979 Competing risk model for animal mortality. *Ecology 60*: 750-757

Singhal A and Lucas A 2004 Early origins of cardiovascular disease: is there a unifying hypothesis? *The Lancet 363*: 1642-1664

Slotow R, Garaï ME, Reilly B, Page B and Carr RD 2005 Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Wildlife Research 35*: 23-32

Sukumar R 1989 *The Asian Elephant: Ecology and Management.* Cambridge University Press: Cambridge, UK

Sukumar R, Krishnamurthy V, Wemmer C and Rodden M 1997 Demography of captive Asian elephants (*Elephas maximus*) in Southern India. *Zoo Biology 16*: 263-272

Sukumar R 2003 *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation.* Oxford University Press: Oxford, UK

Sukumar R 2006 A brief review of the status, distribution and biology of wild Asian elephants. *International Zoology Yearbook 40*: 1-8

Taylor VJ and Poole TB 1998 Captive breeding and infant mortality in Asian elephants: a comparison between twenty western zoos and three eastern elephant centers. *Zoo Biology 17*: 311-332

Terio KA, Marker L and Munson L 2004 Evidence for chronic stress in captive but not free-ranging cheetahs (*Acinonyx jubatus*) based on adrenal morphology and function. *Journal of Wildlife Diseases 40*: 259-266

Tiley HA, Geor RJ and McCutcheon LJ 2007 Effects of dexamethasone on glucose dynamics and insulin sensitivity in healthy horses. *American Journal of Veterinary Research 68*: 753-759

van Aarde RJ and Jackson TP 2007 Megaparks for metapopulations: Addressing the causes of locally high elephant numbers in Southern Africa. *Biological Conservation 134*: 289-297

Vitetta L, Anton B, Cortizo F and Sali A 2005 Mind-Body Medicine: Stress and its impact on overall health and longevity. *Annals of the New York Academy of Science 1057*: 492-505

Waithaka J, Osborne L and Saiwana L 1998 Captive breeding of elephants. *Pachyderm 25*: 100-101

Whitehouse AM and Kerley GIH 2002 Retrospective assessment of long term conservation management of elephants in Addo Elephant National Park, South Africa. *Oryx 36*: 243-248

Wiese RJ 2000 Asian elephants are not self sustaining in North America. *Zoo Biology 19*: 299-309

Wiese RJ and Willis K 2004 Calculation of longevity and life expectancy in captive elephants. *International Zoo Yearbook 23*: 365-373

Wiese RJ and Willis K 2006 Population management of zoo elephants. Calculation of longevity and life expectancy in captive elephants. *International Zoo Yearbook 40*: 80-87

Wingfield JC and Sapolsky RM 2003 Reproduction and resistance to stress: when and how. *Journal of Neuroendocrinology 15*: 711-724

Wittemyer G, Daballen D, Rasmussen H, Kahindi P and Douglas-Hamilton I 2005 Demographic status of elephants in the Sambusu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology 43*: 44-47

Zoo Licensing Act 1981 *Statutory Instrument 2002, No 3080 Amendment (England and Wales).* http://www.opsi.gov.uk/si/si2002/20023080.htm