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Supplementary information for

Capture from the wild has long-term costs on reproductive success in Asian elephants

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Mirkka Lahdenperä*, John Jackson*, Win Htut and Virpi Lummaa

*These authors contributed equally to this work.
Correspondence should be addressed to M.L. (email: Mirkka.Lahdenpera@utu.fi).

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S1. Data selection

Age-specific reproduction

The demographic dataset of Myanmar timber elephants for age-specific analyses includes 2,685 females with known birth origin (captive-born vs. wild-caught) and survival information, which lived beyond the earliest age of reproduction, 5 years. Of these females, 1,323 were captive-born between 1942-2011 and 1,362 were wild-caught, captured between 1951-2002 at estimated ages of 0-55 years (mean capture age 16.13 ± 10.91). Exact lifespan was known for 1,079 females. Elephants were born (or estimated to be born) between 1921-2011 and come from 11 out of 14 regional divisions in Myanmar: Ayeyarwaddy (N = 39), Bago (N = 314), Chin (N = 31), Kachin (N = 266), Magway (N = 104), Mandalay (N = 401), Rakhine (N = 91), Sagaing (N = 928), Shan (N = 242), Tanintharyi (N = 6), Yangon (N = 8) and unknown (N = 255). In these analyses, we grouped regions together based on proximity and elevation, where conditions for elephants were more similar: Ayeyarwaddy, Tanintharyi, Bago, Rakhine and Yangon were grouped together, Chin and Shan were grouped together, and Magway and Mandalay were grouped together. Accounting for spatial variation in reproduction in our analyses was important because MTE elephants from different regions experience differences in forest cover, habitat availability and climatic conditions, which may influence survival and reproduction. Furthermore, grouping regional divisions based on elevation and proximity made sample sizes in each region group more comparable for analyses. Approximately 95% of the original demographic data was retained with reliable birth, capture, departure and death information.

Calf survival and mother's birth origin

To investigate whether captive-born and wild-caught females show differences in calf survival before age 5, we analyzed 2423 calves (F = 1,235, M = 1,188; 1,290 born to captive-born females and 1,133 born to wild-caught females) born between 1960 and 2016 to 1030 mothers (500 captive-born and 530 wild-caught mothers). Generally, age-specific mortality in this population is greatest within the first 5 years [1], and therefore we concentrated on this age range in the analysis. We excluded stillborn calves, calves born to mothers captured before 1952, twins, and calves with mistakes or missing information (on sex, maternal presence, or exact/censored lifespan). These calves come from 11 regions in Myanmar: Ayeyarwaddy (N = 59), Bago (N = 282), Chin (N = 4) Kachin (N = 130), Magway (N = 344), Mandalay (N = 255), Rakhine (N = 29), Sagaing (N = 956), Shan (N = 196), Taninthary (N = 7), Yangon (N = 9) and unknown (N = 152). In the analyses, regions were grouped in the same way as in age-specific reproduction analyses above resulting in 6 grouped regions.

Calf age was included as a linear and quadratic term to control for the quadratic age effect on calf mortality before age 5 [1]. Birth cohorts and regions were also controlled for in the model (grouped the same way as in age-specific reproduction analyses, see SI). Maternal death is known to increase calf mortality [2], and maternal presence was therefore coded as a time-dependent variable in every year from birth to calf age 5 (0 = mother died during the focal year/had died during previous years; 1 = mother was alive during the focal year). We also included an interaction term between calf age and maternal presence to control for the changing effect of maternal death on calf mortality at different calf ages [2]. Maternal age at the birth of the calf was included in the model, which ranged from 7-63 years old in the current sample. Maternal ages above 60 were grouped together because of small sample sizes (N = 6 calves). Short previous birth intervals are known to increase calf mortality [1], and we categorized birth intervals as short, medium, long, and firstborn categories based on the 25% and 75% quartiles of birth-interval length (3.84 and 7.44 years, respectively; average = 6.28 ± 3.75 years). Birth order was not included because of its collinearity with maternal age and birth interval. We also controlled for the differences in survival between male and female calves [1], and an increased effect of maternal death on male calves by including calf sex and an interaction between maternal presence and calf sex in the model [2]. Finally, the mother's individual identification number was included as an intercept-only random effect to account for repeated births by the same female (ranges of 1-8 calves for wild-caught mothers and 1-10 calves for captive-born mothers; average = 2.35 calves).

S2. Age-specific reproduction model selection – additional details

The model selection was carried out in two phases. First, we explored the full set (21,089 models) of age term models with generalized linear models (GLMs) with binomial error structures, incorporating all fixed effects, but excluding the random effects terms. Then, we re-ran the best 100 models using GLMMs, to incorporate the random effects terms of individual ID number and regional division group. We used this approach to reduce the computational power needed to assess all models, while maintaining a large enough subset of models incorporating the random effects. We compared the predictive performance of each model using the Akaike Information Criterion (AIC) [3]. The use of AIC was appropriate for the current study because each of the model parameters and interactions were considered *a priori* in the base model, and so all models contained the same number of parameters and interactions. The best 'final' model was the model with the lowest AIC value (Table S1). We assessed the significance of the terms in the best-fit model using likelihood ratio tests (LRTs) with the Chi-squared ($\chi2$) distribution. Where a model term was included as both a fixed effect and an interaction, all terms with that effect were removed in the LRT calculation.

The AIC value of the best model was 0.04 lower than the second explanatory model with three thresholds (different thresholds at 20 and 44, as opposed to 19 and 44 years of age; Table S2; Figure S1). This small difference is therefore consistent with a peak of reproduction of between 19 and 20. The difference between the best and twentieth explanatory models was 2.74, indicating clear support for the best model relative to other competitive models (Figure S1). The best-fit 20 three-threshold models are shown in Table S2. Of the best 100 models, all were three-threshold models, and we found little support for linear, quadratic or cubic age terms relative to threshold models.

References

1. Mar KU, Lahdenperä M, Lummaa V. 2012 Causes and correlates of calf mortality in captive asian

elephants (Elephas maximus). *PLoS One* **7**, 1–9. (doi:10.1371/journal.pone.0032335)
2. Lahdenperä M, Mar KU, Lummaa V. 2016 Short-term and delayed effects of mother death on calf mortality in Asian elephants. *Behav. Ecol.* **27**, 166–174. (doi:10.1093/beheco/arv136)
3. Burnham KP, Anderson DR. 2003 *Model selection and multimodel inference: a practical information-theoretic approach.* Springer. (doi:10.1016/j.ecolmodel.2003.11.004)

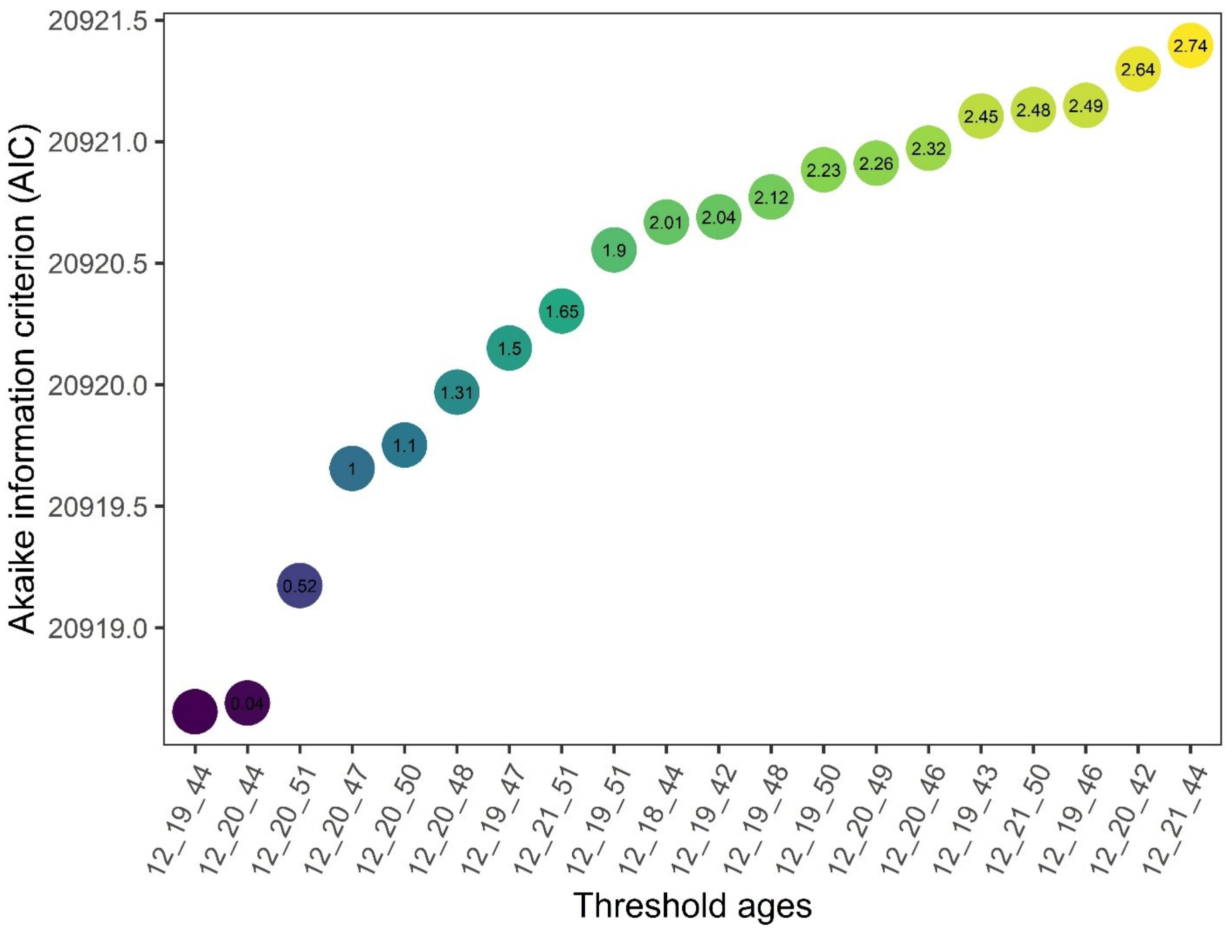

Figure S1. The best age-specific model was a three-threshold model with a peak reproductive age of 19. Figure shows AIC scores and threshold ages for the best-fit 20 models incorporating age terms. Colour denotes the AIC value, and the numbers within the points are the differences with respect to the best-fit model. The AIC differences indicate small differences between the first- and second-best models, but clear support for peak age of reproduction between 19 and 20.

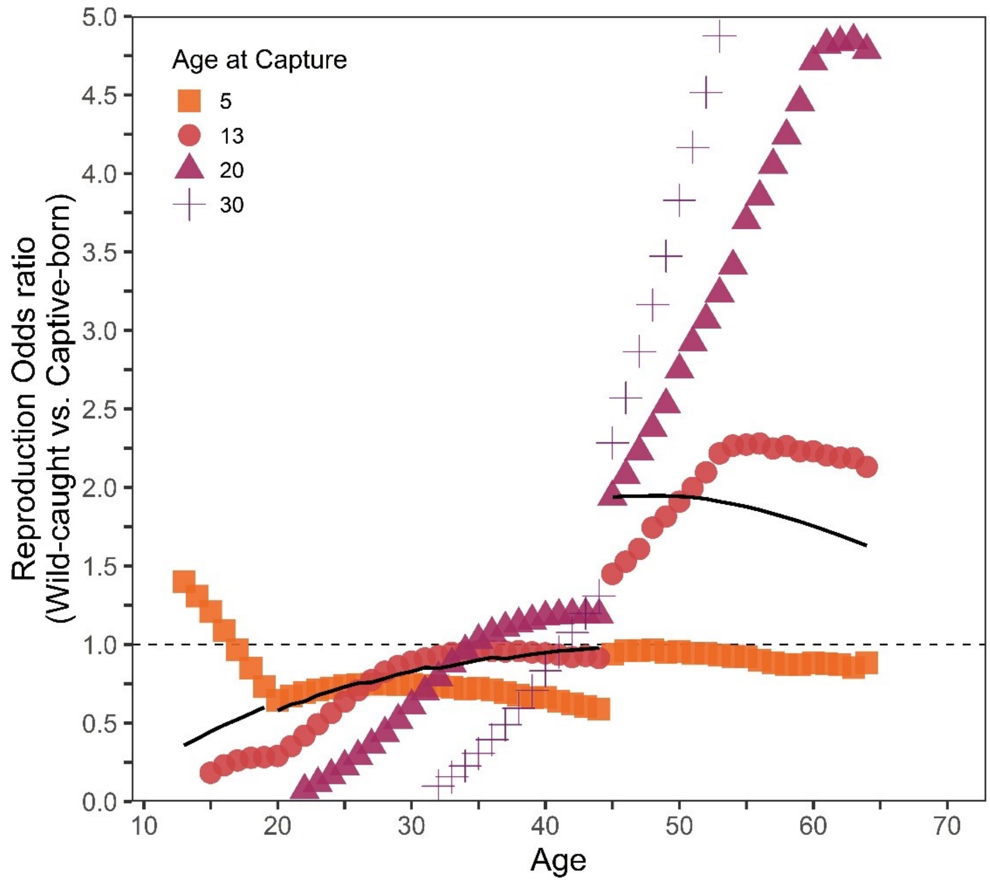

Figure S2. Wild-caught females had a greatly reduced odds of reproduction at peak reproductive ages (20-44) and at the onset of reproduction (13-19). Furthermore, the decrease in reproductive rates immediately after capture was the most pronounced in wild-caught females that were captured at older ages. Age-specific reproduction odds ratios comparing wild-caught to captive-born, for all individuals (1323 captive-born females and 1362 wild-caught females). Solid black line is the average age-specific odds ratio of reproduction for wild-caught females relative to captive-born females, irrespective of capture age. Points are examples of age-specific odds ratios for wild-caught females at different ages, where the colour and shape denote predictions for specific capture ages (5,13,20,30). Dashed black line at odds 1 indicates an equal odds for wild-caught and captive-born females.

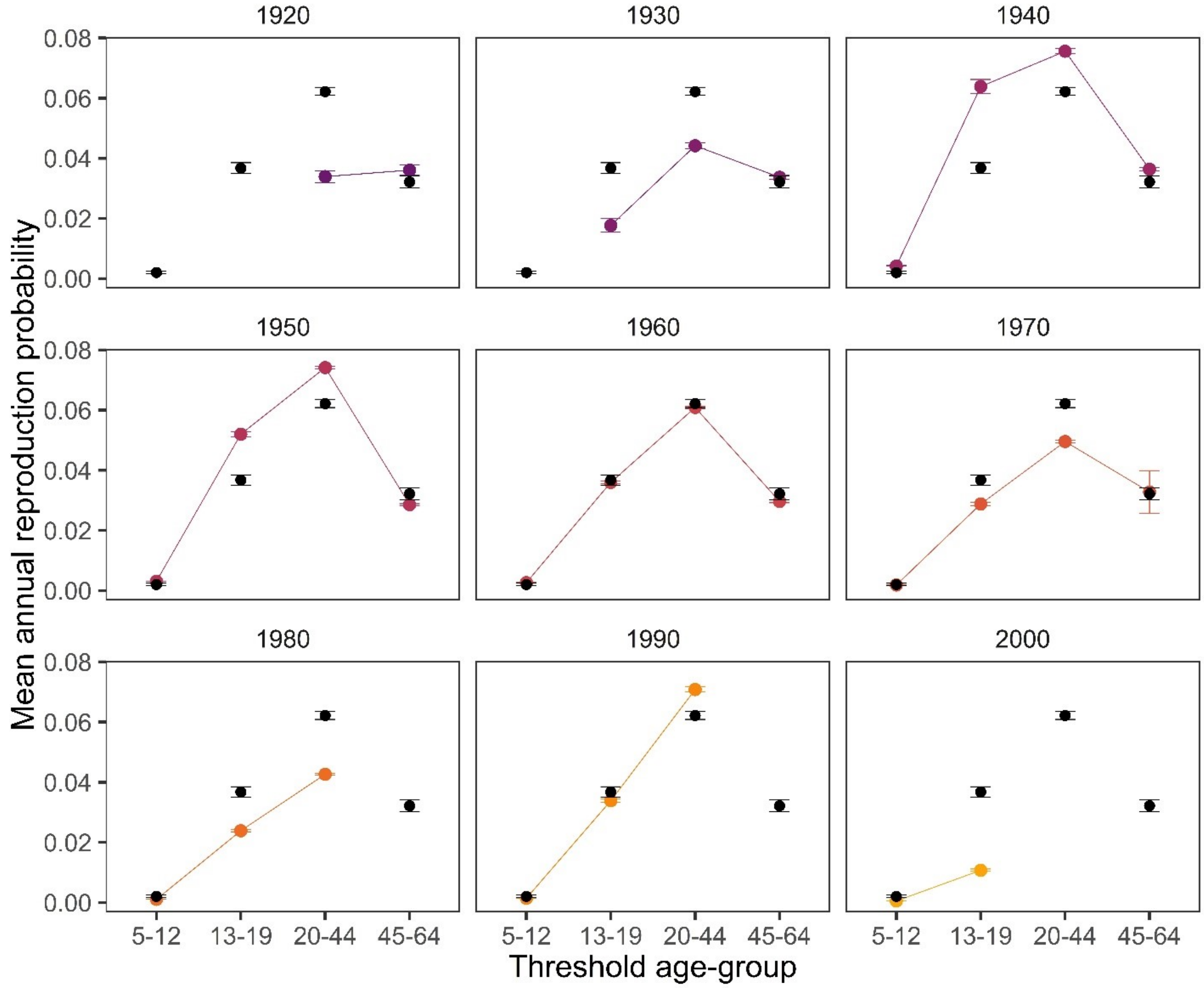

Figure S3. The age-specific birth rates from the 1960 birth cohort most adequately describe the mean reproductive rates in the raw demographic data. Mean annual birth rate in each of the threshold age-groups selected in the best-fit model for all females depending on the birth cohort (decade of birth). Coloured points lines in each panel are the mean±SEM model predicted annual birth rate in each age-group for each birth cohort (decade - panel titles). Black points denote the raw mean±SEM annual birth rate in each age-group from demographic data. There was significant variation in age-specific reproduction depending on birth cohort.

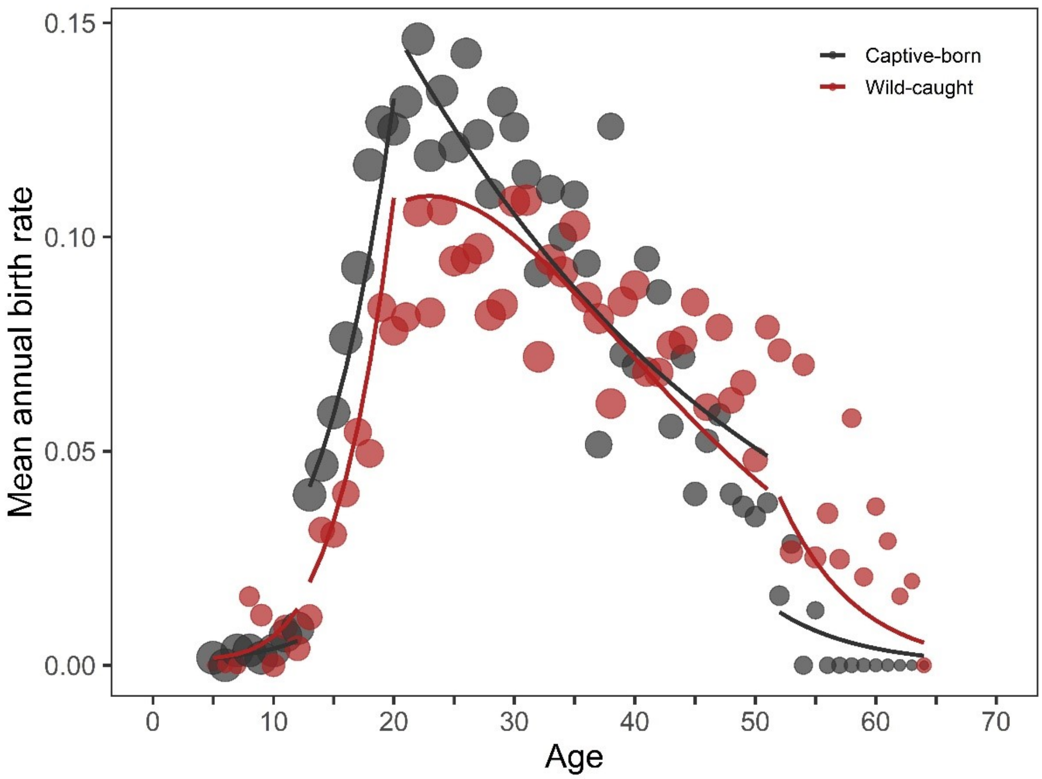

Figure S4. Wild-caught females that reproduced at least once had a reduced age-specific reproductive probability compared to captive-born females. The figure shows age-specific patterns of reproduction for captive-born and wild-caught females that reproduced at least once in their lifetime from the best-fit threshold regression model (age groups: 5-12, 13-20, 21-51, 52-64). Points are the raw mean annual predicted birth rates at each age for reproductive females only, with the size of the points denoting the square root of the sample size at each age (range = 8-580 time-event data points). Lines are the mean predicted values for an extended dataset of the observed females in the 1960 birth cohort, which were most similar to raw mean birth rates.

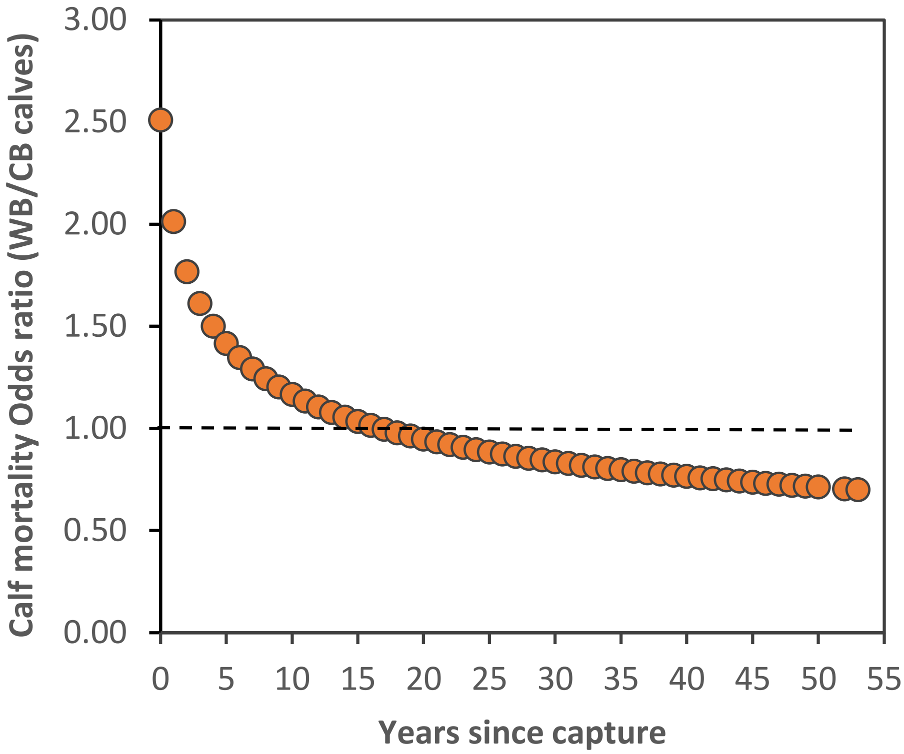

Figure S5. Calves of wild-caught (WB) mothers had increased mortality odds ratios (at each age from birth to age 5) compared to calves of captive-born (CB) mothers, the effect decreasing slowly and lasting ~16 years after mother's capture from wild (n=10,192 observations, 2423 calves, 1030 mothers). Points are yearly odds ratios after the mother's capture for calves born to wild-caught females relative to calves born to captive-born females. Dashed black line at odds 1 indicates an equal odds for calves of wild-caught mothers and calves of captive-born mothers.

Table S1. Parameter estimates and likelihood ratio tests (LRTs) for the effect of birth origin on lifetime reproduction (a- binomial mixed effects model, n = 1678) and log-transformed age at first reproduction (b- linear mixed effects model, n = 843) for female timber elephants. Estimates and standard errors presented on the logit scale for table a). Colon (:) denotes an interaction terms.

a)

Fixed effect	Estimate	Standard Error	LRT χ^2	p value
Intercept	0.02	1.19		
Birth origin			40.1	<0.001
wild-caught	-0.37	0.22		
Censored			15.1	<0.001
dead (1)	0.54	0.17		
Lifespan	0.07	0.01	93.1	<0.001
Birth cohort			17.1	0.02
1940	-1.93	1.11		
1950	-1.99	1.11		
1960	-2.34	1.12		
1970	-2.56	1.12		
1980	-2.53	1.13		
1990	-2.17	1.15		
Birth origin:Age at capture			4.9	0.03
wild-caught:age at capture	-0.04	0.02		
b)				
Intercept	2.67	0.08		
Birth origin			15.3	<0.001
wild-caught	0.08	0.02		
Censored			0	0.90
dead (1)	0.00	0.03		
Lifespan	0.01	0.00	17.3	<0.001
Birth cohort			37.6	<0.001
1950	0.09	0.05		
1960	0.12	0.05		
1970	0.16	0.05		
1980	0.30	0.06		
1990	0.14	0.07		

Table S2. Model selection results for the incorporation of age terms via threshold regression. The best 20 models are shown based on the Akaike information criterion (AIC). All of the best models had three thresholds, and thus four threshold age groups. The best model is highlighted in bold, and was selected in both stages of model selection (GLM and GLMM models).

Threshold age groups	Threshold ages	AIC	ΔAIC	GLM rank
four	**12, 19, 44**	**20918.65**		**1**
four	12, 20, 44	20918.69	0.04	2
four	12, 20, 51	20919.17	0.52	3
four	12, 20, 47	20919.66	1	4
four	12, 20, 50	20919.75	1.1	10
four	12, 20, 48	20919.97	1.31	7
four	12, 19, 47	20920.15	1.5	5
four	12, 21, 51	20920.3	1.65	14
four	12, 19, 51	20920.55	1.9	19
four	12, 18, 44	20920.67	2.01	8
four	12, 19, 42	20920.69	2.04	6
four	12, 19, 48	20920.77	2.12	17
four	12, 19, 50	20920.88	2.23	25
four	12, 20, 49	20920.91	2.26	18
four	12, 20, 46	20920.97	2.32	9
four	12, 19, 43	20921.11	2.45	13
four	12, 21, 50	20921.13	2.48	21
four	12, 19, 46	20921.15	2.49	16
four	12, 20, 42	20921.3	2.64	12
four	12, 21, 44	20921.4	2.74	11

Table S3. Parameter estimates from the best model of age-specific reproduction for only reproductive females (n = 1175; 38,492 elephant-year observations), fit using binomial generalised linear mixed effects models (GLMMs). Estimates and standard errors are present on the logit scale. The colon (:) depicts interaction terms. LRT denotes likelihood ratio test statistics.

Fixed effects	Estimate	Standard Error	LRT χ^2	p value
Intercept	-5.28	1.05		
Age	0.19	0.10	309.0	<0.001
Age group			973.2	<0.001
ages 13-20	1.99	1.06		
ages 21-51	6.51	1.01		
ages 52-64	10.63	2.58		
Birth origin			167.3	<0.001
wild-caught	-2.24	0.55		
Lifespan	-0.09	0.01	59.5	<0.001
Average age	0.15	0.02	48.0	<0.001
Birth cohort			88.7	<0.001
1930	-0.96	0.26		
1940	-1.06	0.25		
1950	-1.42	0.26		
1960	-1.61	0.27		
1970	-1.76	0.28		
1980	-1.97	0.29		
1990	-1.61	0.30		
2000	1.67	1.16		
Censored			9.53	<0.01
dead (1)	-0.14	0.05		
Age:Age group			142.1	<0.001
age:ages 13-20	-0.01	0.11		
age:ages 21-51	-0.23	0.10		
age:ages 52-64	-0.34	0.11		
Age:Birth origin			30.5	<0.001
age:wild-caught	-0.06	0.01		
Age group:Birth Origin			28.5	<0.001
ages 13-20:wild-caught	-1.76	0.49		
ages 21-51:wild-caught	-1.92	0.50		
ages 52-64:wild-caught	-0.53	0.69		
Birth origin:ln time since capture			96.4	<0.001
wild-caught:ln time since capture	1.67	0.18		

Random effects	Variance	Standard deviation
Individual ID	0.00	0.00
Regional division group	0.004	0.06

Table S4. Discrete-time survival model of the effects mother's birth origin on offspring risk of death during 0-4 (4.99) years in semi-captive timber elephants in Myanmar (Total n = 10,192 observations (2,423 calves and 1030 mothers). Positive estimates reflect increasing mortality risk. Reference categories are given in brackets. Mother's identity was fitted as a random term. The colon (:) depicts interaction terms. CB= captive-born, time= years since mother's capture, prev. =previous, M=male, F=female.

Fixed effects		**Estimate**	**Std. Error**	**F value**	**Numdf, Dendf**	**P value**
Intercept		-3.4812	0.2627			
Calf age		-0.5587	0.1214	51.96	1,9183	<0.0001
Calf age:calf age		0.1549	0.02785	30.92	1,9183	<0.0001
Mother's Origin (CB)		0.9266	0.4079	5.16	1,9183	0.0231
Mother's Origin:time (CB)		-0.3221	0.1355	5.65	1,9183	0.0175
Prev. birth-interval (medium)				3.54	3,9183	0.0141
	first-born	0.4380	0.1754			
	short	0.5981	0.1996			
	long	0.3532	0.2097			
Calf age:prev. birth-interval (medium)				5.61	3,9183	0.0008
	first-born	-0.2062	0.07229			
	short	-0.3786	0.1013			
	long	-0.2054	0.09526			
Birth cohort (1980)				2.86	5,9183	0.0138
	1960	0.07900	0.2241			
	1970	0.003297	0.1480			
	1990	0.1421	0.1260			
	2000	-0.3903	0.1627			
	2010	-0.4369	0.2270			
Mother's death (alive)		2.0369	0.4230	23.19	1,9183	<0.0001
Calf age:Mother's death (alive)		-0.4704	0.1668	7.95	1,9183	0.0048
Calf sex (F)		0.4366	0.2470	3.12	1,9183	0.0771
Calf sex (F):Mother's death (alive)				2.92	1,9183	0.0876
	M, mother dead	2.4734	0.5337			
	M, mother alive	0.01554	0.09558			
	F, Mother dead	1.6158	0.4415			
Calf division (Sagaing)				40.51	5,9183	<0.0001
	Ayeyarwaddy group (see S1)	-0.4616	0.1781			
	Chin and Shan	0.8292	0.1807			
	Kachin	1.6393	0.1828			
	Magway and Mandalay	0.2806	0.1304			
	Unknown	2.1089	0.1882			
Mother's age		0.01108	0.006420	2.98	1,9183	0.0844

Random effects	**Variance**	**Std. dev.**
Maternal ID	0.33	0.13