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LETTER

Senescence and age-specific trade-offs between reproduction and survival in female Asian elephants

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Abstract

Although studies on laboratory species and natural populations of vertebrates have shown reproduction to impair later performance, little is known of the age-specific associations between reproduction and survival, and how such findings apply to the ageing of large, long-lived species. Herein we develop a framework to examine population-level patterns of reproduction and survival across lifespan in long-lived organisms, and decompose those changes into individual-level effects, and the effects of age-specific trade-offs between fitness components. We apply this to an extensive longitudinal dataset on female semi-captive Asian timber elephants (*Elephas maximus*) and report the first evidence of age-specific fitness declines that are driven by age-specific associations between fitness components in a long-lived mammal. Associations between reproduction and survival are positive in early life, but negative in later life with up to 71% of later-life survival declines associated with investing in the production of offspring within this population of this critically endangered species.

Keywords

Ageing, fitness, reproductive costs, reproductive success, survival.

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Senescence, by definition, refers to a decline in both an individual's age-specific reproductive rate and underlying latency of survival (Williams 1957; Hamilton 1966; Kirkwood 1977). Evolutionary theory predicts that these changes can occur because of a decrease in the force of selection on age-specific mutations over adult lifespan (Williams 1957; Hamilton 1966; Kirkwood 1977), and because of competing demands of reproduction which result in less effort invested in the maintenance of somatic tissues than is necessary for indefinite survival (Kirkwood 1977). Within a population, individuals will differ both in their reproductive rates and in their underlying probability of survival, and these fitness components may also interact in different ways across ontogeny. For example, some individuals of a given age, perhaps those who can obtain greater resources, may have a higher latent probability of surviving over a given time period. In this scenario, correlations between reproductive success and survival may be positive, and individuals with higher reproductive performance may live longer, predominating older age classes (Vaupel & Yashin 1985). Alternatively, due to limited resources for growth, reproduction and cellular repair (Kirkwood 1977), or antagonistic gene effects (Williams 1957), there may be trade-offs where individuals of high reproductive performance live for a shorter time (for example Descamps *et al.* 2006). Understanding the evolution of life histories requires examining the performance of individuals and changes in that performance over life, and thus it is important to determine the extent to which population-level changes are driven by both age-specific individual-level changes and age-specific relationships between different fitness components across ontogeny.

Studies across populations of a wide variety of species have shown within-individual declines in reproductive performance, whilst accounting for the effects of survival on population composition. In general, reproductive performance for many species of bird and mammal increases at the earliest reproductive ages, and then declines in later life (Reid *et al.* 2003; Bowen *et al.* 2006; Jones *et al.* 2008; Reed *et al.* 2008; Bouwhuis *et al.* 2009; Rebke *et al.* 2010). The most long-lived species studied to date include birds with ages at last reproduction of 20–40 years maximum (Catry *et al.* 2006; Charmantier *et al.* 2006; Reed *et al.* 2008), and mammals with lifespan longer than 15years (Loison *et al.* 1999; Nussey *et al.* 2009; Bronikowski *et al.* 2011). Although there is some debate (Turbill & Ruf 2010), evidence suggests that the onset and rate of senescence scales with generation time across taxa, and thus for a given pace of life organisms senesce at the same rate (Jones *et al.* 2008). Although these patterns are now well documented, identifying the processes associated with rates of senescence at the population level, and the factors that lead to (co)variation in rates of senescence between life-history traits and individuals has received less attention.

For long-lived species which produce one offspring at a time, decomposing mean population reproductive rates across all ages into ontogenetic changes in surviving individuals has proved challenging. Recently, Rebke *et al.* (2010) described a version of the Price equation (Price 1970) applied to phenotypes (Coulson & Tuljapurkar 2008) where rather than just describing population and individual-level changes as in previous studies, changes in population mean reproduction across ages can be exactly decomposed into ontogenetic changes in surviving individuals, plus compositional population changes due to the effects of phenotypic selection. For long-lived organisms these methods must be adapted to decompose changes in reproduction across ontogeny, because often only one offspring is produced per breeding attempt at any one time. Cam *et al.* (2002) present a method for examining reproductive and survival probabilities which can be combined with the methods of Rebke *et al.* (2010). This would enable: (1) a comparison and exact decomposition of population- to individual-level changes in fitness across ontogeny to examine when differences occur; (2) examining relationships between different fitness components across ontogeny, to test for the effects of current reproduction on survival across ages and to exactly determine the effects of these relationships on population-level patterns of reproduction and survival; (3) test the extent to which relationships between reproduction and survival reflect the production of offspring or reflect investment in raising offspring to adulthood, by examining both reproductive probability and the probability of producing offspring which recruit back into the population as adults. Herein, we outline this framework and apply it to decompose rates of change in both reproductive performance and survival across ages, in a unique dataset from a semi-captive population of Asian elephants.

MATERIAL AND METHODS

An approach to decomposing reproduction and survival in long-lived organisms

The approach of Rebke *et al.* (2010) decomposes changes in population mean reproduction across age into ontogenetic changes in surviving individuals, plus compositional population changes due to the effects of phenotypic selection. In brief, this is done by estimating the change in trait value from one age to the next for individuals who survive, and comparing it to the change in population mean. The difference between population-level change and individual-level change gives the change in population composition due to differential survival. For long-lived organisms where one offspring is produced per breeding attempt at any one time, this method must be adapted to decompose changes in reproduction across ontogeny. Here, we modelled reproductive investment as the probability of breeding (ø) across life by adopting the approach of Cam *et al.* (2002):

$$\text{logit}(ø) = f_{ø}(\text{age}) \times g_{ø}(\text{survived}) + \alpha_{ø}(\text{individual}) \tag{1}$$

where breeding probability (binary: 0 not bred/1 bred) ø is modelled as a logit function of age and its interaction with whether the individual survives to the following age step or not, with individual differences modelled as random. This approach of modelling breeding rates stems from a large number of studies using capture-recapture data from individually marked animals (Lebreton *et al.* 1992; Nichols 1992). By treating individual factors as random effects in a hierarchical model, more precisely, a generalised linear mixed model with individual effects modelled as random (Hedeker *et al.* 2000), we account for individual heterogeneity in breeding probability. This model provides all the information required to decompose population-level changes in reproduction over age, as it provides age-specific mean breeding probabilities for individuals which survive each age step and those which do not. We then define age-specific population-level changes in reproduction ($\Delta_{ø}$) as:

$$\Delta_{ø} = (ø_{t-1} \times N_{t-1}) - (ø_t \times N_t) \tag{2}$$

where ø is the predicted breeding probability and N is the number of individuals at age *t* and *t*–1. We also define individual-level changes in reproduction ($\delta_{ø}$) as:

$$\delta_{ø} = N_t(ø_{st-1} - ø_t) \tag{3}$$

where ø is the predicted breeding probability at the population level at age *t*, $ø_s$ is the breeding probability of survivors at age $t - 1$ and N is the number of survivors at age *t*. The change due to selective disappearance is the difference between $\Delta_{ø}$ and $\delta_{ø}$ as a proportion of $\Delta_{ø}$. Thus, 'selective disappearance' denotes a change in the mean of a phenotypic trait due to mortality (Rebke *et al.* 2010).

Using this methodology (Cam *et al.* 2002) we can also model survival probability (β) as:

$$\text{logit}(\beta) = f_{\beta}(\text{age}) \times g_{\beta}(\text{bred}) + \alpha_{\beta}(\text{individual}) \tag{4}$$

where survival probability is modelled as a logit function of age and its interaction with whether the individual breeds during the age step or not. This approach is based on models incorporating latent random variables (Dupuis-Sammel & Ryan 1996), where 'latent' reflects unobserved realisations of an underlying random variable. In the context of studies of survival, each individual has its own mortality risk which cannot be directly observed but its distribution can be assessed using individual realisations of this probability. Therefore, we can estimate the deviation of subject-specific responses around the response assessed at the level of the overall population by including individual effects modelled as random (i.e. subject-specific inference as opposed to population-averaged inference; Hu *et al.* 1997). This type of approach is standard in human demography (e.g. Manton *et al.* 1981; Hougaard 1984, 1986, 1991; Vaupel & Yashin 1985). This model provides all the information required to examine the effects of age-specific reproductive investment on changes in the number of survivors across ages, as it provides age-specific survival probabilities for individuals who reproduced at each age step and those which do not. We define age-specific changes in the number of survivors (Δ_{β}) as:

$$\Delta_{\beta} = N_t(\beta_{t-1} - \beta_t) \tag{5}$$

where β is the survival probability and N is the number of individuals at age *t* and *t*–1. We also define changes in the number of survivors for individuals that reproduce (δ_{β}) as:

$$\delta_{\beta} = N_t(\beta_{Rt-1} - \beta_t) \tag{6}$$

where β_t is the breeding probability at the population level at age *t*, β_R is the breeding probability of individuals that reproduce at age *t*–1 and N is the number of survivors at age *t*. The change in the number of survivors due to the effects of age-specific reproductive investment is the difference between Δ_{β} and δ_{β} as a proportion of Δ_{β}. We also extend [4] to examine survival probabilities for individuals which produced offspring that did not survive to recruit (died before age 5), and for individuals which produced offspring that recruited (survived to age 5) back into the population as adults.

Application

Here, we apply this approach to a unique multigenerational demographic dataset on semi-captive populations of Asian elephants from timber industry camps in Myanmar. Elephants represent an ideal model system for studying the patterns and underlying life history correlates of senescence: their longevity, with survival commonly into 60years in the wild and maximum known age of > 80 years (for details on African elephants see: Moss 2001; for Asian elephants see Mar 2007), represents the upper end recorded for mammals along with humans and some species of whales.

The Asian elephant is classified as critically endangered species on International Union for Conservation of Nature (IUCN) Red List of threatened species because of its high risk of extinction in the wild. It is distributed discontinuously across the Asian continent with the total wild population of 38 500–52 500, and a further 16 000 in captivity. The largest (> 5000) remaining population of captive elephants is in the timber camps of Myanmar (676 553 km^2) where elephant draught power has been utilised extensively in timber harvesting for more than a century. State law requires that elephant logbooks and annual extraction reports be archived and maintained by the Extraction Department, Myanmar Timber Enterprise for this population (Mar

2007; Clubb *et al.* 2008). The traditional elephant logbooks documented on individual elephants after taming are equivalent to the 'studbooks' kept in Western zoos. State ownership of thousands of elephants over half a century makes it possible to compile and transfer data of all registered individual elephants from the logbooks to a database containing a chronology of a captive population, listing vital information on animal identities, sex, maternity, birth-death dates and ages. Life-history traits are thus comprehensively documented and we have data on a total of 8006 individuals for up to four generations of elephants born between 1925 and 1999. Data recorded for each individual include: registration number and name of elephant; origin (wild caught or captive born); date and place of birth; mother's registration number and name; method of capture (if wild-captured); year of capture; place of capture; year or age of taming; dates and identities of all calves born; date of death or last known date alive; and cause of death (Mar 2007).

The population is semi-captive because individuals are free to forage unsupervised in the forest for up to 14 h per night, where they mix and breed with captive and wild elephants. Breeding rates are natural and not managed by humans, and calves born in captivity are cared for by their biological and allo-mothers and are suckled until lactation no longer supports their demands (Mar 2007). However, as the elephants are used in the timber industry they are subject to set work-loads of up to 230 working days per year, with official rest periods of up to 120 days per year. Females are given rest from mid-pregnancy (11 months into gestation) until the calves reach their first birthday (Mar 2007). Mothers are then used for light duties but allowed to nurse the calves on demand. The elephants receive veterinary attention in the form of regular health checks to determine individual working ability, but veterinary workers do not assist with mating or births. The individual elephant logbooks are maintained and updated by local veterinarians and regional extraction managers at least bi-monthly to check the health condition and ability of each elephant to work. Between-individual variation in workload or rest periods is limited by law: all state-owned elephants are subject to the same regulations set by central government for hours of work per week, working days per year and tonnage to extract per elephant. For example, in 2010 all mature elephants (> 17–55 years) worked 3–5 days a week (depending on weather and forage availability) 5–6 h a day (maximum 8 h) with a break at noon. All elephants finish their work season by mid-February each year, and work resumes around mid-June depending on the arrival of monsoon. Finally, the elephants 'retire' at 55 and live out the rest of their lives in comparative freedom with their logbooks maintained until death (Mar 2007). Approximately half of the timber elephants used in Myanmar are captive born, and half are caught from the wild (usually < 5 years), although wild capture was banned in 1997. The elephants live in forest camps, where they are used during the day as riding, transport and draught animals. At night the elephants forage in forests in their family groups unsupervised where they find food and encounter tame and wild conspecifics. The maximum lifespan recorded to date is 83 years for a wild-captured individual with estimated birth year; the longest living captive-born individual with known birth date is at present 55 years.

Our data comprise records taken from 1111 females from 260 camps born 1925–1999. These records are of female elephants that were captive born because precise dates of birth are recorded and thus ages are known accurately, and because methods of capture are associated with reduced later fitness in wild-caught elephants (Mar 2007) and we did not wish to bias our results through the use of these records. Since we were interested in adult life these females all survived until the age of five, which we classify as adulthood because it represents the first breeding age within our data. The youngest female breeding was 5.28 years, and the oldest was 53 years, with the average inter-birth interval being 5 years (range = 1.8–21.4 years) and the maximum lifetime number of calves 10. In this population, 26% of all calves born failed to reach their fifth birthday. These elephants receive no direct veterinary intervention, but there are attempts to ascertain the cause of death (Mar 2007). Most of these life-history patterns mirror those data found for several wild populations of African (*Loxodonta africana*) and Asian elephants which show an earliest age at first reproduction of between 6 and 9 years (Evans 1910; Taylor & Poole 1998; Sukumar 2003), with a mean of 17–18 years (Sukumar 2003), a mean inter-birth interval of 2.5–4 years (Shoshani & Eisenberg 1982; Sukumar 2003), a maximum number of calves produced of 12 (Sukumar 1989) and first year mortality of 10–15% (Moss 2001).

After the age of 5 years we classified breeding and survival probabilities into 5-year age groups (Table 1), by recording whether individuals survived or died (1/0), and reproduced or not (1/0) within each age-group. This was because there were ages where few individuals bred and we did not want to bias our results on the bases of either limited sample size, or low probability values at young or old ages. There were occasions where females produced multiple offspring within a given age group and thus we may underestimate reproductive investment in middle-life, however, these occurrences were rare (of 1013 reproductive occurrences, 38 were of more than one offspring within an age group) and occurred only at ages 15–25. Survival within age groups was known for all females included within the analyses. The maximum age group we considered was 45–50 years because this was the last age where multiple birth events occurred within our sample.

Breeding and survival probabilities (Eq. 1 and Eq. 4) were modelled using generalised linear mixed effects models with a Bayesian MCMC framework in the R package MCMCglmm (Hadfield 2010). The residual variance was fixed to be one and we used a non-informative variance expanded prior for the individual-level random effects. Models were run for one and a half million iterations, with a half million burn-in period and 1000 interval sampling. As the models are run in MCMC we gained 1000 estimates of the posterior distribution of the effects, which we used to gain predicted values at the data scale whilst marginalising the random term. We use these predicted estimates within the equations outlined above to decompose age-specific population-level changes into individual-level changes and

Table 1 Age-specific survival, number of births and number of births resulting in recruiting offspring across different age groups in a semi-captive population of Asian elephants

Age	Survivors	Deaths	Births	Recruiting offspring
5–9	879	238	7	2
10–14	681	198	69	45
15–19	532	149	225	153
20–24	448	84	260	172
25–29	342	106	228	147
30–34	240	102	150	107
35–39	156	84	96	61
40–44	74	82	55	25
45–49	51	23	21	5

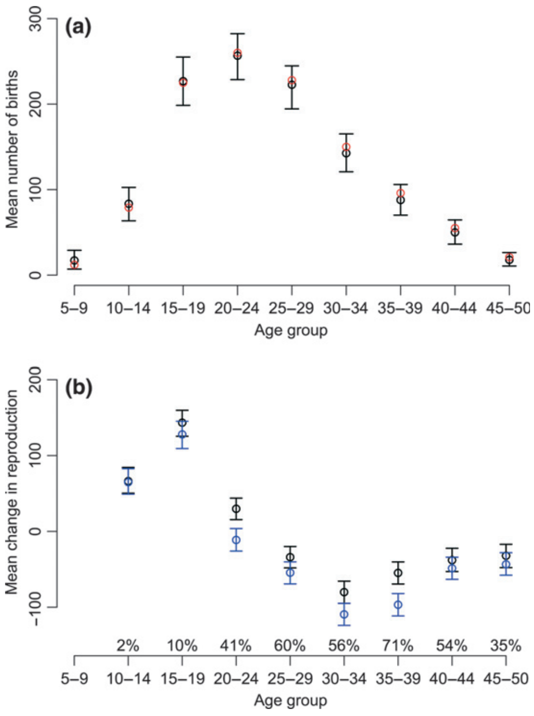

Figure 1 (a) Model predictions for the number of births across age groups are shown in black, along with the actual number of births that occurred in the population (red circles). The mean change in the number of births across age groups is shown in (b), both at the population- (black circles) and at the individual-level (blue circles). The percentage of population-level change in reproduction at each age that is due to the effects of selective disappearance is given in (b). Ninety-five per cent credible intervals are shown and we do not draw our conclusions from these but instead use the 95% credible intervals of the model estimates in Table 2.

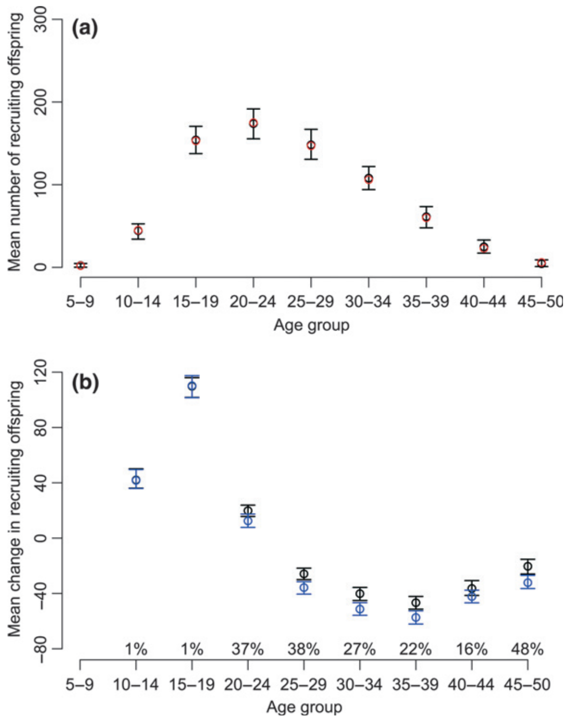

Figure 2 (a) Model predictions for the number of recruiting births across age groups are shown in black, along with the actual number of recruiting births that occurred in the population (red circles). The mean change in the number of recruiting births across age groups is shown in (b), both at the population- (black circles) and at the individual-level (blue circles). The percentage of population-level change in the number of recruiting births at each age that is due to the effects of selective disappearance is given in (b). Ninety-five per cent credible intervals are shown and we do not draw our conclusions from these but instead use the 95% credible intervals of the model estimates in Table 2.

changes due to age-specific associations between fitness components (Figs 1–3). We present the 95% credible intervals of the predicted values as the error in our estimates presented within Figs 1–3, but due to difficulties in estimating predicted values from hierarchical mixed effects models we use these simply to display the effects. The results of the models are shown in Table 2 and we use only the 95% credible intervals of these effects to assess significant differences between groups.

RESULTS

First, we compared population- to individual-level changes in breeding probability across ontogeny. We classified breeding and survival probabilities into 5-year age groups (Table 1), by recording whether individuals survived or died (1/0), and reproduced or not (1/0), within each age-group (Table 1). At the population level, the number of births increased up to the age of 25 years and then began to decline (Fig. 1a; Table 1), a pattern that is accurately matched by our model predictions (Fig. 1a; Table 2). A similar pattern was observed when we examined individual-level changes in reproduction (δ_o), with reproduction increasing until the age of 25, and then declining from age 30 onwards (Fig. 1b). Figure 1b shows the change in reproductive probability from one age to the next, calculated for surviving and non-surviving individuals by back-transforming the estimates from the model presented in Table 2 and using the values within Eq. 2 and 3 to estimate changes in the rate of age-specific reproduction. Table 2 shows model results demonstrating different age-specific mean breeding probabilities for surviving individuals as compared to non-survivors, and this translated into individual-level rates of reproduction for surviving individuals which were lower as compared to the population level from the age of 20 onwards (Fig. 1b). For example, the change in age-specific reproductive rate from 15–19 years to 20–24 years was negative for individuals that survive those time periods (blue circles, Fig. 1b), but at the population level the change in reproductive rate was positive (black circles, Fig 1b). Therefore, female elephants show reproductive senescence in the number of births across ages, and in this population, surviving individuals are those with greater declines in reproductive output in later life (Fig 1b).

In long-lived species, individuals failing to raise successfully offspring may reproduce frequently to 'replace' lost offspring. Therefore, we examined these effects by re-running our model of breeding probability where a reproductive event was recorded if the offspring survived to age five and a zero given if the offspring died. We found similar patterns for this reproductive measure as compared to simply examining the probability of birth (Fig 2a,b). It thus appears that female elephants also show reproductive senescence in their ability to produce recruiting offspring across ages, and in later-life surviving individuals are less likely to produce recruiting offspring as compared to the population-level patterns (Fig 2b).

Third, we then examined age-specific survival probabilities. Visual examination of the data shows a linear decrease in the number of

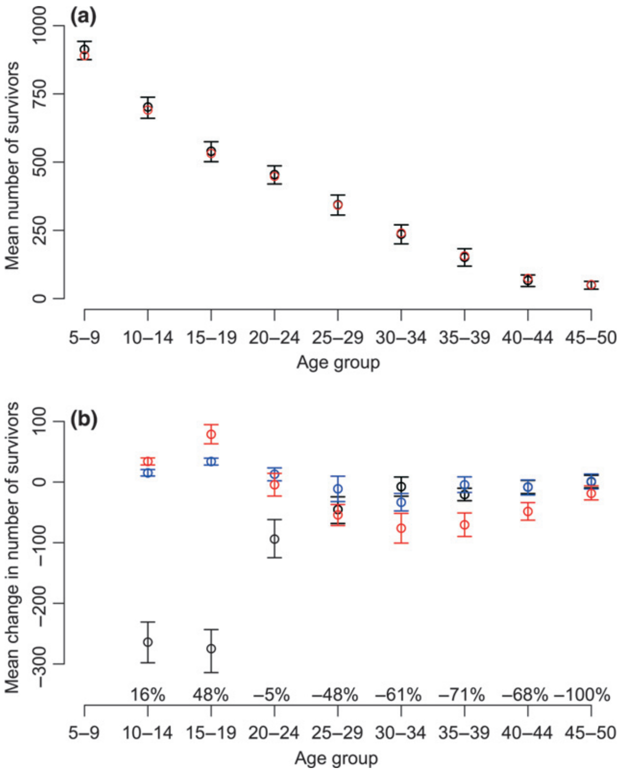

Figure 3 (a) Model predictions for the number of surviving elephants across age groups are shown in black, along with the actual number of survivors observed in the population (red circles). Mean changes in survivors is given in (b) for individuals that did not reproduce (black circles), for individuals producing non-recruiting offspring (blue circles) and individuals producing recruiting offspring (red circles). The percentage change in survivors at each age due to the effects of producing recruiting offspring is given in (b), with negative values indicating the reduction due to these effects. Ninety-five per cent credible intervals are shown and we do not draw our conclusions from these but instead use the 95% credible intervals of the model estimates in Table 2.

survivors across ages (Fig. 3a), which reflects a constant survival probability until age 25 (see Table 2 for model results showing no differences in survival probability between age groups until after age 25). Survival probabilities then decrease at a faster rate after age 25 with the exception of the final age class (Table 2). Therefore, we present evidence that these female elephants show survival senescence from the ages of 30–45 years.

Finally, we then examined the effects of reproductive investment on age-specific changes in survival probability. Fig. 3b shows the change in survival probability from one age to the next, calculated for breeding and non-breeding individuals by back-transforming the estimates from the model presented in Table 2 and using the values within Eq. 5 and 6 to estimate changes in the rate of age-specific survival. We find differences in the mean number of survivors (Δ_β) between individuals who give birth to non-recruiting offspring, individuals who produce recruiting offspring, and individuals who do not give birth (Fig 3b). Table 2 shows model results demonstrating both lower and higher mean survival for those which do not breed depending upon the age considered. Individuals that reproduced prior to the age of 25 years showed higher survival across these ages as compared to individuals that did not reproduce (Fig 3b; Table 2). Within these ages individuals that bred contributed to 5–48% higher survival compared to the population level (Fig 3b). From the age of 30 years onwards this association reversed and individuals that produced surviving offspring had reduced survival as compared to individuals that did not breed (Fig 3b). These results suggest that reproduction and survival trade-offs are greater following peak reproduction as investing in offspring after the age of 30 decreases survival probabilities. Long-lived female elephants are thus likely to be those with fewer births over their lives.

DISCUSSION

The framework presented herein builds upon the approach presented by Rebke *et al.* (2010), allowing age-specific patterns of reproductive success to be decomposed into individual-level changes in long-lived organisms, and quantifying the extent to which changes in survival probability are driven by age-specific relationships between fitness components. Our application of this method to a semi-captive Asian timber elephant population, provides evidence in long-lived mammals for reproductive and survival senescence in females, and for age-specific survival declines that are driven in part by trade-offs with reproduction and survival. Our results support findings in many natural vertebrate populations which have demonstrated within-individual declines in reproductive performance and survival, whilst accounting for the effects of survival and patterns of population-level change. They also support findings that high reproductive investment can relate to reduced subsequent survival (Orrell & Belda 2002; Reid *et al.* 2003; Carranza *et al.* 2004; Bowen *et al.* 2006; Charmantier *et al.* 2006; Descamps *et al.* 2006; Nussey *et al.* 2006, 2008; Reed *et al.* 2008). However, in this study, associations between reproductive investment and survival depend on the age examined, with differences between population- and individual-level reproductive rates becoming more apparent in later age groups where surviving individuals are less likely to reproduce and individuals who have invested highly in reproduction are more likely to die. In contrast at early ages, selective disappearance is associated with individuals that do not reproduce and individuals who have invested highly in reproduction are more likely to survive.

The extent to which patterns of reproductive and survival senescence are driven by age-specific relationships between these components are likely to vary between species and even between populations of the same species that experience different environmental conditions. Our findings demonstrate that there are specific ages at which reproduction comes at the greatest risk to survival, and where individual-level declines are most prominent. These patterns may reflect trade-offs that operate at different levels: (1) associations may be non-metabolic, for example reproductive activity may reduce survival by either increasing risk exposure or through wear and tear, with both increasing throughout life; (2) trade-offs may be metabolic with reproduction and maintenance drawing directly from the same supply of resources within the organism (Kirkwood 1977), and either underinvestment accumulates with age or a greater number of resources are required for maintenance at older ages making reproduction more costly; (3) genes of beneficial effect on both survival and reproduction in early life, have opposing effects later in life. Future research should aim to elucidate whether these effects act in unison or whether a particular factor plays a greater role across taxa.

Assessing differences in fitness among phenotypes is a central objective in evolutionary biology, and our results highlight the need for an age-specific approach to identify how investment in reproduction trades off against later-life survival. Until now, lack of appropriate

Table 2 Models of age-specific (a) breeding probability, (b) recruiting birth probability and survival (c) in a semi-captive population of Asian elephants. For (a) and (b) age-specific breeding probabilities are estimated for those which died and those which survived each age class and for (c) survival probabilities were calculated for individuals that did not reproduce (not bred: *nb*), those which gave birth to non-recruiting offspring (non-recruit: *nr*) and those which gave birth to recruiting offspring (recruit: *r*). Separate intercepts were fitted for (a, b) those which died and those which survived at age$_{5-9}$, and (c) for *nb*, *nr* and *r* females at age$_{5-9}$

	Posterior mean (95% CI)	Posterior mean (95% CI)		Posterior mean (95% CI)
	(a) Model of breeding probability	(b) Model of recruiting birth probability		(c) Model of survival probability
Died	−7.463 (−10.385 : −5.295)	−9.682 (−19.503 : −1.563)	Not bred	1.594 (1.416 : 1.818)
Survived	−6.994 (−8.225 : −5.919)	−0.821 (−3.356 : 1.541)	Non-recruit (*nr*)	2.151 (−0.611 : 5.275)
Age$_{10-14}$	1.752 (−0.785 : 4.630)	8.279 (−3.419 : 20.731)	Recruit (*r*)	10.568 (0.609 : 24.969)
Age$_{15-19}$	3.358 (0.737 : 6.402)	12.370 (0.666 : 25.056)	Age$_{10-14}$	−0.212 (−0.498 : 0.057)
Age$_{20-24}$	4.413 (2.066 : 7.599)	9.303 (−1.382 : 23.084)	Age$_{15-19}$	−0.613 (−0.967 : 0.252)
Age$_{25-29}$	4.889 (2.991 : 7.737)	9.500 (1.681 : 21.595)	Age$_{20-24}$	−0.197 (−0.697 : 0.239)
Age$_{30-34}$	4.823 (2.557 : 7.767)	9.967 (1.041 : 22.124)	Age$_{25-29}$	−0.986 (−1.533 : −0.474)
Age$_{35-39}$	5.170 (3.006 : 8.404)	10.500 (0.929 : 23.251)	Age$_{30-34}$	−1.273 (−1.891 : −0.726)
Age$_{40-44}$	5.007 (3.535 : 6.803)	8.149 (−0.497 : 20.006)	Age$_{35-39}$	−1.338 (−2.019 : −0.728)
Age$_{45-49}$	5.415 (4.205 : 9.042)	9.518 (−1.383 : 22.593)	Age$_{40-44}$	−2.310 (−3.228 : −1.607)
s : age$_{10-14}$	1.727 (−1.375 : 3.714)	−10.853 (−24.740 : −0.412)	Age 9	−0.228 (−1.403 : 0.794)
s : age$_{15-19}$	2.790 (−0.402 : 3.547)	−6.305 (−18.235 : 1.385)	*nr* : age$_{10-14}$	2.209 (−1.686 : 6.227)
s : age$_{20-24}$	2.349 (−0.923 : 3.935)	−7.393 (−20.777 : 0.758)	*r* : age$_{10-14}$	−2.123 (−10.619 : 3.745)
s : age$_{25-29}$	2.039 (−0.806 : 3.929)	−7.642 (−20.741 : 1.785)	*nr* : age$_{15-19}$	0.479 (−2.807 : 3.344)
s : age$_{30-34}$	1.751 (−1.613 : 2.367)	−7.496 (−19.211 : 1.431)	*r* : age$_{15-19}$	−2.895 (−12.030 : 5.615)
s : age$_{35-39}$	0.672 (−2.269 : 2.438)	−8.625 (−22.286 : 1.282)	*nr* : age$_{20-24}$	−0.209 (−3.203 : 2.853)
s : age$_{40-44}$	1.622 (−1.308 : 3.505)	−6.446 (−19.299 : 1.687)	*r* : age$_{20-24}$	−6.547 (−14.284 : 3.916)
s : age$_{45-49}$	−4.351 (−8.650 : −0.478)	−11.977 (−25.677 : −0.691)	*nr* : age$_{25-29}$	0.195 (−3.331: 2.872)
Female identity	2.111 (1.606 : 2.735)	0.768 (0.114 : 1.507)	*r* : age$_{25-29}$	−6.305 (−14.783 : 3.462)
			nr: age$_{30-34}$	−0.360 (−3.341 : 2.574)
			r: age$_{30-34}$	−7.552 (−19.970 : 0.317)
			nr : age$_{35-39}$	−0.346 (−3.589 : 2.551)
			r : age$_{35-39}$	−9.683 (−22.053 : −2.092)
			nr : age$_{40-44}$	−0.732 (3.856 : 2.336)
			r : age$_{40-44}$	−10.940 (−20.488 : −3.832)
			nr : age$_{45-49}$	−2.166 (−5.471 : 1.269)
			r : age$_{45-49}$	−12.599 (−27.478 : −2.521)
			Female identity	0.209 (0.105 : 0.798)

statistical tools constrained biologists to assess selective values using estimates of mean fitness corresponding to classes defined on the basis of factors of interest (e.g. age), trait values, or arbitrary criteria assumed to be associated with individual quality (Coulson 1968; Bjornstad & Hansen 1994; McNamara & Houston 1996; but see McGraw & Caswell 1996). Models permitting description of the distribution of fitness values in the population, or in sub-populations defined on the basis of some factor of interest, are more realistic. In addition, the use of approaches permitting the description of the genuine influence of age on survival and reproduction (i.e. eliminating the confounding effect of within-cohort phenotypic selection) is critical to robust inference in comparative studies of senescence and of evolution in age-structured populations in general. Future research could extend this framework to a bivariate model where survival and reproduction are modelled simultaneously with individual-level covariance directly estimated across ages.

Understanding age-specific changes in survival and reproduction also has important conservation and welfare implications. Elephants are an iconic species with extreme conservation interest, and one of the few endangered species used by humans in a non-domesticated form. Understanding the factors which influence the ability of animals to reproduce in captivity, and finding ways in which to mitigate any costs, will prevent the need to capture elephants from the wild and maintain a healthy population that can hopefully produce a surplus of individuals that could then be used to increase the wild population. It is clear from this work that this captive management needs to mitigate trade-offs between reproductive components ensuring that breeding in captivity does not come at a compromise to their survival. Elephants of breeding age, particularly old multiparous (30+ years) females must be provisioned and reduced work load, balancing resource availability and the energetic demand of daily activities. This study also provides broader implications to zoo elephant management. Current zoo elephant population are not self-sustaining with reported high mortality and low breeding rates and assisted reproductive technology is well underway to boost breeding in zoo elephants (Wiese 2000). This study highlighted the fact that birth spacing should be taken into consideration for old (30+ years) females to prevent early reproductive senescence. The approach taken herein provides a framework where-by data collected can be used to examine patterns in wild or captive populations of long-lived organisms to test whether changes in environmental variables or management practices are having an effect on individual-level changes, and associations between reproductive effort and survival.

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REFERENCES

Bjornstad, O.N. & Hansen, T.F. (1994). Individual variation and population dynamics. *Oikos*, 69, 167–171.

Bouwhuis, S., Sheldon, B.C., Verhulst, S. & Charmantier, A. (2009). Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proc. R. Soc. Biol. Sci.*, 276, 2769–2777.

Bowen, W.D., Iverson, S.J., McMillan, J.I. & Boness, D.J. (2006). Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. *J. Anim. Ecol.*, 75, 1340–1351.

Bronikowski, A.M., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A. *et al.* (2011). Aging in the natural world: comparative data reveal similar mortality patterns across primates. *Science*, 331, 1325–1328.

Cam, E., Link, W.A., Cooch, E.G., Monnat, J.Y. & Danchin, E. (2002). Individual covariation in life-history traits: seeing the trees despite the forest. *Am. Nat.*, 159, 96–105.

Carranza, J., Alarcos, S., Sanchez-Prieto, C.B., Valencia, J. & Mateos, C. (2004). Disposable-soma senescence mediated by sexual selection in an ungulate. *Nature*, 432, 215–218.

Catry, P., Phillips, R.A., Phalan, B. & Croxall, J.P. (2006). Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. *Proc. R. Soc. Biol. Sci.*, 273, 1625–1630.

Charmantier, A., Perrins, C., McCleery, R.H. & Sheldon, B.C. (2006). Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. *Proc. Natl Acad. Sci. USA*, 103, 6587–6592.

Clubb, R., Rowcliffe, M.J., Lee, P.C., Mar, K.U. & Mason, G.J. (2008). Compromised survivorship in zoo elephants. *Science*, 322, 1649.

Coulson, J.C. (1968). Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature*, 217, 478–479.

Coulson, T. & Tuljapurkar, S. (2008). The dynamics of a quantitative trait in an age-structured population living in a variable environment. *Am. Nat.*, 172, 599–612.

Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.-M. (2006). Best squirrels trade a long life for an early reproduction. *Proc. R. Soc. Biol. Sci.*, 273, 2369–2374.

Dupuis-Sammel, M. & Ryan, L.M. (1996). Latent variable models with fixed effects. *Biometrics*, 52, 650–663.

Evans, G.H. (1910). *Elephants and Their Diseases*. Government Printing, Rangoon, Burma.

Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J. Stat. Soft.*, 33, 1–22.

Hamilton, W.D. (1966). The moulding of senescence by natural selection. *J. Theor. Biol.*, 12, 12–45.

Hedeker, D., Siddiqui, O. & Hu, F.B. (2000). Random-effects regression analysis of correlated grouped-timed survival data. *Stat. Methods Med. Res.*, 9, 161–179.

Hougaard, P. (1984). Life table methods for heterogeneous populations: distributions describing the heterogeneity. *Biometrika*, 71, 75–83.

Hougaard, P. (1986). Survival models for heterogeneous populations derived from stable distributions. *Biometrika*, 73, 387–396.

Hougaard, P. (1991). Modeling heterogeneity in survival data. *J. Appl. Probab.*, 28, 695–701.

Hu, F.B., Goldberg, J., Hedeker, D., Flay, B.R. & Pentz, M.A. (1997). Comparison of population-averaged and subject-specific approaches for analyzing repeated binary outcomes. *Am. J. Epidemiol.*, 147, 694–703.

Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H. *et al.* (2008). Senescence rates are determined by ranking on the fast–slow life-history continuum. *Ecol. Lett.*, 11, 664–673.

Kirkwood, T.B.L. (1977). Evolution of ageing. *Nature*, 270, 301–304.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.*, 62, 67–118.

Loison, A., Festa-Bianchet, M., Gaillard, J.M., Jorgenson, J.T. & Jullien, J.M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, 80, 2539–2554.

Manton, K.G., Stallard, E. & Vaupel, J.W. (1981). Methods for comparing the mortality experience of heterogeneous populations. *Demography*, 18, 389–409.

Mar, K.U. (2007). *The Demography and Life-History Strategies of Timber Elephants of Myanmar*. PhD Thesis, University College of London, London, UK.

McGraw, J.B. & Caswell, H. (1996). Estimation of individual fitness from life-history data. *Am. Nat.*, 147, 47–64.

Moss, C.J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J. Zool.*, 255, 145–156.

Nichols, J.D. (1992). Capture-recapture models using marked animals to study population dynamics. *Bioscience*, 42, 94–102.

Nussey, D.H., Kruuk, L.E.B., Donald, A., Fowlie, M. & Clutton-Brock, T.H. (2006). The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecol. Lett.*, 9, 1342–1350.

Nussey, D.H., Wilson, A.J., Morris, A., Pemberton, J., Clutton-Brock, T. & Kruuk, L.E.B. (2008). Testing for genetic trade-offs between early- and late-life reproduction in a wild red deer population. *Proc. R. Soc. B.*, 275, 745–750.

Nussey, D.H., Kruuk, L.E.B., Morris, A., Clements, M.N., Pemberton, J.M. & Clutton-Brock, T.H. (2009). Inter- and intra-sexual variation in aging patterns across reproductive traits in a wild red deer population. *Am. Nat.*, 174, 342–357.

Orrell, M. & Belda, E.J. (2002). Delayed cost of reproduction and senescence in the willow tit *Parus montanus*. *J. Anim. Ecol.*, 71, 55–64.

Price, G.R. (1970). Selection and covariance. *Nature*, 227, 520–521.

Rebke, M., Coulson, T., Becker, P.H. & Vaupel, J.W. (2010). Reproductive improvement and senescence in a long-lived bird. *Proc. Natl Acad. Sci. USA*, 107, 7841–7846.

Reed, T.E., Kruuk, L.E.B., Wanless, S., Morten, F., Cunningham, E.J.A. & Harris, M.P. (2008). Reproductive senescence in a long-lived seabird: rates of decline in late life performance are associated with varying costs of early reproduction. *Am. Nat.*, 171, E89–E101.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (2003). Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *J. Anim. Ecol.*, 72, 765–776.

Shoshani, J. & Eisenberg, J.F. (1982). *Elephas maximus*. *Mamm. Species*, 182, 1–8.

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

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

Taylor, V.J. & Poole, T.B. (1998). Captive breeding and infant mortality in Asian elephants: a comparison between twenty western zoos and three eastern elephant centers. *Zoo Biol.*, 17, 311–332.

Turbill, C. & Ruf, T. (2010). Senescence is more important in the natural lives of long- than short-lived mammals. *PLoS One*, 5, e12019.

Vaupel, J.W. & Yashin, A.I. (1985). Heterogeneity's ruses: some surprising effects of selection on population dynamics. *Am. Stat.*, 39, 176–185.

Wiese, R.I. (2000). Asian elephants are not self-sustaining in North America. *Zoo Biol.*, 19, 299–309.

Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, 11, 398–411.

AUTHORSHIP

KUM and VL conceived the research and collection of long-term data and KUM collected the data. MRR conceived the study, designed and conducted the research, and wrote the manuscript along with contributions from VL and KUM.

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