PROGRESS REPORT

Early reproductive investment depresses age-specific survival and fitness in female Asian elephants

Khyne U Mar[†], Matthew R. Robinson[†], Andrew F. Russell[§][‡] & Virpi Lummaa[†]

[†]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K. § Daphne du Maurier School of Biosciences, University of Exeter Cornwall Campus, Penryn TR10 9EZ, UK

‡4La Station d'Ecologie Experimentale du CNRS à Moulis, 09200 Moulis, France

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SUMMARY

Little is known of the consequences of early reproduction on life history strategies late at life in vertebrates with extreme longevity. Here we use an extensive longitudinal dataset on semi-captive Asian elephants (*Elephas maximus*) to investigate the effects of early-life reproduction on subsequent female age-specific survival, offspring number, quality and annual fitness. Myanmar female elephants show clear reproductive priming, with age-specific fecundity peaking at age 30 and declining thereafter. While high early-life (<30 years) fecundity has no effect on age-specific decline in fecundity or offspring quality, it significantly impairs a female's own survival at later ages. Consequently, annual fitness declines after age 30 with those investing in early reproduction showing fastest fitness decline in old age. Age-specific fitness of high and low early-investment mothers cross after peak reproduction but despite this high early-investment females still achieve greater overall reproductive success. Our results are the first to document that survival and fecundity in female Asian elephants depend on their age and previous investment on their reproductive effort. This study also highlights the importance of well-planned birth spacing and provisioning for high-productive young females to prevent adverse pregnancy outcomes.

INTRODUCTION

High early-life reproductive investment has been shown to be associated with reduced subsequent survival in many natural populations (Carranza et al. 2004, Reed et al. 2008) and reduced breeding performance later in life (Beamonte-Barrientos et al. 2010). For example, female red deer (Cervus elaphus) with high early-life fecundity show stronger subsequent declines in offspring birth weight and delays in calving dates (Nussey et al. 2006). It is currently unclear how the general theories of senescence apply to species with relatively long lifespan. The most long-lived species studied to date include turtles (Chrysemys picta), killer whales (Orcinus orca) and birds such as mute swans (Cygnus olor), common guillemots (Uria aalge) and grey-headed albatrosses (Thalassarche chrysostoma), with maximum ages of reproduction approximating >50 (Ward et al. 2009), >55 (Congdon et al. 2003), 20 (Charmantier et al. 2006), 30 (Reed et al. 2008) and >40 (Catry et al. 2006) years, respectively. In order to have a full appreciation of the generality of results on how early life reproductive investment affects later life senescence, we need to investigate whether the same patterns can be found in species with extreme lifespan. The one long-lived mammal studied in detail so far is humans (Lahdenpera et al. 2004). The closest other mammal with a comparable life-history to that of human is elephants, which are known to breed into their 60s and can live into their 80s (Moss 2001). Thus, not only do elephants provide a much needed data-point on the patterns of, and underlying life-history correlates of,

senescence at the top end of the longevity distributions in wild vertebrates, but understanding the effects of early-life reproduction on subsequence survival and reproductive performance is likely to be important to improve the welfare management and conservation of the species.

MATERIALS AND METHODS

Our data stems from the semi-captive population of Asian elephants from timber camps in Myanmar (Burma). In this study, we used biodata of 376 adult female timber elephants born between 1941 to 1968 who survived until at least age 30, with 141 individuals producing 251 offspring. Individual females and their offspring have known dates of birth and death. The youngest female breeding for the first time was 6 years (range = 6-40 median = 18 years) and the oldest mother in the data set was 53 years with the average inter-birth interval being 5 years (range = 1.8-21.4 years, medium = 4.9) and the maximum lifetime number of calves 10. These elephants are used in the timber industry with set work-loads (<230 working days per year). They are free to forage unsupervised in the forest for up to 14 hours per night and during official rest periods (up to 120 days per year) during which time they mix and breed with captive and wild elephants. Calves born in captivity are cared for by their biological and allo-mothers, and are suckled until lactation no longer supports their demands. Elephants 'retire' at 55 years and live out the rest of their lives in comparative freedom.

In all analyses we control for a range of potentially confounding effects, including temporal (birth cohort) and geographic (forest camp) differences in living conditions, and the selective appearance and disappearance of different-quality individuals from the study cohort. We used Cox proportional hazard model for survival analyses and a generalised liner mixed model (GLMM) of annual fecundity. Models were conducted in Genstat v8.1 (VSN International, Hemel Hempsted, UK) and R (R foundation for statistical computing).

RESULTS

We find strong support that in female elephants, survival, reproductive rate and offspring quality senesce with age. First, the mortality hazard increases from the age of 30 onwards ($\chi^{2}_{1} = 27.36$; P <0.001; Figure 1a). Second, females show clear evidence of senescence in age-related reproductive rates (model of fecundity with age: $\chi^{2}_{1} = 416.37$; P < 0.001 and its quadratic term: $\chi^{2}_{1} = 365.74$; P < 0.001; Figure 1b). Reproductive priming occurs from the age at first reproduction to the age of 30 years; with the reproductive rate (probability of reproducing at given age) increasing during this period, but such an increase is followed by subsequent senescence (Figure 1b). By the peak fecundity age at 30, an average female elephant has produced 1.5±SE 0.059 offspring (range=0-5). Of the females reaching the peak fecundity age, 38% survive from age of 30 to 54. The average number of offspring produced during the latter reproductive period for all females equals 1.0±0.068 (range=0-5).

Figure 1. Panel (a) presents Kaplain-Meier survival curve for female elephants, and (b) shows birth probabilities with age from the fitted values gained from a generalized linear mixed model of female fecundity.



We categorized early-life fecundity as 0, 1, 2 or 3 or more offspring born prior to peak age in fecundity at 30 years and examined the effects of early-life fecundity on: (a) the survival of each female after the age of 30; (b) later-life fecundity; (c) later-life survival of offspring to five years of age or not; and (d) annual fitness (sum of genetic contribution to following year). Female's early-life reproductive investment is related to her survival rates at older ages (Figure 2a). Females that invest heavily in reproduction in early-life (i.e. produce more calves by age of 30 years) show a reduced chance of surviving each subsequent year until age 54, compared to females that produce fewer or no calves by age 30 (Figure 2a). When we examine the relationship between later-life fecundity and survival, we find that giving birth past the age of 30 increases a female's probability of death ($\chi^2_3 = 8.81$; P = 0.032). Decline in offspring quality (recruitment) with maternal age beyond 30 is not modified by the mother's early reproductive investment (Figure 2 c).

Although females with high early-life fecundity have the best age-specific fitness at peak reproductive ages, their age-specific fitness decreased at a greater rate than the age-specific fitness of females with low early-life reproductive effort (Figure 2b). The age-specific fitness gains of high and low early-investment mothers cross over so that those females with low reproductive investment prior age 30 have higher annual fitness than females with high early-life reproductive investment (Figure 2d). Females with high early-life fecundity still achieve on average greater overall reproductive success in their lifetime by producing numerous offspring early in life (numbers of offspring raised to independence over entire lifetime: $\chi^2_1 = 35.81$; P < 0.001); average depending on the number of offspring produced before age 30: none: 0.17 ± 0.05 ; one: 1.45 ± 0.10 ; two: 2.58 ± 0.13 ; three or more: 4.26 ± 0.24).

Figure 2. Figures (a) a parametric survival analysis; (b) female fecundity - whether a female bred or not in each year of her later life, between the ages of 30 and 54; (c) offspring survival – whether an offspring produced by a female survived to independence (age 5) across each year of her life, between the ages of 30 and 54; (d) a female's annual fitness each year between the ages of 30 and 54 (see Methods). To aid interpretation, the results are presented by grouping a female's early-life fecundity (ELF: the number of offspring produced before 30 years of age) into four categories (0: no offspring shown by solid line in (d); 1: one offspring produced before the age of 30 shown by long dashed line in (d); 2: two offspring produced before 30 shown by dot-dash line in (d); and 3+: three or more offspring produced before 30 shown by short dashed line in (d)).



DISCUSSION

Understanding age-specific changes in survival and reproduction has important conservation and welfare implications. When large animals, such as camel, horses, buffalo or elephant, are used for draught purposes, the associated stress of inadequate nutrition and work load could influence the survival, reproduction and draught power because the energy requirements of working individuals were higher than those of non-working, resting or exhibiting animals(Lawrence 1990, Pearson and Dijkman 1994). Here in this study, we reported that declines in age-specific fitness resulted from high-early life reproductive investment but the reproductive output or offspring quality with age were unaffected. More studies need to clarify the impact of work-related stress, malnutrition and adverse environmental conditions (e.g. extreme heat/cold/rain) on survival and fecundity schedules of captive elephants. Interestingly, in zoo elephants, the increasing infertility problems in females have been attributed by the failure to breed in early (<30 years) ages (Hermes et al. 2008). Our study shows that Myanmar elephants that invested a large amount of resources in early reproduction however paid a survival cost because they also attempted to reproduce often at older ages. While we acknowledge that the costs of reproduction may differ between populations depending on the nutrition and workload, it is generally agreed that birth-spacing has profound impact for maternal behaviour and offspring survival (Abebe and

Yohannis 1996, Conde-Agudelo et al. 2007) with widely-spaced infants likely receiving more maternal attention than closed-spaced groups. This study endorsed the fact that time has now arrived to advice the managers and conservationists to organize a far-sighted, well-managed, properly-spaced and fully-provisioned elephant breeding programme for high-productive young females to prevent adverse pregnancy outcomes.

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