Compromised Survivorship in Zoo Elephants

Ros Clubb,[1] Marcus Rowcliffe,[2] Phyllis Lee,[3,4] Khyne U. Mar,[2,5] Cynthia Moss,[4] Georgia J. Mason[6]*

Wild animals can experience poor welfare when held captive (*1*), an effect with ethical and practical implications. In zoos, the welfare of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) has long caused concern. Infanticide, *Herpes*, tuberculosis, lameness, infertility, and stereotypic behavior are prevalent (*2*), and zoo elephant populations are not self-sustaining without importation (*3*). We compiled data from over 4500 individuals to compare survivorship in zoos with protected populations in range countries. Data representing about half the global zoo population (1960 to 2005) came from European "studbooks" and the European Elephant Group (*4*). We focused on females as relevant to population viability ($N = 786$, both wild-caught and captive-born; 302 African and 484 Asian). African elephants in Amboseli National Park, Kenya ($N = 1089$), and Asian elephants in the Burmese logging industry (Myanma Timber Enterprise, M.T.E., $N = 2905$, wild-caught and captive-born) acted as well-provisioned reference populations [for details, see (*2*) and (*5*)].

For African elephants, median life spans (excluding premature and still births) were 16.9 years [95% confidence interval (CI) 16.4 to unknown; upper estimate for median not reached] for zoo-born females and 56.0 years (95% CI 51.5 to unknown) for Amboseli females undergoing natural mortality (35.9 years with human-induced deaths, 95% CI 33.8 to 40.3). Neither infant nor juvenile mortality differed between populations (Fig. 1A and tables S1 and S2), but adult females died earlier in zoos than in Amboseli (Fig. 1B and table S2). Zoo adult African survivorship has improved in recent years [$z = –2.75$, $P < 0.01$ (*5*)], but mortality risks in our data set's final year (2005) remained 2.8 times higher (95% CI 1.2 to 6.5) than that of Amboseli females undergoing natural mortality.

For Asian elephants, median life spans (excluding premature and still births) for captive-born females were 18.9 years in zoos (95% CI 17.7 to 34.0) and 41.7 years in the M.T.E. population (95% CI 38.2 to 44.6). Zoo infant mortality rates were high (over double those of M.T.E.): A female's first pregnancy therefore had only a 42% chance of yielding a live year-old in zoos compared with 83% in M.T.E. (table S1). Rates have not significantly improved over time (e.g., live births controlling for parity: $z = 1.19$, $P > 0.10$). For juveniles, captive-born survivorship did not significantly differ between populations, whereas wild-born survivorship was poorer in Burma (Fig. 1C and table S2) because of after-effects of capture (*5*). In adulthood, however, survivorship was lower in zoos (Fig. 1D and table S2), with no detectable improvement in recent years ($z = –1.48$, $P > 0.10$).

Within zoos, captive-born Asians have poorer adult survivorship than wild-born Asians (Fig. 1D and table S2). This is a true birth origin effect: Whereas zoo-born elephants are more likely to have been born recently and to primiparous dams, neither dam parity ($z = 0.86$, $P > 0.10$) nor recency ($z = –1.48$, $P > 0.10$) predict adult survivorship (controlling for recency makes birth origin more significant: $z = –3.52$, $P < 0.001$). Because the median importation age of wild-born females was about 3.4 years, this suggests that zoo-born Asians' elevated adult mortality risks are conferred during gestation or early infancy.

Interzoo transfers also reduced Asian survivorship (see supporting online text), an effect lasting 4 years posttransfer ($z = –2.10$, $P < 0.05$, controlling for birth origin). Additionally, survivorship tended to be poorer in Asian calves removed from mothers at young ages ($z = –1.92$, $P < 0.10$) (*5*).

Overall, bringing elephants into zoos profoundly impairs their viability. The effects of early experience, interzoo transfer, and possibly maternal loss, plus the health and reproductive problems recorded in zoo elephants [e.g., (*2*)], suggest stress and/or obesity as likely causes.

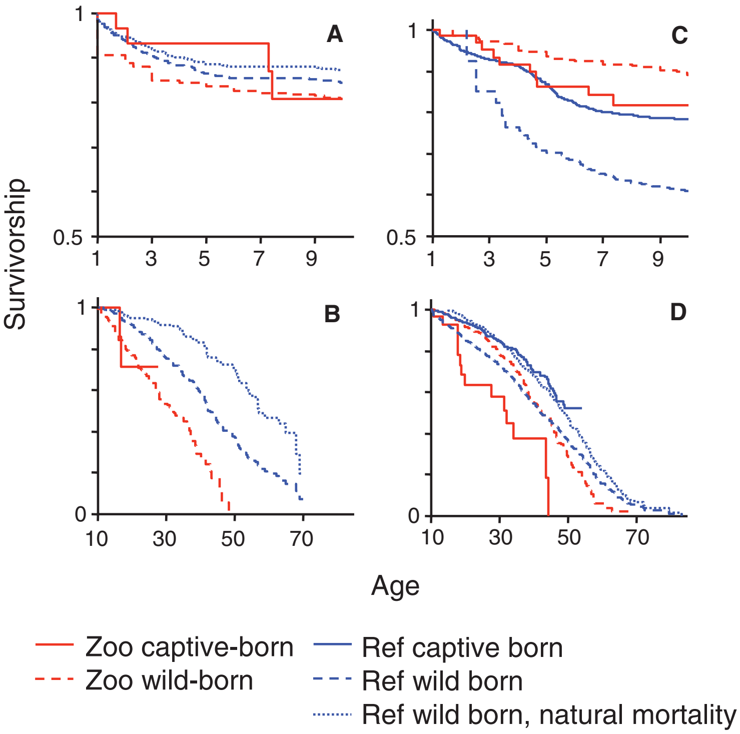

Fig. 1. Kaplan-Meier survivorship curves for female African (**A** and **B**) and Asian (**C** and **D**) elephants aged 1 to 10 [juveniles in (A) and (C)] and 10+ years [adults in (B) and (D)]. For wild-born reference (Ref, Amboseli or M.T.E.) populations, natural mortality excludes human-caused deaths; all mortality includes them (*5*). Results of statistical comparisons are given in table S2.

References and Notes

1. R. Clubb, G. Mason, *Nature* **425**, 473 (2003).
2. R. Clubb, G. Mason, *A Review of the Welfare of Zoo Elephants in Europe* (RSPCA, Horsham, UK, 2002).
3. M. Hutchins, M. Keele, *Zoo Biol.* **25**, 219 (2006).
4. European Elephant Group, "Elefanten in zoos und safariparks Europa" (European Elephant Group, Grünwald, Germany, 2002).
5. Methods and supplementary results are available as supporting material on *Science* Online.
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Supporting Online Material

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[1]Royal Society for the Prevention of Cruelty to Animals (RSPCA), Wilberforce Way, Southwater, West Sussex, RH13 9RS, UK. [2]Institute of Zoology, Zoological Society of London, London NW1 4RY, UK. [3]Psychology Department, University of Stirling, Stirling FK9 4LA, UK. [4]Amboseli Trust for Elephants, Post Office Box 15135, Nairobi, Kenya. [5]Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK. [6]Animal Sciences Department, University of Guelph, Guelph N1G 2M7, Canada.

*To whom correspondence should be addressed. E-mail: gmason@uoguelph.ca

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Supporting Online Material for

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Ros Clubb, Marcus Rowcliffe, Phyllis Lee, Khyne U. Mar, Cynthia Moss, Georgia J. Mason*

*To whom correspondence should be addressed. E-mail: gmason@uoguelph.ca

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This PDF file includes:

Supporting Online Material

Methods

Survivorship analyses (Cox Proportional hazards) were run using 'R' (v. 1.9.1), where survival was the time between population-entry (birth; or importation/capture -- the latter being treated as left-censored) and an 'event' (death; or living/lost to follow-up -- the latter being treated as right-censored). Proportionality of hazards was tested using scaled Schoenfeld residuals; data were divided into age-classes (1-10: Juvenile; 10+: Adult) to ensure proportionality. Infant deaths were non-proportional and so compared using Fisher Exact tests (Table S1).

Human-caused deaths in reference populations were also treated as censored, in 'Natural mortality' analyses that conform closer to fully-protected populations and provide more valid benchmarks. In Amboseli, this affected 142 females (e.g. speared, shot or killed in accidents); these animals were treated as right-censored. In the M.T.E. population, this affected 42 elephants killed for ivory or by insurgents, plus all 1344 wild-born animals captured and 'broken', which elevates mortality (e.g. *S1*). To quantify these capture effects, all wild-caught M.T.E. elephants living longer than x years after capture, T, had their histories split at age $T+x$, where x was varied between one and 14 years. Comparing survivorship before and after x showed significantly elevated mortality for up to eight years post-capture ($z = 8.69$, $P < 0.0001$; *S1*). The first eight years of wild-caught histories were therefore left-censored in 'Natural mortality' analyses for this species.

'Recency' was investigated, by including year of entry into a zoo as a covariate, because zoo husbandry has changed since the 1960's, and recency (plus dam parity) could account for apparent 'birth origin' effects.

Transfer effects were explored in Asian elephants experiencing one or two moves (sample size precluded investigating further moves) via the approach used to assess capture effects. In elephants transferred twice, only effects after the second transfer were investigated. Initial imports for wild-borns were included.

In Amboseli, females who lose a mother before nine years of age show reduced survivorship up to the age of first reproduction (*S2)*. Effects of the age when zoo-born elephants were separated from their mothers were therefore investigated in Asians (whose sample size allowed this) by including as a covariate the age at which each calf was moved from her birth zoo and mother; calves still with their mothers, i.e. right-censored data, were included.

Supporting text

In Africans, recency markedly improved adult survivorship (see paper), but not juvenile (recency: $z = -0.83$, $P > 0.10$, birth origin: $z = -0.19$, $P > 0.10$) or zoo-born infant survivorship (recency: $z = -0.26$, $p>0.10$; dam parity: $z = 0.002$, $P = 0.10$). In Asians, recency did not affect survivorship in adults (see paper), juveniles (recency: $z = 1.24$, $P > 0.10$; birth origin: $z = -0.94$, $P > 0.10$), nor zoo-born infants (recency: $z = 1.19$, $P > 0.10$, dam parity: $z = 1.27$, $P > 0.10$).

Compared to subsequent years, mortality hazards were 50% higher four years following transfer (see paper). Wild-borns experienced lower hazards; but birth origin and transfer number did not interact. Adding transfer age had no significant effect.

Table S1. Infant mortality data (for female calves) in the first year. For Amboseli elephants, natural mortality ('natural') excludes human-caused deaths, 'All mortality' ('all') includes them. Censored infants were excluded from analyses. However, for illustration, proportions were re-calculated assuming they were all (A) dead or (B) alive by one year.

Liveborn infant mortality			
	Primiparous dams	**Multiparous dams**	**Fisher's Exact Test Zoo *cf.* Reference**
Africans, 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%	*Natural mortality*: Primiparous: $P > 0.10$ Multiparous: $P > 0.10$ *All mortality:* Primiparous: $P > 0.10$ Multiparous: $P > 0.10$
Africans, reference – natural	**29/164 = 17.7%**	**41/604 = 6.8%**	
Africans, reference – all	**29/164 = 17.7%** ***(i.e. unchanged)***	**50/604 = 8.3%**	
Asians, 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%	*Natural & all mortality:* Primiparous: $P < 0.05$ Multiparous: $P < 0.05$
Asians, reference	**34/257 = 13.2%**	**30/430 = 7.0%**	
Total infant mortality, i.e. premature and still-births included (NB. reference values are probably under-estimates due to inability to sex all neonates at birth)			
	Primiparous dams	**Multiparous dams**	**Fisher's Exact Test Zoo *cf.* Reference**
Africans, European zoos	**7/27 = 25.9%** A: 8/28 = 28.6%; B: 7/28 = 25.0%	**0/7 = 0%** A: 4/11 = 36.4%; B: 0/11 = 0%	*Natural mortality*: Primiparous: $P > 0.10$ Multiparous: $P > 0.10$ *All mortality*: Primiparous: $P > 0.10$ Multiparous: $P > 0.10$
Africans reference - natural	**31/166 = 18.7%**	**51/614 = 8.3%**	
Africans, reference – all	**31/166 = 18.7%** ***(ie. unchanged)***	**60/614 = 9.8%**	
Asians, 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%	*Natural & all mortality:* Primiparous: $P < 0.0001$ Multiparous: $P < 0.10$
Asians, reference	**47/270= 17.4%**	**42/442 = 9.5%**	

Table S2. Statistical analyses of survivorship data.
Cox Proportional Hazards regression analysis results from the data presented in Figure 1 are given here (Figure 1 sub-sections are referred to by letters A, B, C and D). For significant interactions, *post hoc* pairwise comparisons are also shown. 'Environment' refers to Zoo vs. Reference (Amboseli/M.T.E.); 'Ref' to Reference; and 'Birth Origin' to whether captive-born (CB) or wild-born (WB). For WB Ref populations, Natural mortality ('natural') excludes human-caused deaths, while All mortality ('all') includes them.

A: African juveniles	Natural mortality**:** No significant Environment or Birth Origin effects (z = 1.52, P > 0.10) All mortality: No significant Environment or Birth Origin effects (z = 0.417, P > 0.10)			
B: African adults	Natural mortality: Significant Environment effect (z = 10.9, P <0.0001) All mortality: Significant Environment effect (z = 6.66, P < 0.0001)			
C: 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	P<0.001	--
Ref.	**WB, all**	P<0.05	P<0.0001	P<0.001
D: Asian adults	Natural mortality: Significant Environment by Birth Origin interaction (z=3.37, P<0.001 All mortality: Significant Environment by Birth Origin interaction (z=3.37 P<0.001)			
		Zoo CB	**Zoo WB**	**Ref. CB**
Zoo	**WB**	P<0.05	--	--
Ref.	**CB**	P<0.0001	P<0.0001	--
Ref.	**WB, natural**	P<0.0001	P<0.0001	NS
Ref.	**WB, all**	P<0.05	NS	P<0.0001

References

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S2. C. J. Moss, P. C. Lee in *The Amboseli Elephant: A long term perspective on a long lived species* C. J. Moss, H. Croze, Eds. (Univ. Chicago Press, in press, publication date 2009).