



# Asynchrony of senescence among phenotypic traits in a wild mammal population



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## ABSTRACT

The degree to which changes in lifespan are coupled to changes in senescence in different physiological systems and phenotypic traits is a central question in biogerontology. It is underpinned by deeper biological questions about whether or not senescence is a synchronised process, or whether levels of synchrony depend on species or environmental context. Understanding how natural selection shapes patterns of synchrony in senescence across physiological systems and phenotypic traits demands the longitudinal study of many phenotypes under natural conditions. Here, we examine the patterns of age-related variation in late adulthood in a wild population of Soay sheep (*Ovis aries*) that have been the subject of individual-based monitoring for thirty years. We examined twenty different phenotypic traits in both males and females, encompassing vital rates (survival and fecundity), maternal reproductive performance (offspring birth weight, birth date and survival), male rutting behaviour, home range measures, parasite burdens, and body mass. We initially quantified age-related variation in each trait having controlled for annual variation in the environment, among-individual variation and selective disappearance effects. We then standardised our age-specific trait means and tested whether age trajectories could be meaningfully grouped according to sex or the type of trait. Whilst most traits showed age-related declines in later life, we found striking levels of asynchrony both within and between the sexes. Of particular note, female fecundity and reproductive performance declined with age, but male annual reproductive success did not. We also discovered that whilst home range size and quality decline with age in females, home range size increases with age in males. Our findings highlight the complexity of phenotypic ageing under natural conditions and, along with emerging data from other wild populations and laboratory models, suggest that the long-standing hypothesis within evolutionary biology that fitness-related traits should senesce in a synchronous manner is seriously flawed.

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## 1. Introduction

The identification of genetic and environmental manipulations that extend the lifespan of laboratory model organisms has revolutionised our understanding of the ageing process and is central to modern biogerontology (Partridge, 2010). It is becoming increasingly clear that senescent declines in health and function may begin well in advance of eventual mortality in both humans and laboratory organisms (Herndon et al., 2002; Papadopoulos et al., 2002; Christensen et al., 2009; Bansal et al., 2015). A question of growing importance, especially given the continued increase in human life expectancy, is whether interventions that extend lifespan in the laboratory also extend so-called ‘healthspan’, or instead leave individuals in a frail state for longer

(Christensen et al., 2009; Bansal et al., 2015). A perhaps more fundamental biological question is to what degree senescence is synchronous across physiological systems and phenotypic traits in a given species (Promislow et al., 2006; Martin et al., 2007). Whilst influential evolutionary biologists have hypothesised that natural selection should shape senescence to be synchronous across physiological systems (Maynard-Smith, 1962; Williams, 1999), empirical data from humans and laboratory model organisms suggests that asynchrony is commonplace and that health- and life-span are readily uncoupled (Herndon et al., 2002; Martin et al., 2007; Christensen et al., 2009; Bansal et al., 2015). However, the benign and protected conditions experienced by laboratory model organisms and modern human societies are associated with lifespans hugely in excess of those observed under natural conditions. To understand how patterns observed in the laboratory generalise to more challenging environments and how natural selection has shaped the multifaceted process of senescence, we require studies that investigate patterns, causes and consequences of synchrony of senescence in the wild.

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Age-related declines in survival probabilities and reproductive performance are widely observed in wild vertebrates (Nussey et al., 2013). Investigation of the causes of the dramatic variation in ageing observed among species, populations and individuals in nature could offer important insights into the biology of ageing (Nussey et al., 2013; Jones et al., 2014). To date, the predominant focus of studies of senescence in the wild has been on those traits most proximate to fitness (i.e. survival and fecundity), but efforts to measure other salient phenotypic traits (e.g. body mass, secondary sexual characters, parental investment, ranging behaviour) and markers of relevant physiological processes (e.g. endocrine function, sarcopenia, oxidative stress, telomere length) are rapidly increasing (Nussey et al., 2013). Within this literature, there is mounting evidence for both differences in ageing rates between the sexes and asynchrony among phenotypic traits within sexes in the way they change with age in later life (Nussey et al., 2013). The evidence includes: reproductive cessation well before the end of life in some female mammals (Packer et al., 1998; Ward et al., 2009); evidence from a range of vertebrates for asynchrony of senescence among maternal traits associated with successful reproduction (Nussey et al., 2009; Evans et al., 2011; Massot et al., 2011; Hayward et al., 2013); asynchronous senescence among male secondary sexual traits and male reproductive performance (Nussey et al., 2009; Evans et al., 2011; Kervinen et al., 2015). Furthermore, some studies have observed so-called 'terminal declines' in traits associated with fitness, which are to some degree age-independent and occur over the period immediately preceding death (Martin and Festa-Bianchet, 2011; Nussey et al., 2011; Hammers et al., 2012). Conceivably, phenotypic traits or physiological measures could follow a progressive decline with chronological age, an age-independent and more sudden decline, or a combination of the two. Were declines with chronological age to predict phenotypic variation in later adulthood better than age-independent declines in relation to time to death, it suggests a physiological system selected to be maintained for a set period of time, with weaker selection beyond this. However, if age-independent declines provide a better fit to data than chronological age, it would suggest individual variation in the onset and rate of physiological deterioration. It should be noted, however, that age and time to death are typically confounded and their statistical separation can be challenging (Martin and Festa-Bianchet, 2011; Nussey et al., 2011). To date, few studies in the wild have directly compared the synchrony of senescence patterns among more than a handful of (typically reproductive) traits and thus the evolutionary basis of apparent asynchrony in trait senescence remains poorly understood.

Long-term, individual-based ecological studies provide detailed longitudinal data, commonly encompassing the entire lifespan of individuals, from relatively long-lived species. Survival, reproductive, behavioural, genetic, biometric and, increasingly, physiological data are routinely collected in an increasing number of studies (Nussey et al., 2013). Natural systems are obviously a great deal more variable than their laboratory counterparts, and environmental sources of mortality (e.g. predation, parasites, starvation) may mean that only a relatively small number of individuals survive to experience senescence. Furthermore, the so-called 'selective disappearance' of lower quality phenotypes can readily mask within-individual changes with age in studies in the wild (Nussey et al., 2008). Recent studies of ageing in the wild have sought to account for environmental variability and selective disappearance by statistical means or by decomposing change with age into component processes (van de Pol and Verhulst, 2006; Rebke et al., 2010). Here, we apply the former statistical approach to examine the synchrony of senescence among a wide range of phenotypic traits in an unmanaged population of Soay sheep (*Ovis aries*).

The long-term study of Soay sheep resident in the Village Bay area on the island of Hirta, St. Kilda, is one of the most detailed individual-based studies of a wild vertebrate population anywhere in the world. For three decades (1985 to present day), individuals in the population have been marked and followed from birth to death, with regular recapture of individuals, producing a wealth of information on age-

specific survival, fecundity, maternal reproductive performance, male reproductive behaviour, infection with parasites, ranging behaviour, and morphology (Clutton-Brock and Pemberton, 2004). The Soay sheep on St. Kilda are unmanaged and entirely free from predation. However, they experience many environmental challenges characteristic of temperate wild vertebrate systems including over-winter food limitation, thermoregulatory challenges associated with winter weather, and infection with parasites (Clutton-Brock and Pemberton, 2004). Most mortality occurs over-winter associated with interactions among these environmental pressures, and a characteristic feature of the population is that it experiences occasional severe over-winter mortality, during which the youngest and eldest appear most susceptible (Clutton-Brock and Pemberton, 2004). Although first winter mortality can be high among lambs, individuals that survive to maturity can be long-lived: females can survive up to sixteen years (mean = 5.31 years; median = 5 years) and males to eleven years (mean = 2.67 years; median = 2 years). Phenotypic traits including body mass, parasite burdens, horn size (an important secondary sexual trait in males), and home range size and quality are all known to be associated with over-winter survival or lifetime reproductive success and are thus under natural selection in this population (Hayward et al., 2011; Morrissey et al., 2012; Johnston et al., 2013; Regan et al. in review). Separate studies of the population have documented senescence, typically from around five or six years onwards, in traits including annual survival and fecundity, body mass, parasite burden, and maternal reproductive performance traits (Robinson et al., 2006; Hayward et al., 2009; Nussey et al., 2011; Colchero and Clark, 2012; Hayward et al., 2013), but no direct comparison of senescence patterns among sexes or traits has been made. Furthermore, whilst a previous study of the population found evidence that female body mass follows a pattern of terminal decline rather than a progressive decline with age (Nussey et al., 2011), broader comparisons of such patterns among other traits have not yet been made.

Here, we undertake analyses of age-related variation in twenty different traits measured in males and females during later adulthood. Our principal aims are: (1) to determine whether age-related variation is best-explained by changes with chronological age or by changes associated with time-to-death, and (2) to statistically compare ageing trajectories among functionally-linked groups of traits in order to determine the extent to which ageing rates are synchronous among traits. Available evolutionary theory predicts synchrony of senescence in fitness-related traits (Maynard-Smith, 1962), whilst empirical data on wild populations published to date suggests that some degree of synchrony is usually observed (Nussey et al., 2009; Evans et al., 2011; Massot et al., 2011; Hayward et al., 2013).

## 2. Materials and methods

### 2.1. Study population and data collection

Soay sheep are descendants of domestic sheep that were present throughout northwest Europe during the Bronze age, and probably reached the St. Kilda archipelago 3000–4000 years ago (Clutton-Brock and Pemberton, 2004). A population has lived on the island of Soay since their arrival on the archipelago, but there is compelling evidence that they interbred with the now extinct dunface breed (a precursor of modern blackface sheep) sometime in the mid-nineteenth century (Feulner et al., 2013). The largest island of the archipelago, Hirta (638 ha), was evacuated of its indigenous human population and their modern domestic stock in 1930. In 1932, 107 Soay sheep were reintroduced to the island from the neighbouring island of Soay, following which they increased to carrying capacity and have since remained unmanaged. Monitoring of the population began in 1959. Since then, there have been two periods of intensive study in the Village Bay area: 1959 to 1968 (Jewell et al., 1974) and 1985 to the present (Clutton-Brock and Pemberton, 2004). Our study uses field data collected during

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