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1 **Long-term trends in wild-capture and population dynamics**  
2 **point to an uncertain future for captive elephants.**

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11

12 **Conflicts of Interest:** We have no conflicts of interest.

13

14 **Data accessibility:** The data and code supporting our results are archived in the Dryad Digital  
15 Repository: <https://doi.org/10.5061/dryad.rj237db>

16

17 **Author contributions:** KUM and WH collected the data. JJ, DZC and VL designed the study. JJ carried  
18 out analysis with support from DZC and VL. JJ wrote the manuscript, with contributions from VL and  
19 DZC. All authors approved the manuscript for publication.

20

21

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23

24

25 **Abstract**

26 Maintaining sustainable populations in captivity without supplementation through wild-capture  
27 is a major challenge in conservation that zoos and aquaria are working towards. However, the  
28 capture of wild animals continues for many purposes where conservation is not the primary  
29 focus. Wild-capture hinders long-term conservation goals by reducing remaining wild  
30 populations, but the direct and long-term indirect consequences of wild-capture for captive  
31 population viability are rarely addressed using longitudinal data. We explored the implications  
32 of changes in wild-capture on population dynamics in captivity over 54 years using a  
33 multigenerational studbook of working Asian elephants (*Elephas maximus*) from Myanmar,  
34 the largest remaining captive elephant population. Here we show that population growth and  
35 birth rates declined between 1960 and 2014 with declines in wild-capture. Importantly, wild-  
36 caught females had reduced birth rates and a higher mortality risk. However, despite the  
37 disadvantages of wild-capture, the population may not be sustainable without it, with  
38 immediate declines owing to an unstable age-structure that may last for 50 years. Our results  
39 highlight the need to assess the long-term demographic consequences of wild-capture to  
40 ensure the sustainability of captive and wild populations as species are increasingly managed  
41 and conserved in altered or novel environments.

42 **Keywords**

43 Individual-based model, population viability, demography, ex-situ conservation, life-history

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## 50 **Introduction**

51 Captive management and conservation are considered to be important stop-gap measures in  
52 efforts to ensure that wild animal populations are sustainable [1,2]. Although ex situ  
53 conservation strategies have been implemented successfully (e.g. [3]), captively managed  
54 populations are often small, and fail to be representative of the species as a whole, genetically  
55 robust or self-sustaining [1]. Many studies have found that zoo populations are unsustainable  
56 [4,5]. An assessment of 87 mammalian zoo populations revealed that only half were breeding  
57 to replacement rate [5]. Although an increased effort is now being placed into maintaining  
58 sustainable captive populations through captive breeding and reproductive technology [4,6],  
59 captive populations in zoos and aquaria have long been supplemented through wild-capture  
60 [7]. However, capture from the wild may impose long-term demographic consequences for  
61 captive populations [8], and therefore its implications for population viability must be explored.

62

63 Importantly but often overlooked, animals are also removed from the wild and kept in partially  
64 free-ranging or semi-captive conditions for many reasons other than conservation [9,10], most  
65 notably as research animals or for economic purposes as working animals [11–13]. Large  
66 numbers of individuals may be captured from the wild and conservation is not the primary goal  
67 of many semi-captive populations, but conservation management must still be considered,  
68 particularly where IUCN protection is in place [14]. However, few systems enable the  
69 assessment of how variation in wild-capture rates influences demography and population  
70 viability in captivity. One such species is Asian elephants (*Elephas maximus*), which are  
71 endangered but have a captive population of over 16,000 individuals, up to a third of the total  
72 population, increasing the importance of captive management [15]. Asian elephants are slow  
73 reproducers, exceptionally long-lived (mean lifespan =  $38.4 \pm 11.6$  years and age at first  
74 reproduction =  $19.8 \pm 5.7$  years [16]) and have a matriarchal social structure that has a large  
75 impact on survival [17], making them sensitive to anthropogenic disturbance and slow to  
76 recover [18]. In the wild, although there have been global population estimates and some

77 assessments that indicate large population declines [15,19,20], we have a poor understanding  
78 of population dynamics [21]. In captivity, many studies have emphasized that elephant  
79 populations managed in zoos are not self-sustaining [7,22,23], but this constitutes only a small  
80 number of individuals globally (~1000 individuals; [24]). The vast majority of captive Asian  
81 elephants are partially free-ranging, semi-captive working animals in range countries, used  
82 primarily for timber logging, tourism and ceremonial purposes [12,24]. Traditionally, wild  
83 elephants were captured to supplement the working population, which has been monitored in  
84 countries such as Myanmar for over a century [12,25]. Although the majority of captive  
85 elephants are primarily managed for economic purposes, conservation measures for the  
86 working population have also been incorporated in to local action plans e.g. in Myanmar [14].  
87 The case-study of working elephants therefore provides a unique opportunity to understand  
88 how wild-capture influences population-dynamics in captivity.

89

90 Here, we aim to assess how long-term variation in wild-capture has influenced population  
91 viability in the largest captive population of the long-lived Asian elephant. To address this  
92 issue, we use a detailed longitudinal studbook of government-owned female timber elephants  
93 (N = 3585) that were captive-born or wild-caught in Myanmar between 1960 and 2014. There  
94 has been substantial variation in wild-capture during this period; Aung [26] estimated that at  
95 least 2000 individuals were caught from the wild between 1970 and 1993. Furthermore,  
96 systematic wild-capture was formally banned in 1994 [27]. Thus, this unique dataset enables  
97 us to capture detailed variation in wild-capture and vital rates across several decades, which  
98 provides rare insight into the demographic challenges faced by vulnerable species in captivity  
99 as a result of capture from the wild. From these extensive demographic records, we address  
100 two key questions: 1) Between 1960 and 2014, how much did wild-capture contribute to  
101 observed annual changes in the number of individuals in the population? and 2) Now that  
102 systematic wild-capture is no longer practised, and given observed variation in demographic  
103 rates, will the current population decline in the future? To address the first question, we

104 captured historic trends in age-specific life-history traits in wild-caught and captive-born female  
105 elephants, and related observed changes in population size to wild-capture rates in each year  
106 from 1960-2014. For the second question, using age-specific demographic rates from years  
107 after capture was banned, we constructed individual-based, stochastic projection models to  
108 assess long-term population viability over 250 years. We explored population viability under  
109 model uncertainty of life-history rates, observed variation in the environment and demographic  
110 stochasticity. Finally, we performed sensitivity analyses of the projection models under  
111 different scenarios of changes to life-history rates, to provide targets for sustainable  
112 management in semi-captive elephants.

113

## 114 **Methods**

### 115 Study population

116 The Union of Myanmar has the largest working population of Asian elephants, with more than  
117 5000 individuals, and approximately 2700 are state owned and used for timber extraction  
118 processes [24,25]. The timber elephant population is managed centrally by the state forestry  
119 commission, the Myanma Timber Enterprise (MTE), and keeping systems (including workload  
120 regulations) are consistent across Myanmar [12]. Although MTE elephants are held in  
121 captivity, we describe them as semi-captive: 1) they are free-roaming outside of working hours  
122 and in the 3-month annual rest period and forage naturally without supplementation, 2) there  
123 is no reproductive management of the population and individuals mate freely with captive or  
124 wild conspecifics, 3) there is no human intervention with the weaning of calves, which are  
125 cared for by the mother until training at the age of five [12], and 4) culling is not practised and  
126 elephants only have access to basic veterinary care. Veterinarians diagnose disease and  
127 record deaths and their causes following broad post-mortem exams, increasing the reliability  
128 of mortality estimates [28]. Despite workload and work-related stress having the potential to  
129 influence life-history traits, population vital rates are more comparable to those of wild African

130 elephants [22] and Asian elephants [19] than to those held in zoos [29]. Timber elephants  
131 have been monitored by the state for over a century, and the current studbook has been  
132 collated from individual elephant log-books and annual MTE reports. To our knowledge, the  
133 studbook covers most individuals in the working population between 1960 and 2000, but we  
134 had access to approximately 13% less demographic records between 2001 and 2014. The  
135 final studbook was a female-only dataset (N = 3585, wild-caught = 1215) with individuals from  
136 11 out of the 14 regional divisions (or states) of Myanmar, including Ayeyarwady, Bago, Chin,  
137 Kachin, Magway, Mandalay, Rakhine, Sagaing, Shan, Tanintharyi, Yangon and Unknown  
138 regions (for data selection details, see S1, S2 and figure S1). This female-only dataset was  
139 used in all analyses of life-history traits and population projections.

140

141 Wild individuals were systematically captured in Myanmar until 1994 to supplement the  
142 working population, after which they were protected [12,27]. However, individuals are still  
143 taken from the wild into captivity in instances of human-elephant conflict, but this occurs at  
144 much lower levels than historically [12]. For wild-caught individuals, specific birth date is  
145 unknown, and therefore age is estimated at the time of capture using shoulder height and a  
146 comparison of body condition with elephants of known age [12]. In addition, the extent of  
147 pigmentation on the face (including trunk and temporal areas), folding of the upper ear, tail  
148 hair, and wrinkliness of the skin are used to estimate age in wild-caught individuals [8]. The  
149 exact error in age-estimation for wild-caught individuals is unknown, but thought to be within  
150 couple of years for individuals that continue to grow (up to approximately 25 years old; [30]),  
151 which constitutes the majority (72%) of those captured [8]. Using records of wild-caught  
152 females, we included a measure of wild-capture, which broadly assessed the number of  
153 individuals captured in each year. However, this does not necessarily include all individuals  
154 captured for two reasons. First, an estimated 5-30% of individuals die during capture [31], and  
155 the studbook only includes individuals remaining in the working population [8]. Second, we  
156 only included wild-caught females caught before an estimated age of 25, when their age-

157 estimation is likely to be most accurate. We have no estimate on the level of poaching in the  
158 wild population, and to our knowledge, only very few individuals in the captive population are  
159 removed after they were born/captured. We restricted the studbook to a female-only dataset  
160 because we could not reliably estimate paternity and thus reproductive rates for male  
161 elephants from demographic records. There are differences in life-history traits between male  
162 and female elephants [8], and this is a limitation of the current studbook, but we could not  
163 include the dynamics of males in this study. However, A female-only design was appropriate  
164 for the current study because reproduction was not limited by the number/frequency of males,  
165 with a mean sex ratio of 1.34 across the study period (females:males, range = 1.23-1.45; figure  
166 S6) and 50.54% of births to male calves. Females also mate with both wild and captive bulls  
167 [12]. Thus, population growth and decline can be assessed reliably using the dynamics of  
168 females.

169

170 Long-term trends in the age-specific vital rates of wild-caught and captive-born females

171 Mortality and birth events within the studbook were used to quantify population vital rates  
172 through time for individuals of different birth origins, to parameterise population projection  
173 models. Age-specific rates of mortality and birth were estimated from the raw data using a  
174 generalised additive mixed modelling (GAMM) framework, run using the gam function in the  
175 R package mgcv [32,33]. The raw data was smoothed using an additive modelling approach  
176 because there was a large variation in the density of life-history data spatio-temporally and  
177 across ages. Thus, raw age-specific data in a given year may not be representative of general  
178 population-level trends of life-history. An additive modelling approach also enables us to  
179 flexibly capture non-linear trends in vital rates across an individual's lifespan and through time.  
180 All analyses were carried out in R [33].

181

182 For every year of a female's life from birth/capture (or any years of a female's life after 1960 if  
183 entering before 1960) to death/censoring, we coded the mortality and birth events of each  
184 individual as binary response variables (fitted with binomial error structures and a logit link  
185 function), where a 1 indicated an event (death or birth) in a given observation year. Individuals  
186 exited the analysis at death or at their last known age alive (censor date). The time series  
187 dataset contained 66,528 (wild-caught = 30,287) year-age observations from the 3585  
188 females. We then modelled the probability of death and birth separately as functions of age  
189 (numeric integer), observation year (numeric integer, years from 1960 to 2014), and birth origin  
190 (binary factor, captive-born vs wild-caught). Using model selection, we explored the predictive  
191 performance of 18 models, which incorporated age as a linear predictor or smoothing term,  
192 and observation year as a linear term, factor (decade or half-decade), smoothing term and  
193 random effect smoothing term. We also explored interactions between age, observation year  
194 and birth origin, included as thin plate regression spline smoothers for each birth origin, or as  
195 tensor product interaction smoothing terms [34,35]. Models were selected based on the Akaike  
196 information criterion (AIC) [36,37] (For full details of model selection see S2 and table S1).

197

198 We assessed the distributional assumptions of the best models by testing the  
199 under/overdispersion of scaled model residuals. Scaled model residuals were calculated from  
200 the DHARMA package of R, which uses a simulation-based approach to create readily  
201 interpretable scaled residuals for mixed effects models [38]. We tested for  
202 under/overdispersion and uniformity in simulated residuals using 1000 simulations (figure S2).  
203 Then, we quantified the uncertainty in birth and mortality rate predictions from the best models.  
204 This enabled us to assess how much parameter uncertainty influenced variation in population  
205 size in future projections. Parameter uncertainty was quantified using posterior simulation of  
206 the best model, with 1000 replicates of model coefficients from the posterior mean and  
207 covariance matrix of the model. Posterior simulation was selected ahead of other

208 bootstrapping techniques as it prevented the need to re-fit models, which would risk under-  
209 smoothing.

210

211 How was past population growth influenced by wild-capture?

212 To explore how past trends in population growth were influenced by wild-capture, we  
213 calculated realised changes in the number of females from demographic data. For each year  
214 between 1960 and 2014, we calculated the number of females alive and the realised annual  
215 growth rate was calculated as  $\lambda_{t \text{ realised}} = N_{t+1}/N_t$ , where  $N$  is the number of individuals in  
216 year  $t$ . Population changes from 2000-2001 were ignored because there was a decrease in  
217 the number of demographic records available to us between 2000 and 2001. We partitioned  
218 out population change effects due to wild-capture and to annual vital rates alone by subtracting  
219 the observed annual wild-capture rate from the change in the number of individuals and re-  
220 calculating the realised annual population growth rate. We tested the difference in population  
221 growth rate with and without wild-capture when capture was still practised systematically  
222 (before 1995) using a linear model, with realised annual growth rate as the response variable  
223 and both year (numeric integer) and capture presence (binary factor) as predictor terms.

224

225 Population projection models for a future without wild-capture

226 To assess the future viability of the timber elephant population, we built female-only, stochastic  
227 individual-based projection models using predicted age-specific birth and mortality rates for  
228 years after systematic wild-capture was banned (1995-2014) (more details in S3, figure S9  
229 and figure S10; [39]). We opted to use an individual-based modelling framework to incorporate  
230 demographic stochasticity. All projection models were run on predicted values from the Kachin  
231 regional division; Kachin had a large number of life-history records, whilst having average  
232 predicted vital-rates most consistent with the overall mean vital rates across all divisions. We  
233 did not incorporate density dependence in projection models, as we found that population size

234 did not improve model performance (table S1). Finally, we removed individuals over the age  
235 of 70 in each year of each simulation (i.e. mortality of 1 at age 70), as there was large variation  
236 in life-history parameters at these ages and very few individuals. For each year in all  
237 projections, birth and death events were randomly sampled from a Bernoulli distribution  
238 according to age-specific probabilities from the best models. For all projections, we assumed  
239 that all births were to females.

240

241 We first constructed a projection model for the average vital rates across observation years in  
242 this period (1995-2014), without incorporating parameter uncertainty or environmental  
243 stochasticity (S3). Thus, the first model was intended to explore the average long-term  
244 dynamics of the population with demographic stochasticity alone. The projection began with  
245 the age-structure present in 2014 ( $N = 1369$ ; figure S10). Over 500 iterations, we projected  
246 250 years into the future, which was selected to capture long-term trends over 10-12.5  
247 generations in the future (generation time 20-25 years from [40]). This ensured that we  
248 captured stable long-term dynamics based on the average vital rates between 1995 and 2014.

249

250 We then performed a hierarchical population viability analysis under three levels of  
251 uncertainty; 1) parameter uncertainty from the best model, 2) environmental stochasticity  
252 (variation across years 1995-2014) and 3) demographic stochasticity (figure S11). 1)  
253 Parameter uncertainty was incorporated using posterior simulation of the best birth and  
254 mortality models, from which we calculated 200 sets of predicted values. Each set of predicted  
255 values included interannual (environmental) variation with observation year included as both  
256 a smoothing term and random effect (table S1). 2) Environmental stochasticity was  
257 incorporated by resampling both the random effect and smoothing term of observation year  
258 from the best models. We randomly sampled years for both the smoothing term and random  
259 effect term, and adjusted birth and mortality rates together according to the sampled years.

260 We sampled 10 sets of years for each of the 200 sets of predicted values generated through  
261 posterior simulation. 3) Demographic stochasticity was incorporated by repeating each set of  
262 years 10 times. The total number of simulations when assessing population dynamics over a  
263 50-year period with different levels of uncertainty was 20,000. We then projected 50 years into  
264 the future from the starting population size and age-structure in 2014 (N = 1369). Finally, we  
265 investigated the relative importance of the three different levels of uncertainty on population  
266 size in the population projection. We used nested hierarchical mixed effects models for each  
267 year in the projection, implemented in the lme4 package [41], to partition the variance in  
268 *ln population size* attributable to demographic stochasticity within environmental stochasticity  
269 within parameter uncertainty (figure S11).

270

#### 271 Identifying demographic targets for population management

272 To assess how age-specific rates influence population growth to identify demographic targets  
273 for population management, we performed numeric sensitivity analyses on the average long-  
274 term dynamics of the population excluding environmental stochasticity or parameter  
275 uncertainty. We first split age-specific demographic parameters of captive-born females into  
276 four main stages for life-history: juvenile (0-4 years of age before weaning), pre-reproductive  
277 (5-12 years old), adolescent (13-20 years old), reproductive adult (21-44 years old), senescent  
278 adult (45-70 years old). Life-history stages were selected based on previous findings of life-  
279 history patterns in timber elephants and raw age-specific data [42,43] (figure S7). Then, for  
280 each life-history stage, we increased birth rates by 10% or decreased mortality rates by 10%,  
281 perturbing birth and mortality separately. We selected 10% because it represented a realistic  
282 potential change in management for a given life-history stage, laying beneath the variation in  
283 life-history rates that was observed in the raw data between 1960 and 2014 (SD 19% and 14%  
284 for total birth and death rates, respectively). To assess population viability, we performed  
285 population projections for each scenario, performing 1000 simulations over 200 years,  
286 randomly assigning births and deaths to each individual in each year, with birth and death

287 probabilities adjusted for each scenario. Finally, we compared population dynamics in each  
288 scenario to the baseline under current conditions, to identify targets for management.

## 289 **Results**

290 The average annual birth rate was 3.1% (range = 1.2-5.4%) and the average annual mortality  
291 rate was 2.1% (range = 0.3-4.2%) for female elephants (N = 3585) between 1960 and 2014  
292 (figure S5a). Our measure of wild-capture for females entering the final studbook occurred at  
293 an average rate of 20.6 individuals per year, with the maximum number of individuals captured  
294 in a single year being 117 in 1972 (figure S5b). Capture rates between 1965 and 1975 were  
295 higher than other years within the study period, with 56% of all captures taking place within  
296 this 10-year period (figure S5b).

297

298 Birth rates varied across lifespan and years for both captive-born and wild-caught females  
299 (figure 1a). For captive-born females, birth rates increased at the age of 12 up to an average  
300 initial peak of approximately 10% between the ages of 20 and 22, after which generally there  
301 was a decline later in life (figure 1a; figure S7a). In earlier years before 1970, there were fewer  
302 old-aged individuals and the population was smaller, and so predicted birth rates increased  
303 later into life, but on average birth rates declined beyond the age of 44 (figure 1a; figure S7a).  
304 Birth rates were consistently lower on average in wild-caught females across ages, increasing  
305 more slowly from age 12 and reaching a maximum annual predicted birth rate of only 7%.  
306 However, at older ages wild-caught females exhibited higher birth rates, but also declined after  
307 the age of 50 (figure S7a). Overall, birth rates declined between 1960 and 2014, particularly  
308 for captive-born females (figure 1a; figure S8a). The best model for birth rates included a  
309 tensor product interaction smoothing term between age, year and birth origin, and an  
310 additional term for annual variation with year as a random factor (table S1). We did not find  
311 evidence for an effect of population size on birth rate as it did not improve predictive  
312 performance; the AIC difference between the best model and the model with population size

313 was 0.42, but the more parsimonious model with fewer parameters was selected (table S1;  
314 figure S4a). The best model fit the data well because there was no evidence of overdispersion  
315 or non-uniformity in the simulated residuals (figure S2a). Furthermore, there was no observed  
316 covariance between simulated model residuals and explanatory variables (figure S3a; figure  
317 S3c).

318

319 Mortality rates were high in young individuals, declining until the age of 10 and remaining low  
320 until 45, after which mortality rates rapidly increased into old age (figure 1b). Mortality rates  
321 were also higher in wild-caught females than captive-born females, but at extreme ages (> 50  
322 years of age), there was some evidence that wild-caught females had reduced mortality due  
323 to selective disappearance (figure 1b; figure S7b; [8]). Predicted mortality risk at all ages also  
324 fluctuated across the study period for both captive-born and wild-caught females (figure 1b;  
325 figure S8b). For mortality, the best model also included a tensor product interaction smoother  
326 between age, observation year and birth origin, with an additional random term of year. Again,  
327 we found no clear evidence of an effect of population size on mortality rate, with an AIC  
328 difference of 0.38 compared with the second-best explanatory model with more parameters  
329 (table S1; figure S4b). Furthermore, there was little evidence of non-uniformity,  
330 overdispersion, or covariance with explanatory variables in the simulated model residuals  
331 (figure S2b; figure S3b; figure S3d). For both birth and mortality models, the random effect of  
332 spatial division was accounted for in subsequent projections by using values from Kachin  
333 state, which was closest to the average birth and mortality values across divisions, with a large  
334 population size.

335

336 The number of individuals in the final female-only studbook dataset between 1960 and 2014  
337 increased from 385 to 1369, with a maximum of 1677 individuals in 1992 (figure 2a). To  
338 investigate changes in population growth rate across the study period and to assess the

339 implications of wild-capture for population growth, we calculated the observed annual  
340 population growth rate both with and without wild-capture from raw data. Realised annual  
341 growth rates were highly variable across observation years (figure 2b). Generally, growth rates  
342 declined between 1960 and 2014 (range = 0.93 – 1.14) (figure 2b) but remained above  
343 replacement rate (growth rate  $\geq 1$ ) before 1990 when capture was included. However,  
344 population growth rate was highly dependent on wild-capture, suggesting the population may  
345 not be sustainable, particularly as systematic wild-capture was banned in 1994. Growth rates  
346 excluding wild-capture before 1995 were 2.1% lower than those including wild-capture ( $F_{2,67}$   
347 = 22.1,  $p < 0.001$ ). Together, the historic changes in the female timber-elephant population  
348 suggest that large population increases were accompanied by intensive wild-capture rates,  
349 and population growth rate has fluctuated around 1 beyond 1995, making the population  
350 vulnerable to population decline in the future.

351

352 To assess the future outlook for timber elephants in a world excluding wild-capture, we  
353 performed individual-based, stochastic projection models of the population beginning with the  
354 starting age-structure in 2014. We first investigated long-term (250 years) dynamics over 500  
355 simulations in a scenario excluding model parameter uncertainty or environmental  
356 stochasticity. Generally, as with historic population changes, the average change in the  
357 population was close to a population growth rate of 1, indicating little change over 250 years  
358 (figure 3a). However, the model projection had a long-lasting transient phase of fluctuation in  
359 the population of ~70 years, in which the population declined down to 1176 individuals in 2056.  
360 After this transient phase up to ~2080, the population reached a steady, but small stable  
361 annual growth rate of ~1.005 (figure 3a). Although population growth was predicted in the  
362 long-term, the proximity of the growth rate to 1 indicates that the population is susceptible to  
363 decline given changes in the environment. As expected, the variation in population viability  
364 was far greater when environmental stochasticity and parameter uncertainty were included  
365 (figure 3b). Including uncertainty in the environment and parameter uncertainty, we again

366 found an average population decline of ~150 individuals over 50 years. However,  
367 decomposition of the different sources of uncertainty revealed that although demographic and  
368 environmental stochasticity are drivers of variation in population viability, model parameter  
369 uncertainty was the most important driver of observed population changes (figure 3c). After  
370 50 years, parameter uncertainty explained ~75% of the variance in population size (figure 3c).  
371 This suggests that understanding long-term variation in demographic rates is particularly  
372 crucial in this long-lived species.

373

374 We investigated which age-specific demographic rates had the largest impact on population  
375 growth by performing population projections under scenarios with changes to demographic  
376 rates at key life-history stages and comparing them to the baseline scenario. We investigated  
377 the sensitivity of population viability to 10% changes in each life-history stage (increase for  
378 birth rates, decrease for mortality). The majority of changes to age-specific rates had relatively  
379 little effect on population viability relative to the baseline scenario (figure S12). However, both  
380 a 10% increase to the birth rates of adult reproducers (21-44) and a 10% decrease in mortality  
381 of juveniles (0-4) had a substantial influence on population viability and resulted in a more  
382 rapid population increase (figure 4). Population increases of 5% and 2% were observed under  
383 adult birth rate and juvenile mortality rate scenarios, respectively, compared to a 0.01%  
384 increase under the baseline scenario over the 200-year period. Notably, increases in birth  
385 rates at older ages (45-70) and in early reproducers (13-20) also had an influence on  
386 population growth (figure S12).

387

## 388 **Discussion**

389 Our results challenge the prospect of maintaining viable populations of captive elephants  
390 without the capture of individuals from the wild. Historic trends in population dynamics using  
391 demographic data spanning 54 years revealed that population growth rate was highly

392 dependent on wild-capture. Given this dependence on wild-capture and an accompanied  
393 decline in birth rates between 1960 and 2014, the outlook for captive elephants excluding wild-  
394 capture is uncertain. Long-term population projections predict immediate population declines,  
395 but long-term stable population growths rates that are close to replacement rate, suggesting  
396 that the working population is vulnerable to environmental disturbance. However, due to an  
397 unstable age-structure, immediate transient population declines may last for approximately  
398 half a century, suggesting that management must be tailored to the slow life-history of Asian  
399 elephants. Although population viability excluding wild-capture is uncertain, our results also  
400 suggest that there are long-term demographic consequences for individuals that are caught  
401 from the wild; wild-caught females have lower life-time birth rates and higher death rates than  
402 captive-born females. Wild-capture reduces remnant wild populations, but also has a long-  
403 lasting demographic impact on the demography of the captive population, and we must focus  
404 on managing the demography of captive populations to prevent future declines.

405

406 Between 24% and 29% of the global Asian elephant population is held in captivity [15,40], of  
407 which Myanmar's timber elephant population may constitute as much as a third. Thus,  
408 although this working population is often overlooked as a unit of conservation, sustainable  
409 management is crucial for the viability of this endangered species. However, our study shows  
410 that for decades, this has not been achievable without the capture of wild individuals. Wild-  
411 capture in Myanmar has been detrimental for the wild population, which is important for both  
412 Asian elephants and their surrounding ecosystem [44]. Leimgruber et al. [20] postulated that  
413 capture rates of 100 individuals per year would result in the extinction of the wild population in  
414 under half a century. However, the exact dynamics of Myanmar's wild population in relation to  
415 changes in wild-capture rates is unknown. As well as decreasing the size of the wild  
416 population, we found evidence that wild-caught females have lower birth rates and survival,  
417 which is most likely a result of the stress of the capture process [8]. However, despite the  
418 lower performance of wild-caught females in captivity, there were large declines in captive

419 population birth rates with declines in wild-capture. In other words, the captive population  
420 depended on wild-capture. Furthermore, historic rates of wild-capture do not necessarily take  
421 into account capture-related mortality itself, and many more elephants may have actually been  
422 removed from the wild than are utilised in the timber industry [8]. For example, the estimated  
423 instant mortality rate during the elephant capturing process in Myanmar is high, varying  
424 between 5% and 30% depending on the capture method [26,31]. The ongoing wild-capture of  
425 elephants is not limited to supporting Myanmar's timber elephants (which now continues in  
426 cases of human-elephant conflict, but not systematically): capture continues worldwide for  
427 both legal and illegal purposes (e.g. [45,46]). Asian elephant populations currently held in  
428 Western zoos, safari parks, and circuses are not self-sustaining [22,23], and 60% were wild-  
429 caught and imported from range countries [47]. The reliance of captive Asian elephant  
430 populations on wild-capture is alarming, and management must be addressed to ensure the  
431 sustainability of this species without continued capture.

432

433 Although population viability in captivity is under threat, population extinction was not predicted  
434 in long-term population projections. A handful of studies have also aimed to assess the viability  
435 of semi-captive elephant populations (e.g. [20,48]). Both studies forecasted that extinction was  
436 highly likely. Importantly however, both studies impose carrying capacities on working  
437 elephant populations, which limits population growth [20,48]. We did not find evidence for a  
438 correlation between realised population size and age-specific vital rates in this extensive  
439 demographic dataset spanning 54 years. Furthermore, the notion of density dependence in  
440 semi-captive populations is not trivial; individuals are not always subjected to habitat limitation  
441 or competition as with fully wild populations, because of human management. Another key  
442 difference in the current study was the incorporation of temporal variation in age-specific vital  
443 rates that were estimated directly from the demographic studbook, rather than static age-  
444 specific rates. Historic annual population growth rates displayed a large variation between  
445 1960 and 2014. Understanding temporal differences in demography and life-history are

446 therefore crucial for population dynamics. However, temporal differences in vital rates have  
447 been absent in previous projections in Asian elephants [20,22,48]. Previous work has  
448 suggested that the quality of demographic and life-history data needs to be addressed in  
449 viability analyses [49], but our results suggest that this may be accentuated in long-lived  
450 species, where many decades of data are needed to quantify vital rates. Slow intrinsic growth  
451 rates and life-history in species such as elephants may exacerbate external pressures,  
452 resulting in further population declines [18]. Indeed, we observed transient population  
453 dynamics that last several decades in long-term projections, and previous work has found  
454 long-lasting mortality effects in working elephants [8]. This result is important for the  
455 conservation of long-lived species; an unstable age-structure can lead to long-lasting transient  
456 dynamics with more rapid population declines. However, these changes may occur on  
457 significant timescales, increasing the importance of long-term monitoring and conservation  
458 strategies that reflect the life-history of target species.

459

460 Although our results suggest that captive elephants in Myanmar may not be sustainable  
461 without wild-capture, we are not suggesting that reinstating the capture of wild individuals is a  
462 potential solution, because it is clearly detrimental for the wild population [20]. Instead, we  
463 suggest that management should be focused on sustaining the current individuals in the  
464 captive population. Specifically, our results suggest that increased survival in juveniles may  
465 be an important driver of population growth in long-lived species, which are characterised by  
466 low annual reproductive rates. Although, as expected, birth rates in adult females had the  
467 biggest influence on population viability, increasing adult birth rates does not necessarily  
468 present a tractable target for population management, particularly as adult females are  
469 working animals. Targeting juvenile mortality however provides a clear and tractable target for  
470 population management in this captive population. Currently, juvenile elephants are tamed  
471 around the age of five in order to learn commands and begin light carrying work [12,25,50].  
472 Elephants are removed from the mother at this stage to undergo training, and this stress is

473 may have a negative impact on survival [12]. Furthermore, mortality is highest in neonatal,  
474 pre-weaning elephants [51,52]. This phenomenon is common in other populations and in  
475 African elephants, particularly in captivity [29,53]. Further to previous findings our results  
476 suggest that targeting the factors influencing juvenile mortality may have a disproportionately  
477 beneficial effect on population growth. This could be achieved by adjusting management to  
478 reduce stress during the taming process and for peak reproductive aged females, and to target  
479 neonatal mortality.

480 Ex situ conservation is now common to prevent extinction in wildlife populations, but removal  
481 of individuals from the wild may be detrimental to both populations in situ, and those in  
482 captivity. With human-managed populations becoming increasingly common, there is a need  
483 for an increased understanding of how human intervention influences demography and life-  
484 history.

485

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## 494 **Data**

495 <https://datadryad.org/review?doi=doi:10.5061/dryad.rj237db>

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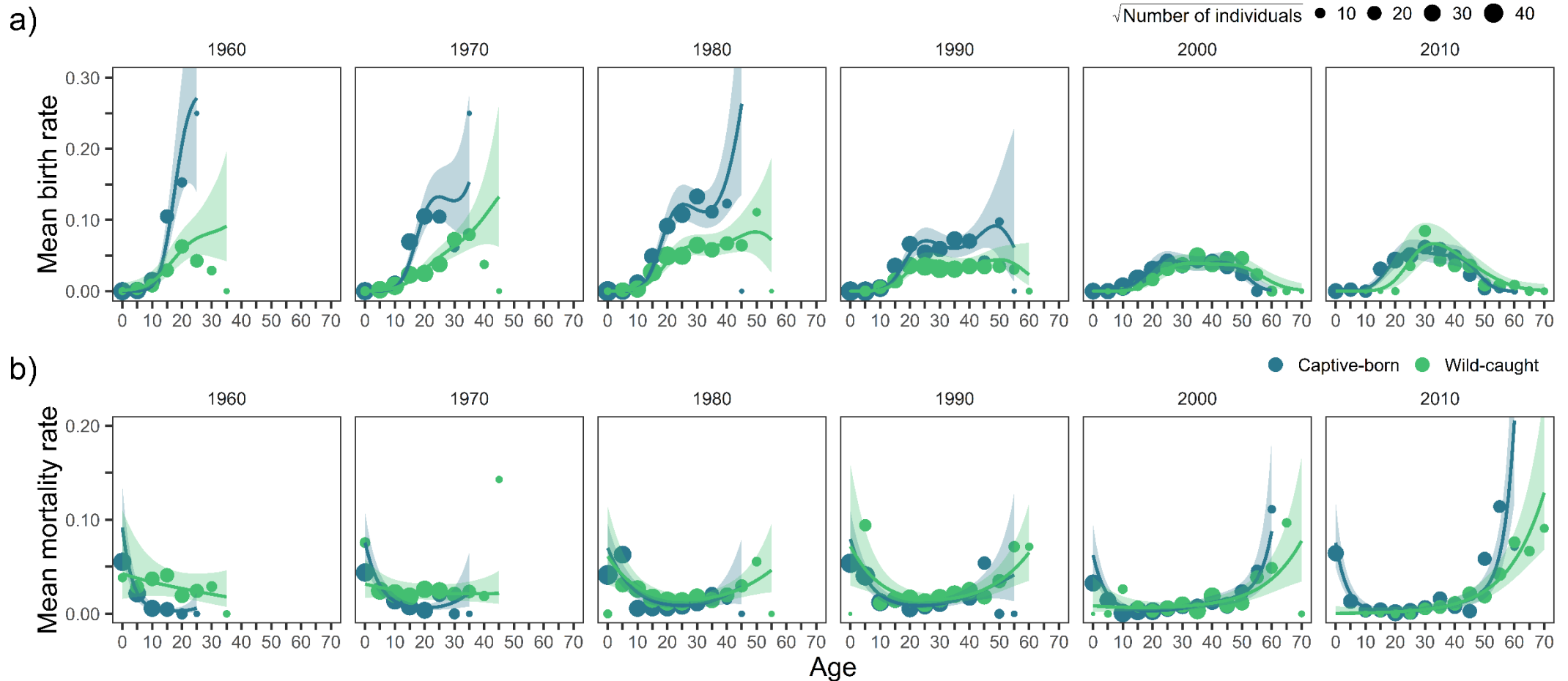
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641 **Figure 1.** Mean age-specific birth (a) and mortality (b) rates in wild-caught (green) and captive-born (blue) female timber elephants for each  
 642 decade between 1960 and 2010. Points are mean age-specific vital rates for each 5-year age-class across all regional divisions in Myanmar for  
 643 each decade, with the size depicting the square root of the sample size (range = 1-1815 individuals). Lines are the mean model predicted values

644 from the best birth (a) and mortality (b) models across regional divisions, with 95% confidence intervals from posterior simulations. Model  
645 predictions between 1995 and 2014 were used to parameterise individual-based projections.

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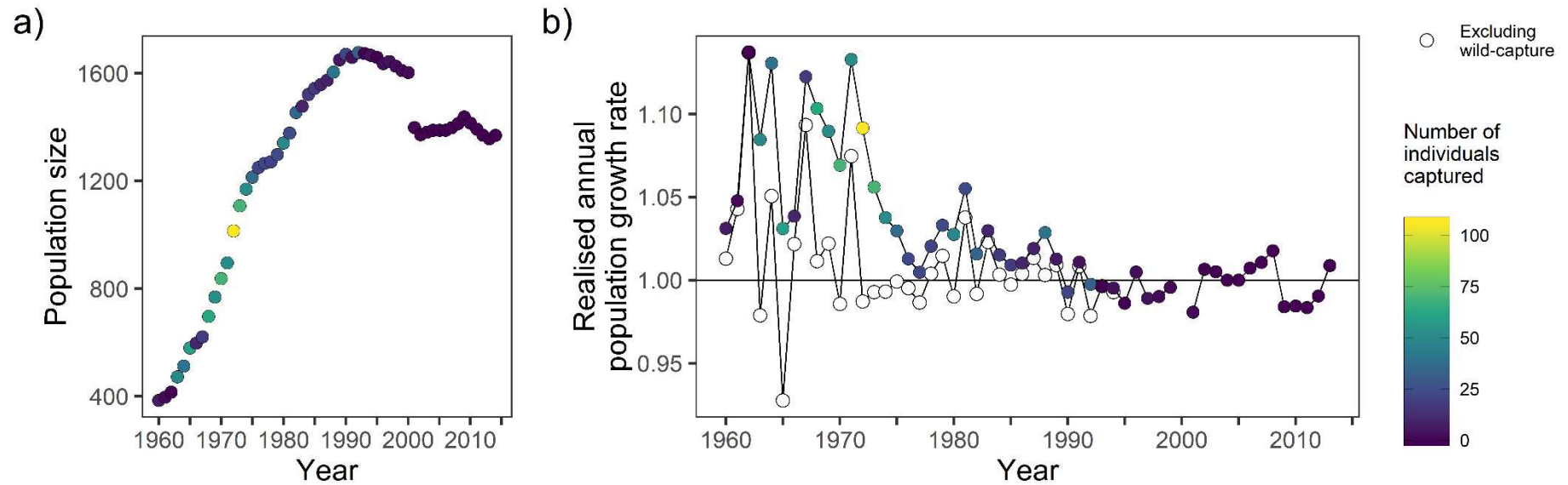
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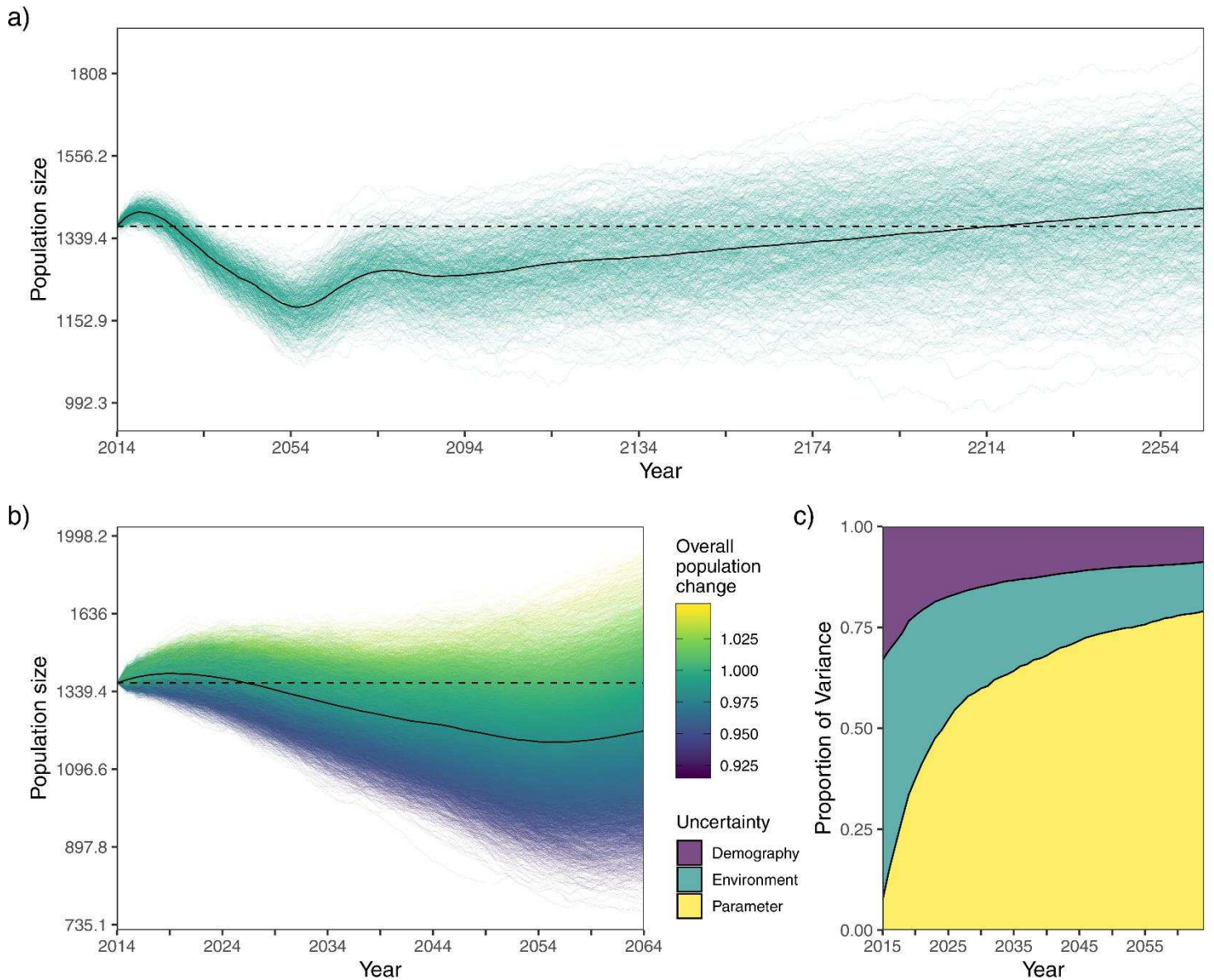
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653 **Figure 2.** Historic trends in the female timber elephant population with wild-capture. a) The number of female timber elephants in each year  
 654 between 1960 and 2014. The decrease in the year 2001 is due to a decrease in the number of demographic records. b) Changes in the realised  
 655 annual population growth rate, both including (coloured points) and excluding (open points) capture from the wild. Solid line indicates annual  
 656 growth rate of 1 i.e. replacement rate. For both (a) and (b), the colour indicates the annual capture rate in each year.

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661 **Figure 3.** Population projections for female timber elephants in a world without wild-capture.

662 a) Population projection over 250 years and 500 simulations representing the average

663 dynamics of the population excluding model uncertainty in parameters and environmental

664 stochasticity. Green lines represent the change in population size for each simulation, and the

665 solid black line indicates the geometric mean. b) Short term changes (50 years) in the timber

666 elephant population incorporating varying levels of uncertainty (parameter uncertainty and

667 demographic/environmental stochasticity). Coloured lines indicate each simulation (20,000),

668 and the colour denotes the overall population change in that simulation. Solid black line

669 indicates the geometric mean of population size. For population projections, population size  
670 is on the natural log scale, and the dashed line indicates the starting population of 1369. c)  
671 The proportion of variance in  $\ln(\text{population size})$  explained by uncertainty in model parameters  
672 (yellow), and with both environmental (green) and demographic (purple) stochasticity over 50  
673 years for 20,000 simulations.

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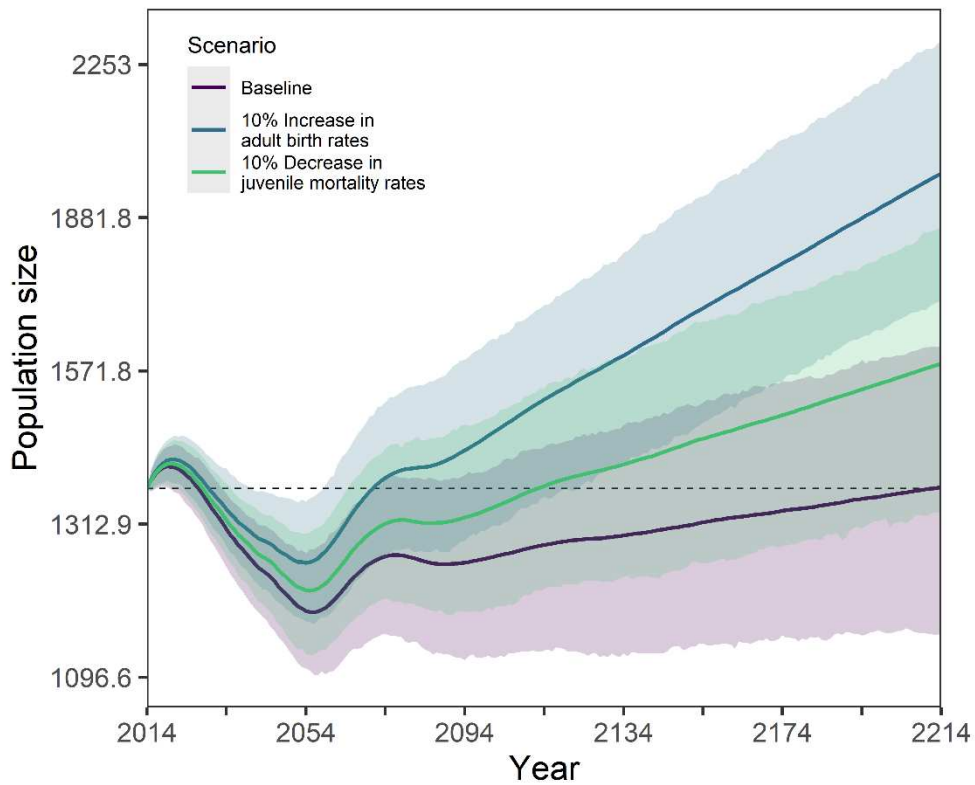
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692 **Figure 4.** Increases to juvenile survival represent a realistic and meaningful target for  
 693 conservation management. Individual-based, stochastic projections excluding parameter and  
 694 environmental stochasticity over 200 years under three scenarios; baseline (average  
 695 observed dynamics – purple), a 10% increase to adult birth rate (age 20-44 – blue), and a  
 696 10% decrease in juvenile mortality (age 0-4 – green). Solid lines are the population size on  
 697 the natural log scale, with 95% CI across 1000 simulations, dashed line indicates the starting  
 698 population size of 1369 females in 2014.

699