Correspondences

Environmental conditions in early life influence ageing rates in a wild population of red deer

Daniel H. Nussey[1,2,*], Loeske E.B. Kruuk[2], Alison Morris[2] and Tim H. Clutton-Brock[1]

The process of ageing, or senescence, is an important focus of current research, but our knowledge of the factors influencing ageing rates in naturally occurring populations remains poor [1]. A growing number of studies of wild vertebrate and human populations has shown that environmental conditions early in life can have long-term effects on fitness-correlated traits [2,3]. However, the consequences of early-life environment for ageing rates remain unknown [4]. Using data collected over 35 years from a wild population of red deer (*Cervus elaphus*), we show that females experiencing high levels of resource competition during early life showed faster rates of senescence as adults. Our results suggest that rather than inducing adaptive shifts in developmental trajectories, harsh early-life conditions may constrain development and ultimately exacerbate the ageing process.

Red deer resident to the North Block study area on the Isle of Rum, Scotland, have been the subject of an individual-based study since 1971. Female deer in this population show clear signs of ageing in both survival probability and reproductive performance [5,6]. They have also experienced recent changes in environmental conditions. The population density in the North Block nearly tripled over the first decade of the study. This increase in resource competition was associated with a reduction in several key reproductive performance parameters [7]. The population then stabilised and has fluctuated around habitat carrying capacity since around 1980 [7] (Supplemental data). We investigated how environmental conditions during development, as indicated by population density in an individual's year of birth ('D_{YOB}'), influenced rates of decline in survival probability and annual fecundity with age amongst adult female deer. We also tested whether early life history traits, including birth weight, age at first reproduction (AFR) and early life fecundity, influenced ageing rates.

Female deer born when population density was high showed more rapid reproductive senescence as adults (Figure 1; age-by-D_{YOB} interaction: $X^2_{(d.f.=1)} = 8.76$, $P < 0.01$). A female's probability of producing a calf in a given year declined more rapidly in old age amongst females that experienced harsh early environments (Figure 1). Although we did not find evidence for a significant direct effect of population density in the birth year on ageing rates in survival probability (effect of dropping age-by-D_{YOB} interaction from survival model: $\Delta AICc = -1.99$), female deer that experienced increased D_{YOB} started to breed later (Figure 2C; $X^2_{(1)} = 14.86$, $P < 0.001$), and individuals that began to breed later showed faster rates of survival senescence (Figures 2A, B; dropping age-by-AFR interaction: $\Delta AICc = +8.56$). Poor early-life conditions were, therefore, also linked to increased survival senescence rates through their effects on the age at first reproduction.

The effects of population density in the year of birth on ageing rates were independent of any effects of population density experienced later in life (Supplemental data). Furthermore, our results were not simply due to the rapid increase in population size over the first decade of our study period. The same effect of D_{YOB} on reproductive senescence was evident when only females born after 1980 were included in our analyses (age-by-D_{YOB} interaction: $X^2_{(d.f.=1)} = 3.86$, $P < 0.05$; Supplemental data). These females experienced fluctuating rather than increasing population densities across their lives (Supplemental data). Similarly, cohorts of these later born females that experienced relatively high D_{YOB} still showed later average ages at first reproduction ($X^2_{(1)} = 7.58$, $P < 0.01$).

We found no evidence that high D_{YOB} was associated with higher early life investment in reproduction ($X^2_{(1)} = 1.23$, $P = 0.27$) or smaller size at birth ($X^2_{(1)} = 0.03$, $P = 0.87$). A female's weight at birth did not influence later ageing rates in survival or fecundity, nor did it affect mean survival probability and fecundity as an adult (Supplemental data). This confirms previous findings that show that birth weight is density-independent and does not influence adult performance in female deer in the North Block population [2,8]. Female deer that invested more in

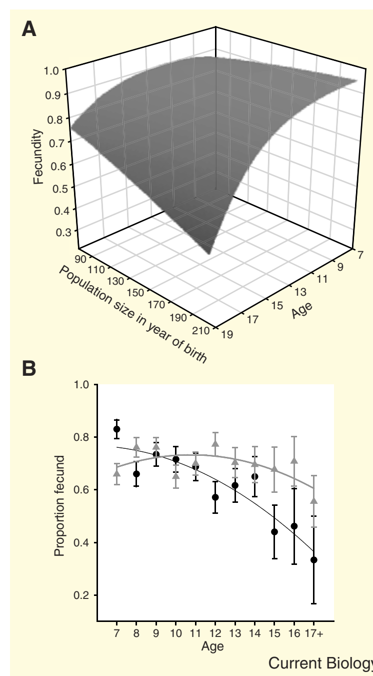

Figure 1. Conditions in early life affect female reproductive senescence rates.

(A) Predicted ageing rates in annual fecundity from the significant age-by-density in birth year interaction in the final fecundity model (Supplemental data). (B) The proportion of fecund females at each age class among females that experienced less than (gray triangles and line), or equal or greater than (black circles and line) the median density in birth year, with standard deviation bars and quadratic functions plotted.

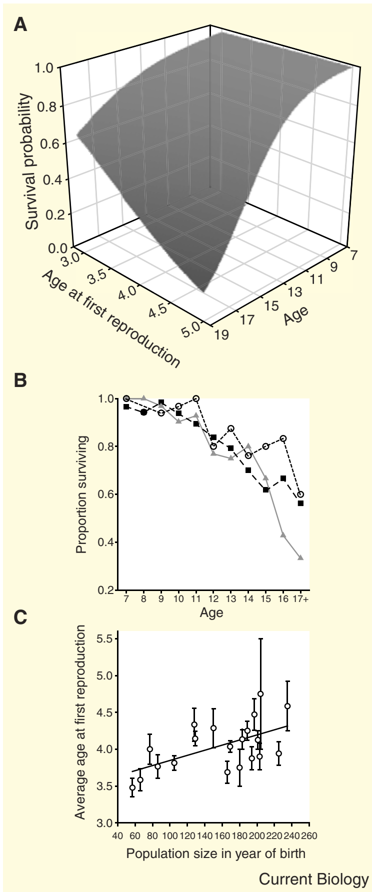

Figure 2. Effects of early environment on the onset of breeding and survival senescence.

(A) Predicted ageing rates in survival probability from the significant age-by-age at first reproduction interaction in the final survival model (Supplemental data). (B) Proportion of females surviving to the next year amongst females that started breeding aged three (unfilled gray circles), four (black squares) and greater than four (filled gray triangles) years of age. (C) Mean ages at first reproduction plotted against population size in year of birth for each cohort of females with standard error bars and regression line.

reproduction in early life (<9 years old) showed higher reproductive senescence rates (age-by-early life fecundity interaction: $X^2_{(1)} = 5.38$, $P < 0.05$). This finding is in support of trade-off theories of ageing [9] and matches previous findings from this population in other traits [6]. However, effects of early life reproduction and D_{YOB} on reproductive ageing rates were independent of one another (Supplemental data). Generally, high D_{YOB} was associated with reduced mean adult fitness and more rapid senescence. Our results, therefore, provide no evidence that individuals experiencing poor early-life conditions showed adaptive developmental responses resulting in more resilient adult phenotypes, as predicted by the 'thrifty phenotype' hypothesis [10]. There was no indication that reduced adult performance was associated with mismatches between conditions in early life and adulthood (Supplemental data).

In the North Block red deer population, increased resource competition associated with relatively high population density may result in maternal nutritional stress during gestation and lactation and thus to less stable conditions for the offspring *in utero* or to reduced maternal provisioning of newborn young. This could represent an insult to development, ultimately reducing overall adult condition and increasing senescence rates later [3,4]. Reduced maternal investment in foetal growth appears unlikely to be responsible for these early-life effects on ageing, as birth weight had no effect on later performance. Poor environmental conditions may instead reduce maternal investment in lactation, or have more subtle effects on foetal development [4].

Several previous studies have demonstrated that conditions during development have long-term effects in wild vertebrates, generating marked variation in survival and fecundity between birth cohorts [2,11]. The present findings constitute, to our knowledge, the first evidence from a wild animal population that early-life environment influences senescence rates. Our results illustrate that ageing rates within a population can vary depending on ecological conditions, leading to strongly delayed effects of environmental variation on population dynamics [11]. Although adaptive responses to conditions in early life are widely believed to have important consequences for human health [3,12], we found no evidence for such adaptive developmental plasticity in wild deer. Under natural conditions such plasticity may be heavily masked by the constraints imposed on development by harsh environmental conditions [3].

Supplemental data

Supplemental data including experimental procedures and acknowledgements are available at http://www.current-biology.com/cgi/content/full/17/23/R1000/DC1

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[1]Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK. [2]Institute of Evolutionary Biology, University of Edinburgh, The King's Buildings, Edinburgh, UK.
*Email: dan.nussey@ed.ac.uk