

1 **Compromised survivorship, fecundity and population persistence in zoo**
2 **elephants**

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14 **Abstract**

15 Keeping elephants in zoos is extremely costly, yet does not yield self-sustaining
16 populations. In Europe, which holds c. half the global zoo elephant population, a long-
17 term decline of c.10% per year is expected in both species, if reliant on zoo-bred animals
18 under historically prevailing conditions. Fitness in zoos is compromised in several ways.
19 Compared with protected *in situ* populations (Burmese working Asians; Kenyan free-
20 living Africans), zoo elephants show premature reproductive senescence and -- despite
21 improving adult survivorship for Africans -- die earlier in adulthood than expected. In
22 Asian elephants, infant survivorship in zoos is also greatly reduced relative to Burmese
23 elephants, and furthermore, zoo-born animals die earlier in adulthood than wild-caught
24 conspecifics kept in zoos, via effects 'programmed' peri-natally. In this species, being
25 transferred between zoos also increases mortality rates. Both survival and fecundity
26 would need to improve to attain self-sustaining zoo populations. Our findings
27 demonstrate deficits in zoo elephant management, particularly for Asians, and implicate
28 stress and obesity as likely problems.

29

The welfare implications of captivity, and the relative cost and effectiveness of *ex* versus *in situ* conservation, determine the value of captive breeding for any given species. Several species apparently thrive in zoo conditions (1), and captive breeding has saved some from extinction (2, 3). However, *ex situ* conservation is typically costlier than *in situ* programs (2, 3); captive-bred individuals often fare poorly in the wild (3); and many species show reproductive failure and elevated mortality in captivity (1-3), raising ethical concerns particularly when stress is implicated (1, 4, 5).

Asian and African elephants exemplify such problems. The zoo elephant populations of North America are non-self-sustaining, and require importation from range countries (6, 7) – a practice criticized by the IUCN (8). Both species are naturally wide-ranging and socially complex (9), and the large disparities between *in situ* and zoo environments have elicited concerns about elephant welfare in captivity (10). Furthermore, zoo elephants have troubling rates of lameness, infertility (e.g. female acyclicity), infanticide, tuberculosis and *Herpes* (10, 11). Nevertheless many zoos argue that their elephants are vital for conservation, and that their viability is improving (6, 7). These arguments underpin commitments to spend very large sums relative to *in situ* conservation costs: c. \$53 million per year in maintenance and, in the last decade, over \$540 million in facility upgrades worldwide (see Table S1 and supporting online text). Here, we use demographic data to identify those aspects of population-level fitness particularly affected by zoo environments, and to suggest biological reasons for zoo elephants' problems at the individual level. We selected these species because of concerns over captive elephant welfare, but our approach could equally be applied to any species sparking similar debates.

To identify the fitness components influenced by zoo husbandry, we compared European zoo populations (N = 786 females) with protected, well-provisioned *in situ* reference populations: working Asian elephants in Myanmar (Burma) (N = 2905 females) and free-living African elephants in Amboseli, Kenya (N = 1089 females) (see supporting online text). Analyses focussed on females only due to the small number of males. For the zoo populations, we also analysed determinants of survivorship and age-specific fecundity, and modelled future zoo population growth under various scenarios (see supporting online text). We found that elephant fitness is reduced in several ways in zoos.

For Asian elephants in zoos, the proportion of elephant calves that die in their first year is between 2.3 and 3.4 times greater than in Burmese working elephants, the greatest differences occurring for first-born calves when stillbirths and premature calves are included (see online supporting material Tables S2 and S3; Fisher's exact $p < 0.05$ in all cases, with one exception where $p=0.054$). In African elephants, however, calf mortality does not significantly differ between the reference and European zoo populations (Fisher's exact $p > 0.4$).

In both species, juvenile zoo elephants aged between 1 and 10 (Figure 1 A & C) survive at least as well as the reference populations undergoing natural mortality. In one instance the survivorship of zoo juveniles is better, due to markedly elevated mortality in wild-born Burmese juveniles induced by capture stress (see 12, and supporting online material, for details). In adults (10 years+), the pattern changes: both species show reduced survivorship in zoos (Figure 1 B & D). Thus overall, captive-born Asians live half as long in zoos as they do working in Burma, while wild-born African females in zoos

80 similarly live half as long as conspecifics undergoing natural mortality in Amboseli (see
81 supporting online text).

82
83 We found three principle risk factors for mortality in zoos. First, being transferred to a
84 new zoo decreases the survivorship of Asian elephants, an effect seen in the first year
85 after the first transfer event ($z=-2.05$, $p=0.04$), but lasting up to six years after the second
86 transfer ($z=-2.23$, $p=0.026$). Small sample sizes precluded similar analyses for Africans.

87
88 The second risk factor is birth origin. In recent times, the proportion of the female zoo
89 population that is captive-born has increased from 6.7% in 1960 to 18.6% in 2004, and in
90 adult Asians, this zoo-born sub-set has significantly poorer survivorship than wild-born
91 animals as adults (see Fig. 1B and supporting online text). Since wild-born female
92 Asians entered the zoo population at a median estimated age of just 3.4 years, yet
93 showed significantly better survivorship as adults than zoo-born Asians, a delayed
94 impact on survivorship is clearly being instigated within a narrow developmental window,
95 prenatally and/or in the first years of infancy. There was no detectable effect of birth
96 origin on survival in Africans, although it should be noted that sample sizes are currently
97 still very small for zoo-born animals.

98
99 The third risk factor is recency of entry to the population, analysed by including year of
100 entry as a continuous explanatory variable. Adult Asians' survivorship shows no
101 significant improvement in recent years ($z = -1.48$, $p = 0.14$). In adult African elephants,
102 in contrast, adult survivorship has improved markedly and significantly in recent years (z
103 $= -2.75$, $p = 0.0059$; see online text for details). Survivorship in zoo-born infants
104 (livebirths) has not improved in recent years, either in Asians ($z=1.19$, $p=0.24$) or in
105 Africans ($z=0.002$, $p=0.10$, both analyses controlling for dam parity).

106

107 Reproductive rates in both species are much lower in zoos than in the reference
108 populations, even for prime-aged animals, and breeding ceases early in adulthood
109 (Figure 2; see also ref. 13). Small sample size precluded any investigation of birth origin
110 effects on reproductive rates. This premature reproductive senescence is the main
111 constraint on achieving self-sustaining zoo populations in future, with improvements in
112 reproduction to reference population levels having a much greater effect than
113 improvements in survival (Figure 3). However, although predicted growth rate comes
114 close to stability for Africans when reproduction alone is improved, for both species it is
115 necessary to improve survival as well to ensure self-sustaining zoo population.

116

117 These findings have implications for welfare, management and conservation. To date,
118 many zoos have responded to their declining elephant populations by advocating the
119 importation of animals from successful *in situ* populations (6, 7), and investing in new
120 enclosures. These and/or other changes do appear to be having some positive effects
121 on survivorship in adult African elephants. However, there is not yet a clear improvement
122 for adult Asians in zoos, and adult survivorship in even the most recent zoo Africans is
123 still lower than that seen in Amboseli animals undergoing natural mortality. Justifying the
124 high costs involved in this approach would thus seem difficult while the physiological and
125 environmental causes of poor breeding and survivorship remain unresolved and poorly
126 understood. Current knowledge indicates that the main causes of zoo elephant infant
127 mortality are prolonged parturition, infanticide, maternal neglect, and, especially in
128 Asians, *Herpes* (10, 11). Adult deaths in zoos reportedly often stem from cardiovascular
129 disease, but frequently are for reasons unknown (10). Fecundity in zoo females is
130 somewhat reduced by mere logistics (limited breeding opportunities); however, their

premature cessation of oestrous cycles and the high stillbirth rates of Asians, along with other fertility issues (10, 13, 14), indicate physiological causes too.

So why might these problems be more serious in zoos than *in situ* reference populations? And why do birth origin and inter-zoo transfer have such marked effects on Asian elephants? We propose two possible biological explanations: chronic stress and obesity. These suggestions are parsimonious, having the potential to explain most or all observed effects, plausible, given what is known about elephant health and husbandry, and testable, making specific predictions about morbid and pre-morbid conditions in the zoo populations. They should also be practically useful, suggesting new indices for identifying at-risk individuals, and for evaluating changes in zoo husbandry and management. Chronic stress, in humans and many other species, causes fertility problems and elevated stillbirth rates (10, 15, 16). Both chronic and acute stress also reduce adult lifespan (16, 17, 18), the post-capture deaths of wild-born Burmese elephants being a likely example. Additionally, stress impairs maternal care and infant survivorship (1, 4, 15, 16), and can induce reproductive senescence (19). Furthermore, early experience can have lasting effects: exposure to elevated stress hormones *in utero* and/or inadequate parental care in infancy (20-22) often disrupts stress responses throughout life. Indeed in adulthood, humans who were abused as children have elevated rates of stress-related disease (23) while rhesus macaques who were maternally-deprived die prematurely (24). Obesity, in humans and many other species, similarly reduces fertility, increases stillbirth risks, and shortens adult lifespan (25, 26). Furthermore, as with stress, early experience can have lasting effects. For example, excess perinatal weight has long-term harmful effects: overweight human babies have

elevated risks of obesity, cancer, cardiovascular disease and Type II diabetes in adulthood (27, 28).

Zoo elephants are often subject to treatments likely to elevate stress (e.g. relatively barren enclosures; unstable social groups; inter-zoo transfer). Adult elephants in zoos are also significantly fatter than *in situ* controls; and furthermore, zoo-born Asian calves are both heavier and fatter than those born into timber camps (see Table S4 in supporting online material). We therefore suggest the following measures for investigating birth origin effects and identifying causal aspects of husbandry/at risk individuals. If early experience and/or events throughout the lifespan predispose elephants to harmful stress responses, then useful screens include: measures of corticosteroid, ACTH and catecholamine outputs; assessments of immune and inflammatory responses (and related diseases); wound-healing rates; and adrenal, thymus and spleen weights *post-mortem* (e.g. 5, 10, 16, 18, 23). If peri-natal and/or adult obesity is the cause of poor fecundity or survivorship, then useful screens include: scores for body fat and its deposition patterns; measurements of serum triglyceride, leptin and cholesterol levels, and kidney fat depot size *post-mortem*; along with indices of insulin resistance such as decreased glucose tolerance and fasting hyperglycaemia (26, 28, 29).

In conclusion, the dramatic under-performance of Asian and African elephants in European zoos raises questions about both animal welfare and the effective allocation of conservation effort. Future work should investigate whether similar effects occur in America, which houses most of the remaining zoo elephants worldwide; pooling American and European studbooks could also provide the statistical power to identify further specific aspects of husbandry influential on survivorship and fecundity. In the

181 interim, we urge that as minimum management responses, i) new tests sensitive to
182 altered stress physiology and morbid obesity are incorporated into zoo elephant health
183 screens; and ii) zoos suspend the importation of elephants from range countries and
184 curtail inter-zoo transfers until it is understood how to mitigate their harmful effects, as
185 well as restricting breeding to zoos where there are demonstrably no harmful effects of
186 being captive-born.

Figure 1. Survivorship curves for female Asian (A-B) and African (C-D) elephants aged 1-10 years (juveniles: A & C) and 10+ years (adults: B & D). The table gives Cox regression results, and, where there are significant interaction terms, the results of *post hoc* pairwise comparisons (** = $p < 0.0001$, * = $p < 0.001$, * = $p < 0.05$, NS = $p > 0.05$). ‘Environment’ refers to whether zoo (Zoo) or *in situ* reference population (Ref.), ‘Birth origin’ to whether captive-born (CB) or wild-born (WB). Effects were tested in two ways, either including all mortality for wild born reference populations (‘All mortality’), or excluding human-caused deaths (‘Natural mortality’). Juvenile Asians (A) have no wild-born natural mortality result because the first eight years of history after capture is removed in this case, leaving insufficient data for a test (see online supporting material).

A: Asian juveniles, Natural mortality: not possible due to removal of capture effects All mortality: Significant Environment by Birth Origin interaction (z = 2.54 p = 0.01)				
		Zoo CB	Zoo WB	Ref. CB
Zoo	WB	NS		
Ref.	CB	NS	**	
Ref.	WB, all	*	***	**
B: Asian adults, Natural mortality: Significant Environment by Birth Origin interaction (- z=3.37, p=0.00075) All mortality: Significant Environment by Birth Origin interaction (z = 3.37 p = 0.0008)				
		Zoo CB	Zoo WB	Ref. CB
Zoo	WB	*		
Ref.	CB	***	***	
Ref.	WB, natural	***	***	NS
Ref.	WB, all	*	NS	***
C: African juveniles, Natural mortality: No significant Environment or Birth Origin effects (z=1.52, p=0.13) All mortality: No significant Environment or Birth Origin effects (z=0.417, p=0.68)				
D: African adults, Natural mortality: Significant Environment effect only (z = 10.9, p < 0.0001) All mortality: Significant Environment effect only (z=6.66, p<0.0001)				

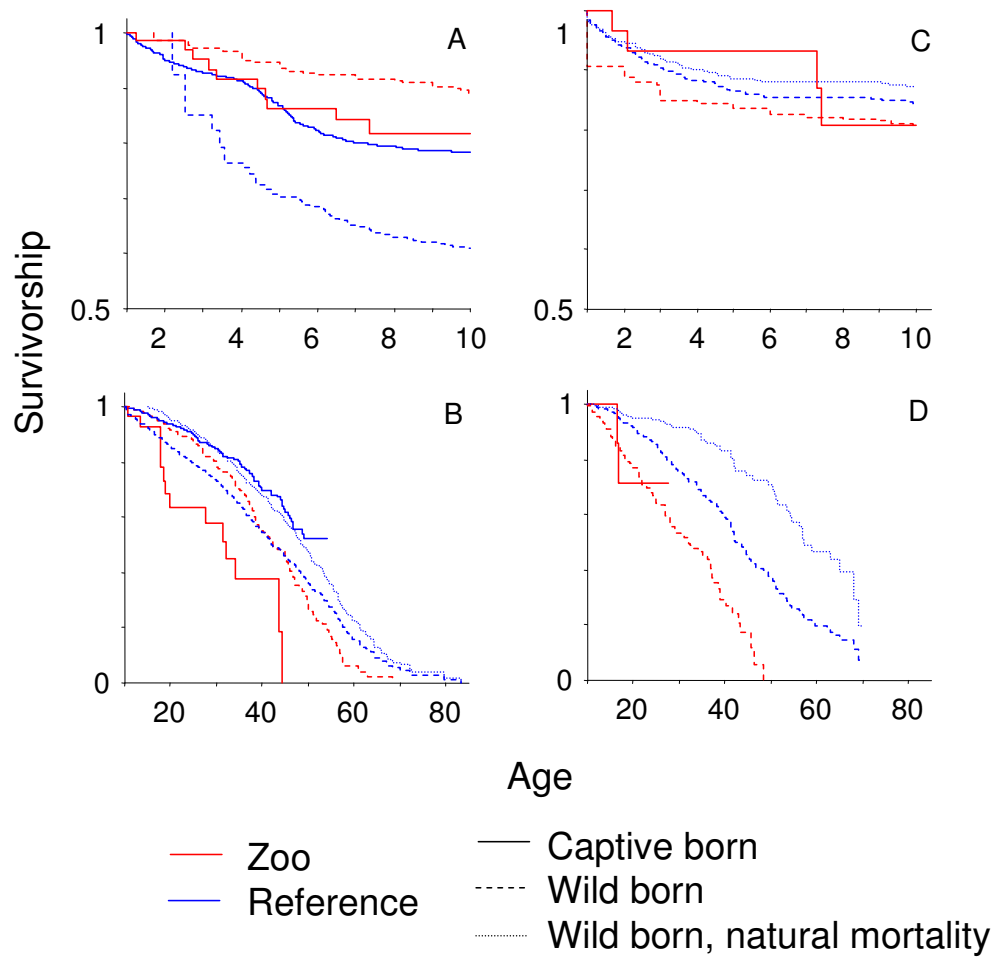
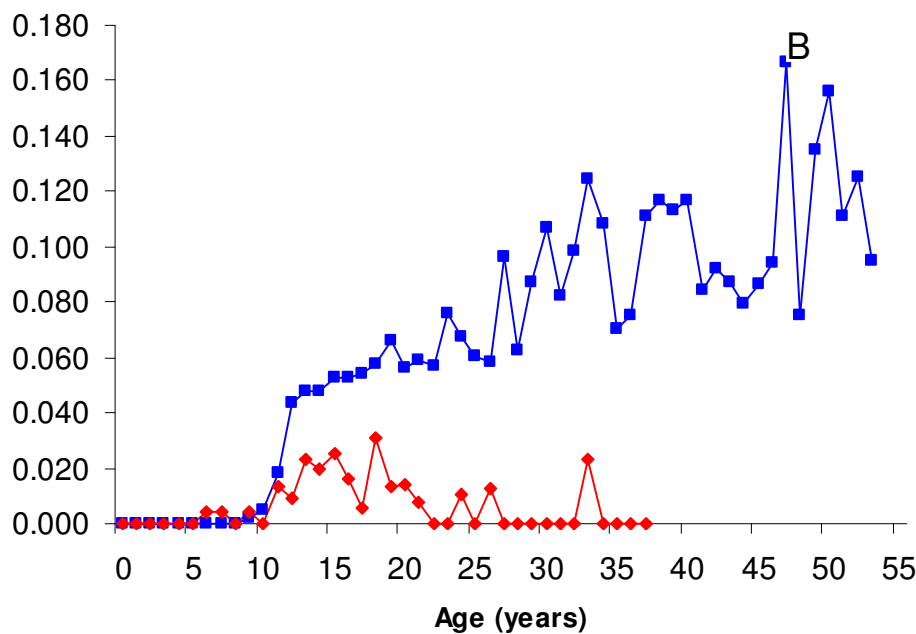
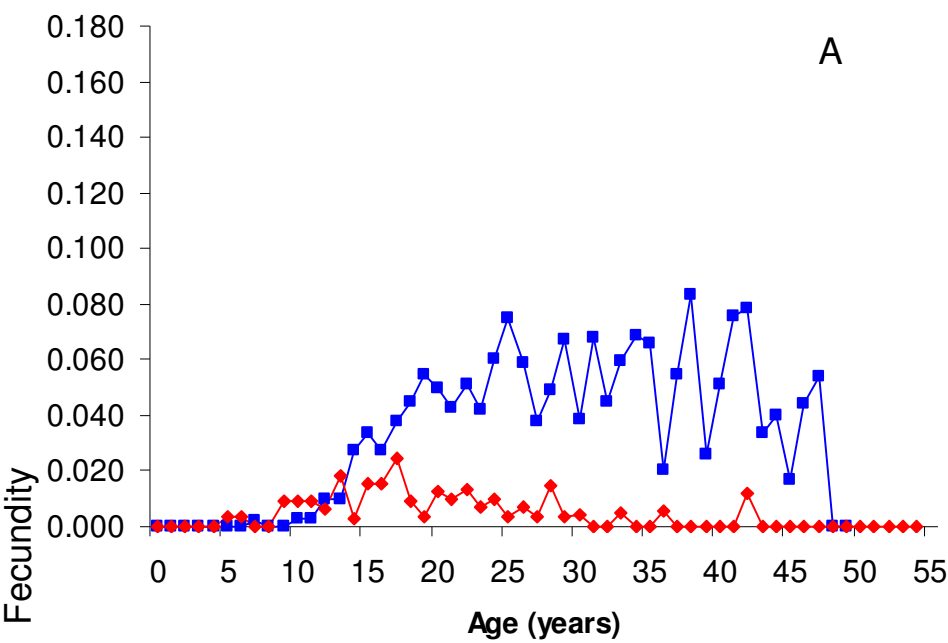


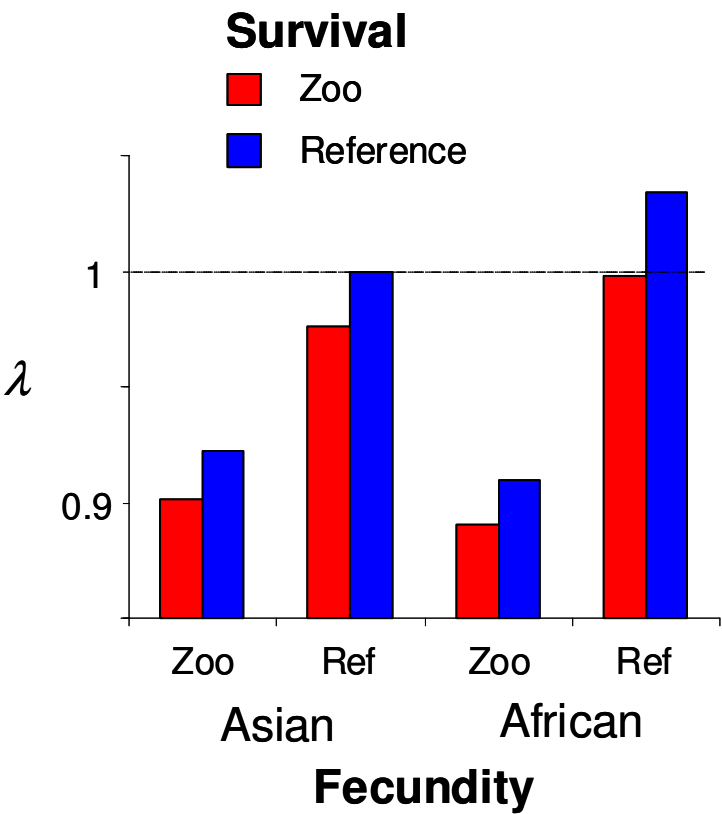
Figure 2. Fecundity curves for female Asian (A) and African (B) elephants, expressed as female calves per female per year.



— Zoo — Reference

208 **Figure 3.** Predicted long-term population growth rate, λ , given by the rate of change at
209 stable age structure of a Leslie matrix model, under various scenarios. A self-sustaining
210 population is reached when $\lambda = 1$, as marked by the dashed line. Survival and fecundity
211 rates are assumed to be either as measured in zoo-born elephants, or, to model best
212 case future scenarios, as measured in the captive-born Asian reference population and
213 the 'natural mortality' African reference population.

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Clubb et al.: Supporting Online Material

1) Materials and Methods

i) The datasets

Zoo elephant data came from the European Endangered Species Programme (EEP) 'studbooks', as accurate to 12 June 2005 (Asian elephants) and 15 July 2005 (African elephants). Data were checked for internal consistency using the 'Clean Up' and 'Data Validation' functions of the SPARKS ('Single Population Analysis and Records Keeping System', Version 1.52) programme used by zoo studbook managers; all errors found were corrected. Supplemental information was added from the European Elephant Group report (EEG 2002), which contained data for additional animals (108 African; 96 Asian) plus some dates absent from studbooks. For our analyses, we used only animals living in the zoo population from 1st January 1960, and excluded the few African forest elephants (*Loxodonta cyclotis*), plus any individual whose birth origin was ambiguous (e.g. unknown, or recorded as 'timber camp') or which had unknown ages/unknown dates of entry to or exit from the zoo population. This resulted in a dataset comprising information on import/birth dates and death dates (where applicable) for 1055 animals (653 Asian and 402 African) from 236 zoos across Europe, Scandinavia and the former Soviet Union. Our analyses here focussed on females only (N = 786; 484 Asian, 302 African) due to the small N for males. In these analyses, birthdates for wild-born females were estimated to the nearest year (*cf.* e.g. Wiese 2000); and those imported when under one year old were assigned the maximum age at import (1 year) to avoid estimated life spans of zero. All zoo elephant data are provided online (www.sciencemag.com/).

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298 To act as reference populations, we used two well-documented *in situ* populations
299 judged to yield demographic benchmarks that zoos should reasonably expect to at least
300 match: thus not hunted/poached and generally well-provisioned with food/water. For
301 Asians, we used captive elephants working for the Myanmar Timber Enterprise (MTE;
302 Mar 1996, Mar and Win 1997, Mar 2007). MTE studbooks cover 5213 animals living in c.
303 260 timber-camps throughout the forested regions of Burma between 1925 and 2000.
304 We excluded records from before 1950; animals with unknown ages or sexes, uncertain
305 birth origins or dams, and/or unknown dates of entry to or exit from the population;
306 records with obvious errors (e.g. birthdates earlier than death dates); and males. For
307 captive-born animals, ages were known precisely. For wild-born animals, age at capture
308 was estimated by experienced elephant handlers, based on shoulder height and a range
309 of other indicators known to reflect age, particularly skin characteristics. The degree of
310 error in these age estimates is unknown, but likely to be within one year for young
311 animals (under 20), which form the majority (68%) of those captured (N = 1344). Animals
312 that escaped, which were stolen, or were transferred to a non-monitored population were
313 right-censored. This left reliable data on 2905 females. Lifetables can be supplied by MR
314 and KUM on request. For African elephants, we used a population continuously
315 monitored in and around Amboseli National Park, Kenya, from 1972 to the present (see
316 e.g. Moss 2001). Data came from 2173 individually-recognised elephants of both sexes.
317 Ages were known with a maximum error ± 6 months for most individuals under the age
318 of 35 at the end of 2004 (N females = 799); estimated either to the nearest year or ± 2.5
319 years for animals aged between 35-45 (N = 125); and estimated to a maximum of ± 5
320 years for animals over 45 years (19% of sample; N = 179). Animals whose ages were
321 estimated at first sighting in 1972 were reassessed at death when jaws were found (from
322 tooth ages) or by changes in size and shape during maturation; maturational changes in

their early photographs were also compared to known-aged reference animals (see Moss 2001). In survivorship analyses, calves of unknown sex were excluded, as were those born to an unknown mother and those that died at birth. Analyses here were based on births, deaths and other events up to the end of 2004 for a total of 1089 females. Lifetables can be supplied on request to PL and CM.

Both reference datasets contained some deaths caused by events that would be absent in fully protected populations, and these were identified in order to allow comparisons between zoo animals and a “natural mortality” baseline or benchmark (see below). In timber camps, for example, the catching and ‘taming’ of wild-born animals involves harsh, potentially fatal, practices (e.g. Lair 1997, Hedges et al. 2006) that do not occur in zoos. To quantify this period of potentially elevated mortality after capture in the MTE population, all wild-caught elephants living longer than x years after capture age, T , had their histories split at age $T+x$, where x was varied in steps of one year between one and 14 years. A new categorical variable was created to define year since capture, and the effects of this variable on survivorship was then assessed (using survivorship analyses described below). Using this technique, a period of significantly elevated mortality was identified in wild-caught MTE animals lasting up to 8 years after capture: mortality rates in this period were twice that seen subsequently ($z = 8.69$, $p < 0.0001$, proportionality test: $\chi^2 = 0.2$, $p = 0.66$; see Mar 2007 for further details). Forty two elephants were also killed deliberately for their ivory or by insurgents. Likewise some animals in the free-living Kenyan population experience human-related causes of death that they would be protected from in zoos, e.g. being speared as part of local Maasai traditions, shot by authorities, poisoned, or killed in traffic accidents. Deaths from such causes totalled 142 females), including 31 calves under the age of two years who lost their mothers. For both reference populations, these human-caused deaths were treated as right-

censored data points in 'natural mortality only' analyses; these conform more closely to fully-protected populations, and thus arguably provide more valid benchmarks for zoos.

ii) Statistical analyses and modelling

Survivorship analyses were run using 'R' (version 1.9.1). Kaplan-Meier survival curves were constructed, and Cox Proportional Hazards Regressions used to investigate the factors affecting zoo elephant survivorship and compare their survival with reference populations. Survival time was defined as the time between entering the population (through importation, capture or birth) and an 'event' (i.e. death, or censorship through loss to follow-up or being alive at the endpoint of the data). Premature and stillborn calves were excluded from all survival analyses. The proportionality assumption was always tested, using scaled Schoenfeld residuals (Grambsch & Therneau 1994).

Comparisons of zoo and reference populations were run using 'natural mortality' (see above) for the reference populations, and also using 'all mortality' (i.e. including human-induced deaths in reference populations) for completeness. Comparisons over the entire lifespan showed strongly non-proportional hazards, indicating that patterns of difference between categories varied between age groups. Data were therefore divided into the following age classes: 0-1 (Infant); 1-10 (Juvenile); 10+ (Adult), within which all natural mortality models were proportional. Birth origin ('Wild-born' versus 'Captive-born') was included in survivorship analyses where possible, since captive-born individuals might be expected to adapt better to captivity than wild-born individuals (in both zoo and MTE populations). *Post-hoc* change in deviance chi-squared tests were used to determine the source of any significant Environment*Birth Origin interactions. Significant results are only presented if they met the assumption of proportionality.

Because infant deaths did not meet the assumption of proportionality, they were compared between zoo and reference populations using Fisher Exact contingency tables, both including and excluding still- and premature births. Calves whose fates by the age of 1 were unknown (e.g. calves still younger than 1 when the database was last up-dated) were initially excluded. However, to investigate the potential impact of these censored animals, infant mortality was then re-calculated assuming that all censored animals were either (a) alive at 1 year of age, or (b) dead by 1 year of age.

For zoo elephants, additional survivorship analyses were run to investigate sources of variance within the zoo populations. These included a series of analyses to explore the 'birth origin effects' in Asians in more detail. First, the impact of age at entry to the zoo population was explored for wild-born animals, to test whether experiencing a relatively long infancy in the wild had an effect additional to being born in the wild. To do this, Import Age was treated as a continuous independent variable. Second, we ran analyses to explore the potential confound of dam parity: because captive-born animals are more likely than wild-born animals to have had primiparous dams, we investigated dam parity effects on progeny survivorship, using data only from captive-born females and wild-born females imported at under six years of age (it was assumed that the latter would not have conceived prior to their entry into the zoo population, and parity could therefore be confidently ascribed). Third, we ran analyses to explore the potential confound of recency: zoo-born animals are also more likely to have been born recently, and so 'recency' was controlled for in re-run birth origin analyses.

'Recency' was also an important factor to investigate in its own right, because, on the one hand, many zoos have up-graded their facilities since the 1960's, while on the other hand, disease agents like *Herpes* may have become more problematic. To include

‘recency’ in survivorship analyses, the year of entry into a zoo was included as a covariate. Dam parity was included in analyses looking for improvements in infant survivorship (live-born calves).

The effects of two aspects of zoo husbandry were investigated: i) age at removal from the mother, and ii) the degree to which each animal was transferred between different sites. These are potentially both important since females have lasting social relationships, daughters being thought to typically remain with their mothers for life in both Asian (Sukumar 2006) and savannah African (e.g. Moss 1988; Moss & Poole 1983) elephants. Age at removal from the mother was quantified as the age at which zoo-born calves were separated from the dam due to movement of either calf or dam to another location. Transfer effects were investigated by looking for elevated hazards after the first and second moves (too few elephants were transferred more than twice to allow further analyses), including initial imports for wild-borns, using the technique employed to investigate capture effects in MTE animals (see above). Elephants that experienced no more than one or two moves were used in these analyses to discount effects of subsequent moves. Birth origin was included as a factor.

Overall, multiple separate survivorship models thus had to be run to fully explore the data. This was necessitated by a) occurrences of non-proportionality, and b) the need to use different sub-sets of data in different analyses (e.g. captive-born calves only for weaning age effects).

Age-specific fecundity was calculated as 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). Small sample sizes precluded detailed analysis of the effects of Environment on fecundity.

427

428 The future population viability (long-term equilibrium growth rate) of zoo elephants was
 429 modelled in order to identify whether populations are expected to be self sustaining
 430 under conditions to date, and exploring the effects of changes in vital rates. Parameter
 431 values were taken from the survivorship and fecundity analyses above, using the
 432 characteristics of captive-born animals where they differed from wild-born since the
 433 analysis aims to understand the possible situation without further importation to zoos.
 434 The model used a female-only Leslie matrix formulation with 70 annual age classes, and
 435 a transition matrix of the following form:

$$\begin{array}{ccccc}
 s_0.m_1 & s_0.m_2 & K & s_0.m_{69} & s_0.m_{70} \\
 s_1 & 0 & K & 0 & 0 \\
 436 & 0 & s_2 & 0 & 0 \\
 M & & O & & \\
 0 & 0 & & s_{69} & s_{70}
 \end{array}$$

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

$$446 \quad \sigma_x = e^{(-a/b)(1-e^{-bx})} e^{-cx} e^{(f/g)(1-e^{-gx})}$$

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

449
$$s_x = \frac{\sigma_{x+1}}{\sigma_x}$$

450 Curve parameters were estimated using a Gauss-Newton nonlinear fitting procedure,
 451 implemented in R. Finally, to model the best possible future scenarios for zoo elephants
 452 and identify the respective benefits of improved fecundity and improved survivorship, we
 453 ran all matrices using the demographic parameters of our *in situ* reference populations.
 454 Using the age-specific fecundities of our reference populations gives a scenario in which
 455 all zoo females have ready access to males, high conception rates, and low stillbirth
 456 rates. Using the 'natural mortality' survivorship of our relevant *in situ* reference
 457 populations gives a scenario in which the zoo elephant mortality rates are reduced to the
 458 lowest level that can be expected.

459

460 **2) Results**

461 **i) The relative costs of *in* and *ex situ* elephant conservation**

462 *Ex situ* conservation costs exceed *in situ* costs for many species, with those of elephants
 463 previously being estimated as an order of magnitude greater *per capita* per year
 464 (Balmford et al. 1995, 1996). Here, using more direct estimates of *in situ* costs than
 465 these authors, we find a difference closer to two orders of magnitude. In North American
 466 zoos, maintenance costs average \$57,900 per elephant per year (AZA 2005) – with the
 467 c. 480 extant European elephants thus costing c. \$28 000 000 per year, and the global
 468 zoo population of 921 (Koehl 2007), c. \$53 000 000 per year. The non-recurring costs of
 469 *ex situ* elephant housing (building etc.) are also large, at c. \$2 000 000 *per capita*: see
 470 Table S1. In contrast, the Kenya Wildlife Service, for example, successfully protects c.
 471 25 000 elephants (Blanc et al. 2007) along with other species, and operates on \$15 -18
 472 000 000 per year (Associated Press 2003, Maliti 2005, Morris 2006); while the Kruger
 473 National Park (South Africa) protects c. 12 500 elephants (SANParks 2006) plus other

species, and operates on \$18-19 000 000 per year (Biggs et al. 2006). Even if all this *in situ* expenditure went on protecting elephants, this would represent just \$600-1520 *per capita* per year Asian elephants are less numerous, more threatened (e.g. Blake & Hedges 2004, Sukumar 2006), and their *in situ* conservation costs are harder to estimate. However, the guarding of protected areas (Hedges et al. 2005) and prevention of elephant-human conflict are just two areas where funding could assist Asian elephant conservation. For example elephant-proof fencing costs between \$300 and \$5000/km (Sukumar 1989, Nelson et al. 1993; Rees 2003), while compensation schemes could reduce retaliatory killing (e.g. \$10 000 000 per year would recompense Sri Lankan farmers for the damage done by this island's 3500 animals: Bandara & Tisdell 2004).

ii) Demographic analysis

a) Zoo and reference population comparisons - survivorship comparisons as summarised in Figure 1 and Tables S2 and S3:

Asians: For juvenile Asian elephants (Fig. 1A), survival was highest among wild-born zoo elephants, intermediate among captive-born elephants, regardless of keeping environment, and lowest among wild-born reference elephants. Note that removing human-caused mortality primarily requires the first eight years of captive history to be censored in wild-born animals, and since no animals in the reference population were younger than two when captured, this makes it impossible to analyse a natural mortality curve for wild-born reference juveniles. The low survivorship observed in this group is likely to be caused by capture stress (see above). For adult Asian elephants (Fig. 1B), when considering natural mortality only, survival was highest in the reference population, regardless of birth origin, intermediate among wild-born zoo elephants, and lowest among captive-born zoo elephants. When all mortality was included for the reference

population, survival among wild-born elephants was lower, similar to that of wild-born zoo elephants, but non-proportional. Median lifespans for captive-born elephants are 18.9 years for zoos, and 41.7 years for the reference population. Infant mortality comparisons are summarised in Table S2.

Africans: For juvenile African elephants, there was no significant effect of Environment (see Fig. 1 C). For adult African elephants, there was a significant effect of Environment (see Fig. 1 D), with zoo animals having poorer survivorship than reference animals, regardless of birth origin if only 'natural mortality' is considered; survival in the reference population is somewhat lower when all mortality is included, but still higher than in zoos. However, the adult captive-born zoo population is still very small, and so all results pertaining to it should currently be treated with caution. Median lifespans are 16.9 years for zoo-born elephants, 35.9 years for the reference population including all mortality, and 56.0 years for the reference population with natural mortality only. Infant mortality comparisons are summarised in Table S3.

b) Exploring variance in survivorship in zoo populations

The nature of the birth origin effect on survivorship evident in zoo Asians (see text of paper, plus above) was explored to see if length of infancy in the wild influenced the adult survivorship of wild-caught Asians. Using Import Age as a continuous independent variable, hazards were proportional, but there was no significant effect of import age ($z=-0.88$, $p=0.38$). Parity of the dam also had no significant effect on their offspring's survivorship (Asians: $z=0.857$, $p=0.39$; Africans: $z=1.36$, $p=0.17$). Thus dam parity was unlikely to be the cause of the birth origin effects in Asians.

Analyses to tease apart recency (i.e. how recently animals entered the population) and birth origin revealed the following. In Asians, controlling for recency increased the significance of the birth origin effect on adult survivorship ($z=-3.52$, $p=0.0004$). The same was not true for Asian juveniles (recency: $z=1.242$, $p=0.21$; birth origin: $z=-0.935$, $p=0.35$) or zoo-born infants (recency: $z=1.19$, $p=0.24$, parity: $z=1.27$, $p=0.21$). In equivalent analyses for Africans, birth origin remained non-significant in adults ($z=0.07$, $p=0.95$), but recency had a markedly beneficial effect on adult survivorship ($z=-2.75$, $p=0.0059$). Again, such effects were not evident in juveniles (recency: $z=-0.825$, $p=0.41$, birth origin: $z=-0.186$, $p=0.85$), or zoo-born infants (recency: $z=0.002$, $p=0.10$; parity: $z=-0.26$, $p=0.79$). In African adults, although recency is improving survival rates in zoos, the survival model suggests a mortality risk at the final year of the data set (2005) that remains 2.8 times higher (95% CI 1.2 – 6.5) than in the reference population (excluding human-caused deaths).

The age at which zoo-born calves were separated from their mothers had no significant effect on the survival of Asians ($z=-1.38$, $p=0.17$) or Africans ($z=-0.002$, $p=1$), although sample sizes of weaned young were very low ($N = 15$ for Asians and 8 for Africans; note that the total number of zoo-borns here differs from the totals in Tables S2 and S3 because dam parity is not known for all births). Testing for periods of elevated hazard post-transfer showed that Asian elephants that were transferred once experienced 71% higher mortality hazard in the year following transfer than in subsequent years ($z=-2.05$, $p=0.04$; proportionality test: $\chi^2=0.75$, $p=0.69$). For elephants that experienced two transfers, this period of elevated hazard lasted for up to six years after the second move ($z=-2.23$, $p=0.026$, proportionality test: $\chi^2=1.48$, $p=0.48$), at which point the hazard was

69% higher than in the following years. It was not possible to test for elevated hazards after a transfer event in Africans due to the small sample size.

iii) How our three populations compare with other in and ex situ populations

Analyses and modelling of the North American Asian zoo elephant population have revealed total infant mortality rates (i.e. deaths under one year, including stillbirths) of c. 40%; they also project population declines, despite using the pooled survivorship of zoo-born and wild-born zoo animals (e.g. Faust et al. 2006). Very similar findings exist for the North American zoo Africans (Olson & Wiese 2000) – which thus have much higher infant mortality than conspecifics in Europe (see Table S3). Overall, European zoos therefore seem similar to or even better than other zoos globally. Turning to our reference Asians, conditions for working elephants in range countries can be harsh, and the capture of wild Asians problematic. However, some well-managed captive populations in southern India and Sri Lanka resemble the MTE population in being self-sustaining, and in having infant mortality rates under 15%, median female lifespans of c. 45 years, and annual fecundities of over 0.05 (Taylor & Poole 1998, Sukumar et al. 1997). Data from wild Asians are sparse, but they likewise indicate good infant survivorship when conditions are good, with annual mortality rates of 5% between 0 and 5 years of age (Sukumar 1989). Such reports suggest that MTE records are indeed representative. Finally, our African reference population likewise seems to provide a representative – even conservative – view of how this species can fare when well-provisioned and protected. Thus, for instance, 5 year cumulative infant mortality is just 10.5% in Samburu National Park, Kenya (Wittemeyer et al. 2005), while populations in range country reserves often increase exponentially at high rates, for example by 4.6% a year in Samburu (Wittemeyer et al. 2005), 6% a year in Addo, South Africa (Whitehouse

574 & Kerley 2002), and by over 8% a year in several other South African reserves (Slotow
575 et al. 2005): all higher than the Amboseli's 3.75% per year (Moss 2001).

576

577

3) Supporting tables

Table S1: Non-recurring expenditure committed by zoos/*ex situ* elephant sanctuaries in the last 10 years.

Items listed here range from completed facilities to those still being planned, and include construction, renovation and elephant acquisition costs. The final total given is an underestimate, since non-Anglophone sites are under-represented; inter-zoo animal transfer costs are not included; and data on several known renovations could not be found (e.g. Disney's Animal Kingdom, Australia Zoo & Woburn Safari Park; also c. 30 American Zoos and Aquariums Association members additional to those listed here, reportedly planning renovations by 2010: e.g. Piper 2007). For costs in non-US facilities, the exchange rates of Sept. 2007 were used.

<u>Year</u>	<u>Zoo/ Sanctuary</u>	<u>\$ Sum (USD)</u>	<u>No. elephants</u>	<u>Source/Notes</u>
Zoos:				
2004-2006	Anchorage Zoo, Canada	1 000 000	1	<i>Anchorage Daily News</i> , May 16 th 2006
2005-/2007- (planned)	Birmingham Zoo, US	15 000 000	6-8	www.bloomberg.com Nov 18 th , 2005; <i>Birmingham News</i> , July 15 th 2007; <i>Birmingham News</i> , Sept. 21 st 2007 (N.B. For other species too)
2006 - 2012	Brookfield Zoo (Chicago), US	'tens of millions'; <i>figure used here = \$20 000 000</i>	6	<i>Chicago Tribune</i> , Dec. 18 th 2006; <i>netscape.com</i> Dec. 19 th 2006
2007 (planned)	Buffalo Zoo, US	1 000 000	3	<i>Olean Times Herald</i> , Feb. 3 rd 2007
2007 (planned)	Calgary Zoo, Canada	10 000 000	4	www.calgaryzoo.org/HelpingTheZoo/ElphantBuilding.htm (accessed Aug. 2007); see also <i>Journal of Commerce</i> , Mar. 7 th 2007
2003 - 2006	Chester Zoo, UK	6 100 000 (for barn only; outside enclosure completed 2000).	15	www.zoolex.org , published Feb. 15 th 2007

2000 + 2006	Cincinnati Zoo, US	6 000 000 +2 600 000	3 (+)	<i>The Plain Dealer</i> , Feb. 27 th 2005 <i>Cincinnati Enquirer</i> , Jan. 2 nd 2006
2005 - 2010	Cleveland Metroparks, US	25 000 000	3 – 10	<i>The Plain Dealer</i> , Feb. 27 th 2005; <i>The Plain Dealer</i> , Dec. 14 th , 2006; WKYC-TV (http://www.wkyc.com/) Dec. 16 th , 2006. N.B. For hippopotamus and other species too
2005	Cologne Zoo, Germany	20 678 000	13	<i>EAZA News</i> , vol. 49 (2005)
2007: under construction	Copenhagen Zoo, Denmark	32 000 000	7	<i>The Copenhagen Post</i> , Oct. 18 th 2006
2006 (plan for future)	Dallas Zoo, US	6 500 000	2	<i>Dallas Morning News</i> , Mar. 4 th 2006
2007 -	Denver Zoo, US	52 000 000	6-8	<i>Denver Post</i> , July 9 th 2007; <i>AOL News</i> , www.aol.com , July 9 th 2007
2000-2005	Dublin Zoo, Eire	20 400 000 <i>allocated to 4 projects including elephants; figure used here = 5 100 000</i>	2	Office of Public Works 'What's New?', Eire; July 28 th 2000
2003-2007	Kamla Nehru Zoo, Kankaria, India	124 000	2	Times of India, Aug. 5 th 2007
2005 (date opened)	Hogle (Salt Lake City) Zoo, US	5 500 000	3	<i>AZA Communiqué</i> , July 2005; <i>Deseret Morning News</i> , June 2 nd 2005.
In progress (2007)	Honolulu Zoo, US	13 200 000	3	<i>Starbulletin.com</i> Feb. 13 th 2003
2006	Houston Zoo, US	6 000 000	3-6	<i>Houston Chronicle</i> , Mar. 25 th 2006
2007: scheduled to open 2009	LA Zoo, US	39-40 000 000 <i>(Sum used here: 39 000 000)</i>	5-10	<i>CNN.com</i> , April 20 th 2006; <i>LA Times</i> , Apr. 19 th 2006; NBC4 TV, Feb. 15 th , 2007; <i>Associated Press</i> July 21 st 2007
2005-2006	Lee Richardson Zoo (Garden City), US	175 000	2	<i>Garden City Telegram</i> , July 9 th 2004
2003; expansion currently delayed	Maryland Zoo, US	11 000 000	5	<i>Associated Press</i> , Nov. 25 th , 2003; <i>MD Board of Public Works</i> , ref. no. D06EO21E; <i>Baltimore Business Journal</i> , Mar. 20 th 2007

2004-6	Melbourne Zoo, Australia	10 850 000 + 5 600 000 (import costs; including those for Taronga Zoo)	3+	<i>Herald and Weekly Times</i> , Dec. 6 th 2006; <i>Herald-Sun (Sunday)</i> , June 25 th 2007
2005	Montgomery Zoo, US	1 000 000	3-4	<i>Montgomery Advertiser</i> , Nov. 13 th 2005
2003-2005	Nashville Zoo, US	3 500 000	3	<i>The Tennessean</i> , June 6 th 2006
2007- (planned; currently on hold)	National Elephant Center, US	3 500 000 (– 5 500 000) (<i>Figure used here: 3 500 000</i>)	13 -15	<i>Associated Press</i> wire, Mar. 8 th 2007; <i>Arkansas Democrat Gazette</i> , Mar. 8 th 2007; <i>Today's THV.com</i> , June 9 th 2007.
2006 (planned for future)	National Zoo (Washington, US	60 000 000	8 - 10	<i>Washington Post</i> , June 21 st 2006; <i>Associated press</i> July 21 st 2007
2005	North Carolina Zoo, US	8 000 000 (paddock) + 2 500 000 (barn)	3 -12	<i>News & Record</i> , Nov. 30 th 2005; <i>Houston Chronicle</i> , Mar. 25 th 2006; <i>WWAY News Channel 3</i> , 30th Nov. 2005, <i>News 14 Carolina</i> , www.news14charlotte.com , Nov. 30 th 2005.
2004	Oakland Zoo, US	100 000	4	<i>Contra Costa Times</i> , Mar. 21 st , 2005
2006 (flooring complete); rest in planning stages 2007	Oregon Zoo, US	51 000 (flooring) + 11-13 500 000 (new enclosure; <i>figure used here: 11 000 000</i>)	6	<i>KXL.com</i> , Oct. 21 st , 2003; <i>Facilities Plan Final Report</i> , Tony Vecchio July 29 th 2007
2006	Pittsburgh Zoo, US	1 500 000 – 2 200 000 (<i>figure used here: 1 500 000</i>)	6 - 20	For other animals too; <i>Pittsburgh Tribune Review</i> , Jan. 6 th and 10 th 2006; <i>Phillyburbs.com</i> , Oct. 4 th 2007
2005-2008	Reid Park Zoo (Tucson), US	8 500 000	2	<i>Tucson Citizen</i> , Mar. 3 rd 2005; <i>KVOA News 4</i> , www.kvoa.com , April 12 th 2006.
2003	Roger Williams Park Zoo (Providence), US	6 200 000	3	<i>Providence Journal</i> , Jul. 14 th 2006

2007-	Rosamund Gifford Zoo (Syracuse), US	7 600 000 (new barn cost estimated at 1/ 3 total i.e. 2 530 000)	3+	<i>The Post Standard</i> , Nov. 17 th 2007 http://www.syracuse.com/articles/news/index.ssf?/base/news-12/119529396728340.xml&coll=1 ; <i>The Post Standard</i> , Dec. 5 th 2007 http://www.syracuse.com/printer/printer.ssf?/base/news-12/1196850275182340.xml&coll=1 (N.B. For a new barn and viewing pavilion for visitors; also renovations to 'Primate Island')
1999	Saint Louis Zoo, US	6 600 000	12	<i>St. Louis Post-Dispatch</i> , Nov. 19 th 2005
2007 - 2009	San Diego Zoo, US	45 000 000 (House alone: 23 000 000)	3	<i>San Diego Union Tribune</i> , Sept. 18 th 2007; <i>Associated Press</i> July 21 st 2007 [Other species are to be included too: http://www.10news.com/news/14139837/detail.html]
2003	Santa Barbara Zoo, US	2 650 000	2	<i>Daily Nexus</i> , Oct. 20 th 2003
2005 - 2009	Sedgwick Zoo, US	6 – 10 000 000 (<i>Sum used here: 6 000 000</i>)	2	<i>Washington Post</i> , Dec. 28 th 2005; <i>American Zoos and Aquaria Assoc. news release</i> , 2005; <i>Associated Press</i> July 21 st 2007
2006 (completed) + Planned	Seneca Park Zoo, US	4 400 000 6 000 000	2	<i>Rochester Democrat & Chronicle</i> , Apr. 19 th 2006; democratandchronicle.com ; <i>Monroe County Executive Press Release</i> (Maggie Brooks), Dec. 22 nd 2004; <i>Rochester Democrat & Chronicle</i> , Aug. 12 th 2006
2003-2005	Taronga Zoo, Australia	44 000 000	5	<i>Annual Report for the Zoological Parks Board of New South Wales</i> , 2003/4; <i>The Sun-Herald</i> , July 10 th 2005; <i>Sydney Morning Herald</i> June 23 rd 2007
2006	Toledo Zoo, US	13 000 000	2	<i>The Plain Dealer</i> , Feb. 27 th 2005; Toledoblade.com Nov. 8 th 2006
2007 (under construction)	Topeka Zoo, US	1 800 000	2-4	www.savezooelephants.com
2007	Tulsa Zoo, US	550 000	3	<i>Tulsa World</i> , Apr. 14 th 2007
2004 - 2005	Western Plains Zoo, Australia	1 200 000	5	www.zoo.nsw.gov.au May 18 th 2005
2002	Whipsnade Zoo, UK	8 100 000	6	<i>The (London) Independent</i> , Jan. 29 th 2002
Sanctuaries:				
1994-present	Elephant Sanctuary, Tennessee, US	20 000 000	19	<i>Philadelphia Inquirer</i> , Nov. 26 th 2006;

2007	PAWS (Performing Animal Welfare Sanctuary), US	1 000 000 (for new planned facility)	11	<i>PAWS press release, Feb. 20th 2007</i>
2007	Salinas Ranch, US	250 000	4	<i>Santa Cruz Sentinel, Apr. 12th 2007</i>
	<i>For all sites including sanctuaries</i>	TOTAL SUM: \$563 358 000	Total. no. of animals: 229 - 278	
	<i>Excluding sanctuaries</i>	TOTAL SUM: \$ 542 008 000	Total. no. of animals: 195 - 244	

Table S2: Asian calf survivorship- Infant mortality data (for female calves)
in the first year.

Liveborn infant mortality			
	Primiparous dams	Multiparous dams	Fisher's Exact Test Zoo cf. Reference
European zoos	6/16 = 37.5% A: 7/17 = 41.2%; B: 6/17 = 35.3%	5/27 = 18.5% A: 6/28 = 21.4%; B: 5/28 = 17.9%	All mortality: Primiparous: p=0.018 Multiparous: p=0.046
MTE reference population – all and natural mortality (data are the same)	34/257 = 13.2%	30/430 = 7.0%	
Total infant mortality (includes some still-births of unknown sex; this value is likely to be an under-estimate for the reference population)			
	Primiparous dams	Multiparous dams	Fisher's Exact Test Zoo cf. Reference
European zoos	14/24 = 58.3% A: 15/25 = 60.0%; B: 14/25 = 56.0%	6/28 = 21.4% A: 7/29 = 24.1%; B: 6/29 = 20.7%	All mortality: Primiparous: p<0.0001 Multiparous: p=0.054
MTE reference population – all and natural mortality (data are the same)	47/270= 17.4%	42/442 = 9.5%	

A = Mortality if all calves that were censored, i.e. missing or still alive, all died in the first year.

B = Mortality if all calves that were censored, i.e. missing or still alive, all lived past the first year.

Table S3: African calf survivorship- Infant mortality data (for female calves) in the first year.

Liveborn infant mortality			
	Primiparous dams	Multiparous dams	Fisher's Exact Test Zoo <i>cf.</i> Reference
European zoos	6/26 = 23.1% A: 7/27 = 25.9%; B: 6/27 = 22.2%	0/7 = 0% A: 4/11 = 36.4%; B: 0/11 = 0%	All mortality: Primiparous: p=0.586 Multiparous: p=1 Natural mortality: Primiparous: as above Multiparous: p=1
Amboseli reference population	29/164 = 17.7%]	50/604 = 8.3%	
Amboseli reference population – natural mortality	29/164 = 17.7% (<i>i.e. unchanged</i>)	41/604 = 6.8%	
Total infant mortality (NB. this value is likely to be an under-estimate for the reference population due to inability to sex all neonates at birth)			
	Primiparous dams	Multiparous dams	Fisher's Exact Test Zoo <i>cf.</i> Reference
European zoos	7/27 = 25.9% A: 8/28 = 28.6%; B: 6/28 = 21.4%	0/7 = 0% A: 4/11 = 36.4%; B: 0/11 = 0%	All mortality: Primiparous: p=0.433 Multiparous: p=1 Natural mortality: Primiparous: as above Multiparous: p=1
Amboseli reference population	31/166 = 18.7%	60/614 = 9.8%	
Amboseli reference population - natural mortality	31/166 = 18.7% (<i>ie. unchanged</i>)	51/614 = 8.3%	

A = Mortality if all calves that were censored, i.e. missing or still alive, all died in the first year.

B = Mortality if all calves that were censored, i.e. missing or still alive, all lived past the first year.

Table S4: Body fat estimates and neonatal body weights.

Body weight (kg) and height at shoulder (cm) used to calculate Ponderal Index ($1000 \times [\text{kg}/\text{cm}^3]$) and Body Mass Index, BMI ($1000 \times [\text{kg}/\text{cm}^2]$).

Group/measure	Population		Population difference	Data source/ notes
	<i>In situ</i>	Zoo		
Asian calves' birth weights	89.5 (n = 5)	102.1 (n = 63)	$F_{1,66} = 8.32$, $p = 0.005$	Hayssen et al. 1993
	74.0 (n = 6)	105.6 (n = 40)	Reported as significant	Kurt & Mar 1996 (sexes pooled)
	-----	118.8 (n = 7)		ISIS 2002 (females only)
	-----	Females, including one stillbirth: 112.9 (n = 7) Males, including 4 stillbirths 117.2kg (n = 14)		European Asian studbook, 2005
Asian calves' ponderal indices	0.124 (n = 5)	0.154 (n = 19)	$F_{1,22} = 252.3$, $p < 0.0001$	Kurt & Mar 1996 (sexes pooled)
Asian calves' BMIs	11.3 (n = 5)	13.5 (n = 19)	$F_{1,22} = 252.3$, $p < 0.0001$	
Asian adults' ponderal indices	0.199 (n = 13)	0.214 (n = 7)	Difference not analysed; summary stats. given only	Kurt & Mar 1996 (adult females only)
	0.216	0.246		Kurt & Kumarasinghe 1998 (females only, aged 20; N not supplied; figures obtained from graphs)
	-----	0.241 (n = 26)		Ange et al. 2001 (females only; mostly adults, but data not broken down by age).
	0.222 (n = 6)	-----		Evans 1910 (adult females only)
Asian adults' BMIs	43.9 (n = 13)	50.5 (n = 7)	Difference not analysed; summary stats. given only	Kurt & Mar 1996 (adult females only)

	45.3	59.0		Kurt & Kumarasinghe 1998 (females only, aged 20; N not supplied; figures obtained from graphs)
	-----	58.5 (n = 26)		Ange et al. 2001 (females only; mostly adults, but data not broken down by age).
	51.1 (n = 6)	-----		Evans 1910 (adult females only)
African calves' birth weights	-----	Females: 88.5kg (n=2) Males: 89.8kg (n=4)		African European studbook 2005 (all liveborn)
African adults' ponderal indices		0.232 (n = 26)		Ange et al. 2001 (females only; mostly adults, but data not broken down by age).
	c. 0.150 (n = 56)			Krumrey & Buss 1968 (females age 20; figures obtained from graphs)
African adults' BMIs		56.7 (n = 26)		Ange et al. 2001 (females only; mostly adults, but data not broken down by age).
	c. 38.4 (n = 56)			Krumrey & Buss 1968 (females age 20; figures obtained from graphs)

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