Ageing in a variable habitat: environmental stress affects senescence in parasite resistance in St Kilda Soay sheep

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Despite widespread empirical evidence for a general deterioration in the majority of traits with advancing age, it is unclear whether the progress of senescence is chronologically determined, or whether factors such as environmental conditions experienced over the lifespan are more important. We explored the relative importance of ‘chronological’ and ‘environmental’ measures of age to changes in parasite resistance across the lifespan of free-living Soay sheep. Our results show that individuals experience an increase in parasite burden, as indicated by gastrointestinal helminth faecal egg count (FEC) with chronological age. However, chronological age fails to fully explain changes in FEC because a measure of environmental age, cumulative environmental stress, predicts an additional increase in FEC once chronological age has been accounted for. Additionally, we show that in females age-specific changes are dependent upon the environmental conditions experienced across individuals’ life histories: increases in FEC with age were greatest among individuals that had experienced the highest degree of stress. Our results illustrate that chronological age alone may not always correspond to biological age, particularly in variable environments. In these circumstances, measures of age that capture the cumulative stresses experienced by an individual may be useful for understanding the process of senescence.

Keywords: ageing; environmental dependence; strongyle helminths; Soay sheep; immunosenescence; faecal egg counts

1. INTRODUCTION

Biological senescence is a general age-specific decline in physiological condition and fitness (Bonsall 2006). It is manifested in a wide range of traits, from key life-history traits, such as age-specific survival and reproductive performance (Monaghan et al. 2008), to aspects of cellular physiology such as telomere length (Monaghan & Haussmann 2006) and oxidative damage (Monaghan et al. 2009). The crux of interpreting senescence within an evolutionary framework is that the number of surviving individuals in any cohort decreases with age owing to extrinsic causes of mortality, and so the strength of natural selection declines with age. Theoretically, the onset and rate of senescence can be perfectly predicted by an individual’s true ‘biological’ age, an indicator that would predict the ageing state of an individual better than ‘chronological’ age (Klemera & Doubal 2006), which equates to the time since birth in units such as days or years. However, chronological age does not take into account additional environmental factors that may influence the proximate mechanisms of ageing (Monaghan et al. 2008), and which may therefore contribute to an individual’s biological age. It has been shown in a number of studies that conditions during early growth and development can have profound effects on fitness (e.g. Kruuk et al. 1999) and on the trajectory of senescence in later life (e.g. Nussey et al. 2007; Reed et al. 2008). Environmental conditions can therefore play a large role in determining life-history trajectories, particularly with reference to senescence. In this context, a metric measuring ‘environmental’ age, encompassing the cumulative environmental conditions experienced by an individual across its lifespan, could aid the understanding of senescence-related changes in key life-history traits, especially in free-living systems where individuals are subject to stochastic environments. ‘Biomarkers of ageing’, such as telomere length, hormonal changes and a range of immunological parameters (Simm et al. 2008), are thought to provide alternative indicators of biological age, but studying such parameters in the wild has proved to be difficult. It is therefore not clear how well alternative measures of ageing describe changes in performance across an individual’s lifetime.

Over the last 20 years, a growing body of work has shown that senescence is pervasive in wild populations (e.g. Jones et al. 2008) and occurs in a range of traits in organisms including insects (Bonduriansky & Brssil 2005), fishes (Reznick et al. 2004), birds (Gustafsson & Part 1990; Brommer et al. 2007; Keller et al. 2008) and mammals (Beauplet et al. 2006; Nussey et al. 2006). Typically, individuals experience declines in survival probability and reproductive performance as they age. Susceptibility to infection also increases, through the process of immunosenescence, an age-specific deterioration in the efficiency of the immune system (Tarazona et al. 2002). This subject has received much attention in the laboratory (Gruver et al. 2007), but there has been limited
work in natural populations and especially in mammals (but see Fest-Bianchet 1989, 1991; Pelletier et al. 2005 for a notable example of a longitudinal study of helminth infection in a wild population). Previous work in wild bird populations has proved to be consistent with a decline in aspects of the immune system with age (Cichon et al. 2003; Palacios et al. 2007). However, such studies are, as far as we are aware, exclusively cross-sectional and as such do not account for the possibility that the observed results are due to individual differences, cohort effects, or interannual variation. In contrast, the use of longitudinal data allows separation of within-individual change from between-individual heterogeneity (Nussey et al. 2008).

The Soay sheep population on St Kilda is the subject of one of the world’s most intensive longitudinal studies of a free-living mammal population (Clutton-Brock & Pemberton 2004). Data have been collected for over 20 years on population dynamics, individual life histories, parasitism and environmental variables, and provide a unique opportunity to examine the effects of ageing on parasitism. By using individual-based longitudinal data on parasite burdens, we attempted to identify how ageing affects resistance to parasites in this population. We use three separate indicators of biological age: chronological age in years, and two alternative measures indicating an individual’s cumulative experience of the environment, which we term environmental age. The first of these sums the number of years of severe mortality an individual has experienced, and the second takes into account environmental conditions experienced in every year of life from birth until sampling to assess the impact of lifetime environmental experience. We also assess how the environmental conditions experienced by individuals across their life histories affect the trajectory of changes in parasitism with chronological age.

Our primary aim was to test, using longitudinal data from a free-living population, for senescence in parasite resistance and to describe age-specific changes in parasitism, with the hypothesis that individuals will experience increasing parasitism as they age. We also test for differences in age-specific parasite infection between the sexes, and predict that males will age more rapidly than females (Clutton-Brock & Isvaran 2007). Secondly, we use chronological and environmental measures of age, and examine how they affect parasitism. Finally, we attempt to identify how age-specific changes are affected by an individual’s cumulative environmental experience. We predict that individuals that have experienced poorer environmental conditions will suffer elevated parasitism compared with individuals of the same chronological age that have experienced relatively favourable conditions.

2. METHODS
(a) Study population and data collection
The feral Soay sheep population of Hirta (638 ha) in the St Kilda archipelago, NW Scotland (57°49’ N, 08°34’ W) has existed in a free-living state since 1932, when 107 sheep were moved from the neighbouring island of Soay. The current individual-based study began in 1985, since when data have been collected on a range of aspects of the population, including population dynamics, individual life-history and morphological traits and parasitology, as well as a suite of environmental measures (Clutton-Brock & Pemberton 2004). The study focuses on the Village Bay area of the island of Hirta, which contains 200–650 sheep, approximately a third of the island’s population. The population exhibits unusual dynamics, with periodic overwinter mortality events (population ‘crashes’) that result in severe reduction in population size (figure 1; Clutton-Brock et al. 1991, 1997). Mortality is determined by a combination of population density (PD), demographic structure, winter weather conditions and low food availability (Grenfell et al. 1998; Coulson et al. 2001).

The sheep are parasitised by a number of parasitic helminth species (Wilson et al. 2004), as well as ectoparasites and 13 species of parasitic protozoa (Craig et al. 2007). The most prevalent parasite species in the population are the gastrointestinal strongyle nematodes Teladorsagia circumcincta, Trichostrongylus axei and Trichostrongylus vitrinus, infections of which are associated with overwinter mortality (Gulland 1992; Craig et al. 2006) and loss of condition as indicated by reduced body weight (Craig et al. 2008). Data on infection with these and less-abundant strongyle species, in the form of faecal egg counts (FECs), have been collected since 1988. The McMaster egg counting technique provides an estimate of the number of eggs per gram of faeces, and has been shown to be a good index of parasite burden in Soay sheep, both on St Kilda and elsewhere (Wilson et al. 2004). In our analyses, we used strongyle FEC as our response variable for estimating resistance to parasite infection.

(b) Data and variables
Analysis was performed on data collected between 1985 and 2006, comprising 1806 faecal samples from 227 females and 683 samples from 70 males. This does not represent the total number of FECs available because we removed a proportion of the full dataset for three reasons. First, lambs and yearlings suffer from extremely high parasite burdens before gradually acquiring immunity (Wilson et al. 2004; Craig et al. 2006), and so we excluded all FECs collected from individuals younger than the age of two. Secondly, during the history of the project, a number of experimental administrations of anthelmintics have been made, and so any samples collected less than a year after anthelmintic treatment were excluded from our analyses. Finally, we only considered individuals that had died, and for which we had complete life-history data.

Chronological age in years was included in all initial models as linear, quadratic and cubic terms, in order to test for a curvilinear effect of age on FEC. We also quantified ‘environmental’ age, which is an individual’s experience of the environment and an estimate of the amount of stress it has experienced up to the point of sampling, using two metrics. Our assumption is that conditions experienced immediately before and during a crash are more stressful than those experienced immediately following a crash because adult female sheep show a larger reduction in body weight between autumn and March in crash years (Clutton-Brock et al. 1991). The first measure of environmental age was given by the number of winter population crashes an individual has survived (figure 1), with more crashes equating to more stress. Secondly, we used a measure of environmental quality, E, which is the proportion of lambs of a cohort surviving for at least 1 year (Wilson et al. 2006). This value provides an indicator of environmental quality based on survival of lambs of both sexes. Although the factors influencing lamb survival and adult survival are not identical (Coulson et al. 2001),
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(c) Statistical analysis
To test for changes in FEC with indicators of age, we used generalized linear mixed-effect models (GLMMs), and all analyses were performed using the GLMM procedure in GENSTAT 11th edition (VSN International). We used a negative binomial error structure, in order to account for the highly overdispersed nature of parasite data, with few hosts containing the majority of parasites (Wilson & Grenfell 1997). The negative binomial distribution is described by the mean and \( k \), a term describing the extent of aggregation \( (k = \mu^2 / \sigma^2 - \mu) \), and we calculated separate values for both sexes combined \( (k = 0.344) \), females \( (k = 0.299) \) and males \( (k = 0.549) \), indicating that FEC is more uniformly distributed among males. We used a log-link function, estimated the dispersion parameter for each model and used the conditional fitting method of Schall (1991).

In all of our analyses, we included individual identity and year of collection as random effects to account for non-independence of samples taken from the same individual or in the same year. Below, we describe a preliminary model testing for sex-specific differences in patterns of FEC with ageing, and then four subsequent models, each of which were performed on data from both female and male sheep, and which attempt to identify the effects of chronological and environmental measures of ageing.

(d) Model 0
We pooled data for females and males and constructed a model designed to assess the factors affecting FEC in adults in this population. We investigated sex-specific differences in variables affecting FEC by fitting sex, season, PD, PPD, NAO, year and linear, quadratic and cubic terms for age, as well as interactions between sex and the other variables, where parentheses indicate random effects: \( \text{FEC} \sim \text{sex} \times \text{season} + \text{PD} + \text{PPD} + \text{NAO} + \text{year} + \text{age}^2 + \text{age}^3 + \text{sex} + \text{season} + \text{sex} : \text{PD} + \text{sex} : \text{PPD} + \text{sex} : \text{NAO} + \text{sex} : \text{year} + \text{sex} + \text{age}^2 + \text{sex} : \text{age}^3 + \text{ID} + \text{year} \). This initial model was simplified using the method described below to a final model, which indicated that FEC followed a quadratic trajectory with age (age est. = -0.248 ± 0.069, d.f. = 1, Wald = 43.1, \( p = 0.038 \); age\(^2\) est. = 0.024 ± 0.005, d.f. = 1, Wald = 13.49, \( p \leq 0.001 \)). There was also a significant interaction between sex and age (male est. = 0.106 ± 0.043, d.f. = 1, Wald = 6.15, \( p = 0.013 \)). Inspection of the parameter estimates reveals that FEC remains effectively constant in males aged 2 to 4, and correlated with parasitism (Morand & Poulin 1998), and so we included Village Bay August PD and previous August population density (PPD) as continuous variables. Parasitism is likely to be influenced by climatic conditions, particularly where they have an effect on host condition and survival, as they do in this population (Milner et al. 1999). The North Atlantic oscillation (NAO) is a general measure of climatic conditions, with high values indicating warm and wet weather, and low values cool and dry weather, and is commonly used in ecological studies (Stenseth et al. 2003). The winter NAO is an average of the monthly NAO values from December to March (Gibraltar–Reykjavik index) and here provides a measure of the climatic conditions during the winter before sampling. Finally, to test for any temporal trend in FEC, and to account for any interannual variation not explained by the specific variables described above, we included year as a continuous covariate in our analyses.

Figure 1. The St Kilda population inhabits a highly variable environment. The system exhibits severe interannual fluctuations in PD (black line), where open symbols show ‘crash years’, and in first-year mortality (grey line), which has varied from 21 to 98 per cent over the course of the study.

Factors that negatively influence lamb survival, such as density and winter weather, have similar effects on female sheep past their reproductive peak and smaller but detectable effects on prime-age adult survival (King et al. 2006; Coulson et al. 2008). March rainfall is negatively associated with survival in all age and sex classes (Catchpole et al. 2000). Our measure of environmental quality, \( E \), is negatively associated with PD, winter weather variables and March rainfall (A. Hayward 2009, unpublished data), indicating that environmental conditions affecting adult survival and performance are similar to those affecting senescent and prime-aged female sheep. To gain a measure of environmental stress experienced by an individual, this measure was inverted to give the proportion of lambs dying within a year, and then summed from the time of an individual’s birth until the time of sampling, giving a measure of environmental age, cumulative environmental stress (CES). As this measure accumulates with, and positively covaries with, chronological age, we required an alternative measure to predict the influence of environmental conditions across the lifespan on changes in FEC. To remove the colinearity between environmental age and chronological age, we took the mean of the yearly values of inverted \( E \) and subtracted it from each yearly value. By summing these mean-centred values from birth until the time of sampling, we obtained a measure of the quality of environment experienced over the lifespan that was age-independent, which we refer to as relative environmental stress (RES). Thus, individuals with more positive values of RES have experienced a poorer environment than individuals of the same age with a more negative RES.

An individual’s age at death (longevity) was included as a covariate in all of our analyses, in order to account for selective disappearance, the heterogeneity in survivorship of individuals that can produce misleading results in longitudinal analysis of age-specific traits (van de Pol & Verhulst 2006). Intra-annual seasonal environmental conditions are likely to have significant effects on parasite infection, and so we included a number of variables to account for this possibility. Females, in particular, experience a peri-parturient rise, an elevation of parasite burden around the time of offspring birth (Houdijk 2008). We considered season of sampling as a factor with two levels: ‘lambing’ (samples collected in April and May), and ‘other’ (all other months, chiefly August). PD is similarly influential, generally being positively
then increases, with the highest FEC in the oldest sheep at age 8. In females, FEC is predicted to initially decline with age, reaching a trough around the age of 5 or 6, before subsequently increasing from the age of 10 onwards. This result, coupled with the differences between the sexes in biology, longevity, parasite aggregation and age distribution of the data, encouraged us to separate the sexes for subsequent analyses.

(e) Model 1
Having established that age-specific changes in FEC differ between the sexes, we described the relationship between chronological age and FEC in each sex separately with a model incorporating current environmental factors and chronological age: \(\text{FEC} \sim \text{longevity} + \text{season} + \text{PD} + \text{PPD} + \text{NAO} + \text{year} + \text{age} + \text{age}^2 + \text{age}^3 + (\text{ID}) + (\text{year})\).

These models allowed us to fit sex-specific aggregation parameters to represent the differences in the distribution of FEC between the sexes.

(f) Model 2
Our second model assessed changes in FEC with the number of population crashes experienced by an individual, as a crude measure of environmental age, while controlling for chronological age. Note that \(\text{AGE}\) indicates the linear and quadratic chronological age terms in females, and solely the linear term in males, because these were the variables that emerged from model 1 in females and males, respectively: \(\text{FEC} \sim \text{longevity} + \text{season} + \text{PD} + \text{PPD} + \text{NAO} + \text{year} + \text{AGE} + \text{crashes} + (\text{ID}) + (\text{year})\).

(g) Model 3
Thirdly, we employed our cumulative measure of environmental age, CES, as an alternative to the number of population crashes experienced, in order to further assess changes in FEC with environmental age, while controlling for chronological age: \(\text{FEC} \sim \text{longevity} + \text{season} + \text{PD} + \text{PPD} + \text{NAO} + \text{year} + \text{AGE} + \text{CES} + (\text{ID}) + (\text{year})\).

(h) Model 4
Finally, to assess the influence of environmental experience on changes in FEC with chronological age, we used a model with an interaction between RES and chronological age: \(\text{FEC} \sim \text{longevity} + \text{season} + \text{PD} + \text{PPD} + \text{NAO} + \text{year} + \text{AGE} + \text{RES} + \text{AGE} : \text{RES} + (\text{ID}) + (\text{year})\).

All initial models were simplified until only significant variables, or those involved in significant interactions, remained. Significance of fixed effects was assessed using Wald statistics and associated conditional \(p\)-values with the appropriate degrees of freedom.

3. RESULTS

(a) Model 1
In female sheep, there was a significant quadratic effect of age on FEC (est. = 0.025 ± 0.001SE, Wald = 19.55, d.f. = 1, \(p \leq 0.001\); figure 2), indicating a decline in FEC from the age of 2 until the age of 5, followed by a rapid increase in later life. Male sheep, on the other hand, showed a significant linear increase in FEC from the age of 2 onwards (age est. = 0.127 ± 0.036, Wald = 12.54, d.f. = 1, \(p \leq 0.001\); figure 2). Hence, there is evidence to suggest that Soay sheep underwent a senescent decline in the ability to resist parasite infection, but that this decline contrasts between sexes, as predicted by the preliminary results from model 0.

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Finally, an interaction model attempting to identify an effect of environmental experience on age-specific changes in FEC yielded a significant interaction between age and RES in females (est. $= 0.052 + 0.021$, Wald $= 6.36$, d.f. $= 1$, $p = 0.012$; figure 4), indicating that the change in FEC with age changes from negative to positive with increasing stress suffered. Therefore, at low stress, FEC decreases with age, while at high stress it increases with age. The trajectory of age-specific changes in FEC with age is, therefore, dependent on an individual's experience of the environment over its life history. In males, the interaction between chronological age and RES was non-significant (est. $= 0.125 + 0.103$, Wald $= 1.49$, d.f. $= 1$, $p = 0.223$), suggesting that FEC in males is independent of environmental conditions experienced over the lifespan.

(d) Model 4
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(e) Other variables
Tables 1 and 2 show other variables that were found to influence FEC in all models in females and males, respectively. Both sexes experienced significantly higher FEC during the lambing season and following winters with high NAO values, indicating warmer and wetter weather. Longevity was negatively associated with FEC in both females and males, indicating that longer lived sheep generally exhibit lower FEC and justifying our attempts to control for selective disappearance. Finally, previous summer's PD was positively associated with FEC in females, but not males, indicating that transmission events occurring prior to winter may influence worm burden during the following year. This demonstrates that specific environmental effects influence parasitism and that simply accounting for interannual variation by including year as a covariate or random effect may not be sufficient in this respect.

4. DISCUSSION
We have presented results showing that, as predicted by previous work on immunosenescence, feral Soay sheep experience declining ability to resist parasite infection as they age chronologically. We have also shown that an alternative measure of ageing, environmental age, also predicts an increase and that chronological age alone is insufficient to describe senescence in this context. Finally, we have demonstrated that the nature of changes in parasitism with age is highly dependent upon the environmental conditions individuals experience across their life histories.

Many life-history traits measured in wild populations can be well explained as a quadratic function of chronological age, with an improvement in the trait from early life until a peak in 'prime age', followed by a senescent decline in later life (Jones et al. 2008). The bulk of studies of immunosenescence either compare age classes (e.g. Saino et al. 2003) or show a linear decline in immunological parameters with age (e.g. Haussmann et al. 2005; Palacios et al. 2007), which therefore contrast with the
fixed effects

| variables | estimate | SE | d.f. | Wald  | p-value |
|-----------|----------|----|-----|-------|---------|
| intercept | 1.193    | 0.128 | 1 | 15.03 | <0.001 |
| longevity | -0.113   | 0.027 | 1 | 0.67 | 0.413 |
| season    | -1.438   |       | 1 | 17.50 | <0.001 |
| lambing   | 0.000    | 0.079 | 1 | 297.86 | <0.001 |

random effects

| variables | estimate | SE | d.f. | Wald  | p-value |
|-----------|----------|----|-----|-------|---------|
| ID        | 0.500    | 0.079 | 1 | 2.56 | 0.114 |
| year      | 0.136    | 0.068 | 1 | 12.59 | <0.001 |

quadratic form described in studies of other traits. A decrease in assayable immune parameters does not necessarily predict an increase in parasitism with senescence because an optimal immune response is not necessarily the strongest possible (Viney et al. 2005), but in both female and male sheep, we show that there is an increase in parasitism with chronological age, suggesting senescence in the efficiency of the immune response to helminth infection. Moreover, it appears that the age-related increase in FEC begins from age 8 in females and age 5 in males (figure 2). This represents data on 93 different females (41% of the individual females in our dataset) and 31 different males (44% of individual males in our dataset), indicating that a substantial proportion of individuals surviving to adulthood reach an age at which they experience increasing parasite burden as they get older. This is, as far as we are aware, the first longitudinal analysis of senescence-related changes in parasite infection or resistance.

Our two indicators of environmental age, number of crashes experienced and CES, both predicted an increase in FEC, and these results also hold whether or not chronological age was included in the model. This indicates that chronological age alone does not describe senescence-related changes in FEC and that incorporating a measure of environmental age in addition to chronological age can provide more information about the process of senescence.

By using RES as a relative measure of environmental age, we have shown that conditions experienced throughout life can have a profound impact upon age-specific changes in an important fitness trait, namely FEC, an estimate of parasite burden and resistance. Thus, when experiencing low levels of environmental stress, females showed an improved ability to resist parasites with age, as estimated by falling FEC. However, when experiencing relatively poor conditions over their lives, females showed a progressively faster increase in FEC with age. This shows that environmental conditions can have a profound impact upon rates of senescence. The results of analyses on males suggested that changes in FEC with chronological age seemed to be independent of RES. A possible explanation could be simply that we lacked the statistical power to detect any interaction, though this is unlikely given that standard errors were lower for males than for females. A second explanation is that the more rapid life history of males (Clutton-Brock et al. 2004) makes them less vulnerable to the cumulative effects of environmental stress because the majority may not live long enough to express its effects. Similarly, because of the lower life expectancy of males, they do not experience the same range of CES as females and so either do not express its effects or do so only weakly.

Although we cannot identify the proximate mechanisms driving these changes, we can comment in broad terms on how cumulative exposure to environmental stress may affect parasite resistance. One possibility is that experience of adverse environmental conditions has irreparable effects on physiology, which are proportional to the cumulative amount of stress suffered. For instance, limited resources in poor conditions may be shifted away from immunocompetence and into maintenance of body weight or to a developing foetus, which may explain the effects of PPD and NAO on the FEC we have shown here. Persistent experience of poor environments and parasite infection may have an adverse effect on the ability of the immune system to respond to infections in later life, as the proliferative capability of T cells becomes exhausted (Akbar et al. 2004; Vleck et al. 2007). It has also been shown that strongyle infection can cause physical damage to the sheep abomasum (Gulland 1992), and such damage accumulated over time could have adverse effects on the ability to assimilate nutrients and, therefore, maintain an effective immune system. A final possibility is that sheep experiencing poorer cumulative environments have faced greater exposure to parasites than other sheep of the same age, and so, for instance, sheep with a higher RES for a given age may simply express past exposure, rather than current state, in higher FEC. As current state depends on the past experience of environmental conditions, it would be extremely difficult to separate these effects.

This longitudinal study suggests that senescence-related changes in parasite resistance are dependent upon the environmental conditions experienced over the lifetime of an individual. We are unable here to identify the mechanistic nature of the relationship between
parasitism, ageing and the immune system, and so a fruitful avenue of future research will be to characterize immunosenescence in a longitudinally monitored natural population and to relate this to actual parasite burdens. We have used a ubiquitous indicator of environmental quality, namely the proportion of first-year mortality, and so identifying specific environmental variables that influence senescence-related changes provides a challenge for further research in this and in other systems. A direct and intuitive route from the current study would be to expand the analyses herein to investigate occurrences at different stages of the life history of individuals and their effects on ageing and parasitism. Conditions experienced during early development, either pre- or postnatally, could contribute to age-specific changes in the same way as environmental ageing. Further, parasitism during development could affect later-life changes in other life-history traits. In relatively constant environments, chronological and environmental age will be virtually equivalent because damage or stresses caused by environmental conditions will accumulate at a constant rate. Our current results indicate that in assessing any influence senescence-related changes provides a challenge for further research in this and in other systems. A direct and intuitive route from the current study would be to expand the analyses herein to investigate occurrences at different stages of the life history of individuals and their effects on ageing and parasitism. Conditions experienced during early development, either pre- or postnatally, could contribute to age-specific changes in the same way as environmental ageing. Further, parasitism during development could affect later-life changes in other life-history traits. In relatively constant environments, chronological and environmental age will be virtually equivalent because damage or stresses caused by environmental conditions will accumulate at a constant rate. We thank the National Trust for Scotland and Scottish Natural Heritage for permission to work on St Kilda, and the Royal Artillery Range (Hebrides) and QinetiQ for logistical support. We especially thank D.A. Elston and R.W. Payne for statistical advice, and D. H. Nussey, T. Coulson, A. L. Graham, M. Festina-Bianchet, L. Raberg and an anonymous reviewer for helpful discussion and/or comments on the manuscript. We also thank the many previous members of the project and all the volunteers who have collected field data, and T. H. Clutton-Brock who conceived the project. The long-term data collection on St Kilda has been funded by the Natural Environment Research Council, the Welcome Trust, the Biotechnology and Biological Sciences Research Council and the Royal Society through grants to T.H.C.-B., J.M.P., L.E.B.K., B. T. Grenfell, M. J. Crawley, T. Coulson and S. Albon. This work presented here was funded by a Biotechnology and Biological Sciences Research studentship to A.D.H., supervised by L.E.B.K. who is supported by the Royal Society.

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