THE EVOLUTIONARY ECOLOGY OF SENESCENCE

Measuring senescence in wild animal populations: towards a longitudinal approach

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Summary

1. A major current challenge in ageing research is to understand why senescence rates vary between individuals, populations and species in wild populations.

2. Recent studies clearly illustrate that senescent declines in key demographic and life-history traits can be observed in many wild animal systems.

3. Here, we summarize the key challenges facing researchers working to understand senescence in the wild. We concentrate on: (i) limited data availability, (ii) the substantial individual heterogeneity typical of wild populations, (iii) incomplete capture histories, and (iv) trade-offs across the life span.

4. We discuss analytical methods to overcome these challenges. We advocate the use of Capture–Mark–Recapture models to remove likely bias associated with re-sampling rates of less than one. We also illustrate that ageing trajectories may vary between different traits in wild populations. Wherever possible, researchers should examine ageing patterns in multiple traits.

5. Numerous models are available to describe the rate and shape of senescence in free-living populations, but there is currently little consensus regarding which is most appropriate in analyses of wild organisms.

6. We argue that only longitudinal studies of marked or recognizable individuals provide reliable sources of information in the study of senescence. Senescence is a within-individual process and only longitudinal studies allow researchers to separate within-individual ageing patterns from between-individual heterogeneity.

7. We examine two analytical approaches to measure ageing using longitudinal data from wild populations: a jack-knifing approach, well-suited to modelling survival probability, and a mixed-effects model approach. Both methods control for sources of between-individual heterogeneity to allow more accurate measurement of within-individual ageing patterns.

Key-words: ageing, Capture–Mark–Recapture, heterogeneity, life-history trade-offs, longitudinal data, mixed-effects models, senescence, ungulates, wild populations

Introduction

The evolutionary ecology of senescence has been the focus of a recent surge in studies of free-living animal populations. These studies build upon the evolutionary literature on ageing: the well-established body of theory to explain the evolution of senescence (Medawar 1946; Williams 1957; Hamilton 1966), and the increasingly detailed understanding of the proximate physiological and molecular mechanisms underpinning senescence in several model laboratory study organisms (Partridge & Gems 2002, 2006, 2007). However, several assumptions of the classical evolutionary theory of ageing may rarely be met in free-living animal populations (Reznick *et al.* 2004; Williams *et al.* 2006). Recent work reveals that under such circumstances, classical theoretical predictions may not apply (Abrams 1993; Williams & Day 2003; Williams *et al.* 2006). Furthermore, the handful of intensely studied model laboratory systems cannot explain the remarkable

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variation in longevity and ageing rates observed both between and within species in nature, nor elucidate how environmental variation or life-history trade-offs really influence the rate of ageing and the force of selection on senescence (Partridge & Gems 2006, 2007). Senescence will reduce individual fitness (or age-specific vital rates) amongst individuals surviving into old age (Partridge & Barton 1996), but the evolutionary and ecological importance of such declines in free-living populations is largely unknown. The recent interest in measuring senescence in life-history traits and testing evolutionary theories of ageing in free-living non-model organisms has already shed light on these important issues (e.g. Bryant & Reznick 2004; Hendry *et al.* 2004; Charmantier *et al.* 2006b).

Ultimately, our capacity to address these gaps in our knowledge relies on our ability to accurately and reliably measure senescence in wild populations. Senescence is a within-individual process caused by deterioration in molecular and physiological function. This deterioration increases an individual's probability of mortality and decreases its likelihood of successfully reproducing. A central challenge when studying free-living populations is to accurately measure either the ageing rates of specific individuals or the average ageing rate across individuals within a population. In this review, we argue that only longitudinal data sets, in which repeated measures are available for individuals across their lifetimes, are suitable for the estimation of ageing rates (Forslund & Part 1995; van de Pol & Verhulst 2006). Collecting such data from free-living populations can be logistically demanding and many potentially confounding factors can mask or emulate within-individual senescence patterns (Blarer, Doebeli & Stearns 1995; Gaillard *et al.* 2000b; van de Pol & Verhulst 2006). Here, we aim to review and assess the challenges associated with research into senescence in the wild; synthesize the approaches taken to measuring senescence to date; and describe analytical solutions to the central challenge of measuring within-individual ageing rates using longitudinal data. Throughout, we illustrate key points with unpublished examples using data from long-term individual-based studies of wild ungulates. We begin by describing four broad challenges to the accurate detection of senescence in wild populations.

The challenges

MORTALITY RATES AND SAMPLE SIZES

In free-living animal populations, annual mortality rates are often high. Wild animals experience sources of mortality (e.g. predation, starvation) that few animals in the laboratory or captivity, or humans in the Western world, have to contend with. This has lead many eminent gerontologists and evolutionary biologists to speculate that senescence should rarely or never be observed in wild populations (e.g. Comfort 1979; Rose 1991; Hayflick 2000). As Rose (1991) puts the argument, 'it is doubtful that many individuals [in free-living populations] would remain for study at the age at which laboratory

populations exhibit aging.' Whilst it is undoubtedly true that sample sizes for senescent individuals in wild populations are reduced by high pre-senescent mortality rates, a growing body of empirical research shows very palpably that declines in life-history traits in old age synonymous with senescence can be detected in wild animal populations. Table 1 shows a selection of studies of wild animals demonstrating age-related declines in a range of different traits, including probabilities of survival, fecundity or reproductive and physiological traits such as body mass, hormone levels and immune function. The list includes studies across a broad range of taxa showing marked variation in life history. Table 1 is not exhaustive and numerous studies have failed to detect senescence in wild populations (e.g. Slade 1995; Pistorius & Bester 2002). However, the list clearly exposes the suggestion that senescence is unlikely to be detected in natural populations as a fallacy. The question that remains largely unanswered is: what causes variation in the detectability and measured rate of senescence in different traits in wild populations?

High rates of mortality in wild populations present problems of statistical power for studies of senescence. High rates of mortality inevitably mean that far lower numbers of individuals will be alive, and therefore available for sampling, in the eldest relative to the youngest age classes. The degree to which the magnitude of the mortality rate limits power to detect and model senescence will vary substantially between study systems. For example, a recent study of a Swedish population of collared flycatchers (*Ficedula albicollis*), a passerine bird experiencing relatively high annual mortality, revealed senescent declines in annual fitness from 5 years of age onwards in females (Brommer, Wilson & Gustafsson 2007). Because only around 7% of adult females survived to this age, an enormous sample (4992 females marked at birth) collected over 25 years was required to detect senescence and model causes of individual variation in senescence rates in this species (Brommer *et al.* 2007). On the other hand, many long-lived vertebrate species (such as ungulates, seabirds, turtles, bats and marine mammals) show relatively low adult mortality rates, with the onset of senescence in survival delayed until many years after maturity (e.g. Weimerskirch 1992; Gaillard *et al.* 1993). In a population of red deer (*Cervus elaphus*) in Scotland, the proportion of adult females surviving into senescent age classes was an order of magnitude higher than in the flycatcher study. Of 328 female deer that survived to maturity (3 years old), 70% survived to the age at which senescent declines in performance began (9 years old; Nussey *et al.* 2007a).

Mortality rates have bearing not just on the statistical power of studies of senescence, but also on theoretical predictions regarding the force of selection in old age and hence future evolutionary trajectories of senescence (Williams 1957; Hamilton 1966). Williams (1957) predicted that populations experiencing increased 'extrinsic' mortality risk should evolve more rapid senescence rates. Laboratory and comparative studies have tested the prediction with mixed success (e.g. Promislow 1991; Ricklefs 1998; Stearns *et al.* 2000; Reznick *et al.* 2004). It has recently been argued that the assumptions

Table 1. Examples of studies of wild animal populations demonstrating declines in life-history traits in old age consistent with senescence. The table is not intended to be an exhaustive list, but rather to illustrate the accumulating evidence from a wide variety of different traits across a wide range of animal taxa for senescent declines in wild populations

Trait	Technique	Function	Species	References
Survival				
Mortality risk	ML	W	*Protopiophila litigate*	Bondurianksy & Brassil 2002
Mortality risk	ML; PH	G; W	*Oncorhynchys nerca*	Morbey *et al.* 2005
Mortality risk	AFT; PH	W	*Aphelocoma coerulescens*	Fox *et al.* 2006
Survival probability	CMR	Age	*Ovis aries*	Catchpole *et al.* 2000
Survival probability	CMR	Age	*Poecilia reticulata*	Bryant & Reznick 2004
Survival probability	CMR	Age	*Lacerta vivipara*	Ronce, Clobert & Massot 1998
Survival probability	CMR	Lt-L	*Cervus elaphus*	Moyes *et al.* 2006
Survival probability	CMR	G; W	*Capreolus capreolus*	Gaillard *et al.* 2004
Reproductive life-history traits				
Probability of reproducing	TM	Lt-Q	*Dama dama*	McElligott *et al.* 2002
Annual reproductive performance	ML	Q	*Accipiter nicus*	Newton & Rothery 1997
Annual fecundity	GLMM	Lt-Q	*Cervus elaphus*	Nussey *et al.* 2007a
Offspring birth mass	GLMM	Q	*Halichoerus grypus*	Bowen *et al.* 2006
Breeding date	GLMM	Q	*Uria aalge*	Reed *et al.* 2008
Arrival time at breeding grounds	ANOVA	Age	*Hirundo rustica*	Moller & De Lope 1999
Other traits				
Adult body mass	ML	Q	*Ovis canadensis*	Bérubé *et al.* 1999
Dispersal behaviour	GLMM	Age	*Sula nebouxii*	Kim *et al.* 2007
Foraging performance	ANOVA	Age	*Thalassarche chrysostoma*	Catry *et al.* 2006
Ectoparasite burden	ANOVA	Age	*Hirundo rustica*	Moller & De Lope 1999
Humoral immune response	ANOVA	Age	*Ficedula albicollis*	Cichon *et al.* 2003
Corticosterone levels	GLM	Age	*Diomedea exulans*	Angelier *et al.* 2007

Abbreviations: *Technique*: ML, maximum likelihood-based linear or nonlinear curve fitting to age-specific trait averages; PH, proportional hazards model; AFT, accelerated failure time model; CMR, Capture–Mark–Recapture model; TM, multi-state transition model; ANOVA, simple analysis of variance; GLM, generalized linear model; GLMM, generalized linear mixed-effects model. *Function*: Age, age class model; G, Gompertz; W, Weibull; L, linear; Q, quadtratic; Lt-L, logit-linear; Lt-Q, logit-quadratic.

underlying this prediction are overly simplistic and are almost certain to be violated in free-living populations (Williams *et al.* 2006). Changing these assumptions can markedly alter how theory predicts senescence should evolve (Abrams 1993; Williams & Day 2003). In practice, it is extremely difficult to separate (or even define) the extrinsic and intrinsic forces driving senescent declines in mortality or reproductive performance in wild populations (Williams & Day 2003; Williams *et al.* 2006). Most often the causes of mortality in such studies are unknown. Even when causes of death can be determined, it is likely that the intrinsic deterioration associated with senescence will interact with extrinsic mortality risks so as to make their separation unfeasible (Williams & Day 2003; Reznick *et al.* 2004; Vaupel *et al.* 2004). For example, older individuals may be at greater risk from predation (e.g. Festa-Bianchet *et al.* 2006; Wright *et al.* 2006). Similarly, extremely rapid declines in life-history traits just prior to death may reflect terminal illness rather than senescence (Coulson & Fairweather 2001), although the likelihood of contracting such an illness may increase with age. The distinction between 'intrinsic' and 'extrinsic' contributions to mortality may not be useful in most field studies, where decompositions of senescence into these components is, at best, challenging, and likely impossible (see Ricklefs 2008 for an alternative view).

CORRECTING FOR INDIVIDUAL HETEROGENEITY

Individuals dying during a given period may not represent a random sub-section of a population (Vaupel, Monton & Stallard 1979; Vaupel & Yashin 1985). The importance of variation in any individual-level component of mortality risk was first noted by demographers, and this component has been termed 'frailty' and was assumed to be constant with age (Vaupel *et al.* 1979; Vaupel & Yashin 1985). If individuals with high frailty are more likely to die young, the average frailty of a cohort will decline with age (Vaupel *et al.* 1979). Consequently, even if within-individual mortality risk increases with age, the age-specific mortality estimated at the cohort or population level could actually plateau or decrease with age as low frailty individuals compose a larger and larger proportion of survivors (Vaupel *et al.* 1979). This individual heterogeneity in mortality risk can explain the puzzling decreases in mortality risk in extreme old age observed in large cohort experiments on fruit flies and nematode worms (Carey *et al.* 1992; Partridge & Mangel 1999).

Ageing is a within-individual process and the accurate measurement of within-individual changes in phenotype across ages is therefore crucial to its study. However, disentangling the contributions of between-individual phenotypic heterogeneity from the within-individual ageing process in wild

populations has proved challenging (Vaupel & Yashin 1985; van de Pol & Verhulst 2006). Heterogeneity in mortality risk is likely to be prevalent in wild populations for a variety of genetic and environmental reasons. It has the potential to mask patterns of senescence when measured among individuals at the cohort or population level. Since mortality can, by definition, only be observed once per individual, separating the within- and between-individual sources of variation in mortality is, strictly speaking, impossible. However, one can model frailty distributions, based on certain assumptions, and attempt to measure ageing in mortality risk at the within-individual level (see 'Dealing with individual heterogeneity' section).

Between-individual variation is also frequently observed in traits other than survival and may have important ecological and evolutionary implications (van Noordwijk & de Jong 1986; Forslund & Part 1995). An individual's average phenotypic performance often covaries with longevity or age at maturity in wild populations (Bérubé, Festa-Bianchet & Jorgenson 1999; Reid *et al.* 2003; Weladji *et al.* 2006). This will generate heterogeneity in the phenotypic composition of different age classes and potentially mask the pattern of within-individual ageing observed at the population level (Curio 1983; Reid *et al.* 2003; van de Pol & Verhulst 2006). We can illustrate the issue using 581 annual body mass measurements from 205 female roe deer born between 1975 and 1996 in Trois Fontaines, France (Gaillard *et al.* 2000b). Females were separated into four age classes: 2, 3, 4–10 and > 10 year olds (following Gaillard *et al.* 2000a). Females measured more than once in an age class were assigned their median mass in that class. Females that were last measured at > 10 years were, on average, heavier than females that were last measured in middle age (4–10 years; $t_{(df=489)} = 3.43$, $P < 0.001$; Fig. 1a). The eldest age class was therefore comprised of females that were heavier than the population mean; this heterogeneity will mask within-individual declines in body mass at the cross-sectional level. Figure 1b (filled squares) shows the mean body mass of females in each age class: there is no evidence of a significant decline from the 4–10 year old age class to the > 10 year old class ($t_{192} = 0.81$, $P = 0.42$). However, the repeated measures available on females allow us to also directly assess within-individual changes in mass between age classes. Changes in mass assessed from females measured in consecutive age classes revealed that females actually lost an average of 1.56 kg (± 0.39 SE; $t_{28} = 4.06$; $P < 0.001$) between the middle and eldest age classes (Fig. 1b, open trianges). Individual heterogeneity can totally mask senescence when measured using cross-sectional age-specific means (Bérubé *et al.* 1999; Cam *et al.* 2002; van de Pol & Verhulst 2006; see also Wilson, Charmantier & Hadfield 2008 for further discussion of implications of heterogeneity for quantitative genetic studies).

SAMPLING ERROR AND DETECTION PROBABILITY

Senescence in wild populations has been assessed using two very different types of information: cross-sectional and
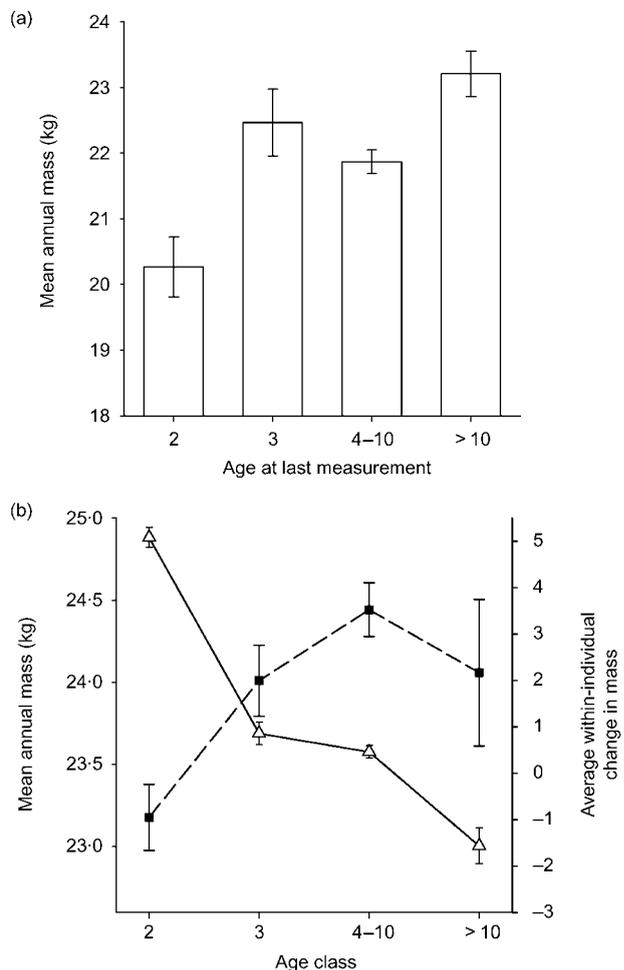

Fig. 1. Cross-sectional and longitudinal ageing patterns of body mass of females in a wild population of roe deer in Trois Fontaines, France. (a) Average individual body mass across lifetime for females of different ages at last weighing (with SEs). (b) Plots of body mass changes with age: cross-sectional average body mass for each age class with SE bars (filled squares, left y-axis) and estimates of within-individual change across age classes for females measured at consecutive ages with SE bars (open triangles, right y-axis).

longitudinal data. Most early studies were based on cross-sectional (or transversal) life tables in which individuals are sampled only once, usually at death (Deevey 1947; Spinage 1972). Such analyses provided the first broad picture of age-specific mortality (e.g. Caughley 1966) and were subsequently used to assess senescence patterns in wild animal populations (Nesse 1988; Promislow 1991; Ricklefs 1998; Mysterud *et al.* 2001). This approach, however, relies on several assumptions that are unlikely to be met (Gaillard *et al.* 1994). Life-table models of ageing assume a stationary demography over the study period, which is rarely likely to be true in free-living populations (Festa-Bianchet, Gaillard & Côté 2003; Coulson *et al.* 2006). They also rely on an accurate means of estimating the age of recovered individuals (Vincent *et al.* 1994), and assume that age-specific carcass recovery (for mortality-based life-tables) or detection (for survival-based life-tables)

probabilities are equal across individuals (Caughley 1966). Because most of these assumptions are typically violated, we contend that reliable conclusions about senescence patterns in free-living populations cannot be drawn from cross-sectional data.

The second type of data collected on wild populations involves the longitudinal monitoring of recognizable individuals, ideally from birth to death. This approach avoids most of the assumptions implicit in transversal approaches. However, in most studies of wild animals, the life-history traits of all individuals are not measured at each age simply because not all individuals are caught or observed each year. In such conditions, the number of animals at risk of mortality at a given age (R_a) and the number alive at the next age (A_{a+1}) are not known exactly. To account for the 'unseen' proportion of the population, a probabilistic approach such as Capture–Mark–Recapture (CMR) is required (Lebreton *et al*. 1992). In the handful of studies of wild animals where detection probabilities are almost one, such considerations do not apply (McDonald, Fitzpatrick & Woolfenden 1996; Bonduriansky & Brassil 2002; Catchpole *et al*. 2004). Where detection probabilities are less than one, but do not vary with age or among years, the ratio $A_{a+1} : R_a$ still provides an unbiased estimate of age-specific survival. However, variation in capture rates or re-sighting probabilities between years, seasons, sex and age classes, and social or reproductive states are common in studies of wild animals. For instance, changes in sampling effort can result in widely varying capture and re-captures rates (Gaillard *et al*. 2000b), and annual variation in re-sighting probabilities have been reported for ibex (*Capra ibex*; Toïgo *et al*. 2007), isard (*Rupicapra pyrenaica*; Loison *et al*. 1999) and mouflon (*Ovis gmelini*; Cransac *et al*. 1997). Likewise, young and adults often differ markedly in capture rates, young being generally easier to catch than adults (Gaillard *et al*. 1997; Cohas *et al*. 2007). Both social status (Cohas *et al*. 2007) and reproductive status (Catchpole *et al*. 2004) are also known to influence detection probability. Ignoring variations in detection rates can lead to biased age-specific survival estimates, and thereby biased estimates of both the onset and rate of senescence (Lebreton *et al*. 1992; Gaillard *et al*. 2000b).

LIFE-HISTORY TRADE-OFFS

Life-history theories of the evolution of ageing, including antagonistic pleiotropy and disposable soma theories, predict trade-offs between investment in reproduction in early life and survival, performance or rate of senescence in later life (Williams 1957; Kirkwood & Holliday 1979; Partridge & Barton 1996). Several studies of human and wild animal populations have provided empirical support for these predictions (Westendorp & Kirkwood 1998; Orrell & Belda 2002; Reid *et al*. 2003; Carranza *et al*. 2004; Bowen *et al*. 2006; Descamps *et al*. 2006; Nussey *et al*. 2006, 2008; Charmantier *et al*. 2006b; Reed *et al*. 2008). However, as with all life-history analyses of trade-offs, several factors could confound a possible functional relationship between early reproduction and longevity or any measure of senescence in survival or reproductive output. For example, individual heterogeneity

in resource acquisition could mean that some individuals perform consistently better than others. This would lead to positive correlations between early and late life performance at the phenotypic level and mask underlying genetic trade-offs between early and late life reproduction (van Noordwijk & de Jong 1986). Environmental variation may also reduce the detectability of early- vs. late-life trade-offs. An analysis of historical data for humans in Germany showed that the predicted trade-off between longevity and lifetime number of children only occurred when economical status was accounted for, with the poorest social groups suffering more costs (Lycett, Dunbar & Voland 2000). The trade-offs predicted by life-history theories of senescence may be less detectable when resources are plentiful (Ricklefs & Cadena 2007).

Life-history trade-offs may also confound studies of survival senescence (Blarer *et al*. 1995). For example, in age-structured populations life-history theory predicts that individuals should increase their reproductive effort as they age because reproductive value declines with increasing age after the first reproduction (Williams 1966; Schaffer 1974). Evidence for increasing allocation of resources to reproduction with age in wild populations is limited (Mysterud, Solberg & Yoccoz 2005; Velando, Drummond & Torres 2006; Descamps *et al*. 2007). However, a 'terminal investment' strategy could mask intrinsic senescent declines in reproductive performance if reproductive effort was increased at the expense of reduced survival probability. Similarly, where short-term trade-offs between reproductive investment and survival occur, increased investment in reproduction late in life would result in an increase in mortality risk driven by allocation strategy rather than senescent deterioration (Blarer *et al*. 1995; Bonduriansky & Brassil 2002).

Life-history theory predicts age-dependent changes in resource allocation that may interact with or be independent of the process of senescence and the integration of life-history theory within studies of ageing in the wild remains an important challenge.

Meeting the challenges: analysis of senescence patterns in wild animal populations

Longitudinal studies clearly are the most powerful approach to studying senescence in the wild. However, even when all individuals in a population are monitored continuously from birth to death, detecting and describing within-individual ageing patterns in free-living systems is challenging. In this section, we discuss issues relating to statistical power, the selection of traits for analysis and the functional form used to describe ageing patterns in field studies. A key challenge for field studies is to harness the power of longitudinal data sets to generate reliable predictions of within-individual ageing rates, whilst controlling for sources of heterogeneity. We present and illustrate two analytical approaches: the first predicts an individual's age-specific survival probabilities based on its phenotype; the second uses a mixed-effects model framework to separate between- and within-individual components of age-dependent variation in life-history traits.

STATISTICAL POWER

The statistical power to detect and model senescence rates will depend on both study effort and the life history and mortality rates of the focal population. The number of individuals sampled and monitored from birth and the length of the study period are crucial. As discussed above, the adult mortality rate, dispersal rates, age at maturity and age at onset of senescence of the study population will also determine the sample size available for senescent age classes. It will be particularly difficult to detect senescence in small, short-lived, highly dispersive taxa, where it is difficult to follow marked individuals from birth to death or to estimate the age of individuals at first capture (Slade 1995; Bonduriansky & Brassil 2002; Muller *et al*. 2004). This has not stopped researchers from successfully undertaking longitudinal studies on amenable species in the wild (e.g. Bonduriansky & Brassil 2002, 2005), or from developing novel methods of estimating the age structure of animals captured in the wild (Muller *et al*. 2004). Longer-lived species which experience relatively low adult mortality, such as large ungulates and colonial seabirds, will yield more powerful data for investigating changes in life-history traits in old age. However, these species may show a late onset of senescence and require data collected over many decades. Ultimately, it is important that any study of senescence in the wild applies analytical techniques that account for the inevitably declining sample size with age (Slade 1995). Several researchers have advocated the use of weighted regression (e.g. Promislow 1991; Jones *et al*. in press), but the problem is typically accounted for within the statistical frameworks applied in studies listed in Table 1 (e.g. maximum likelihood-based survival analyses; CMR models; GLMs).

WHICH TRAIT TO MEASURE?

Studies of senescence in free-living populations should aim to measure longitudinal ageing patterns in as many life-history traits as possible. Most demographic, ecological and evolutionary studies of senescence have focused on measuring patterns of age-related increases in mortality risk (or equivalently decreases in survival probability), also known as actuarial senescence. However, the strength of natural selection in old age, depends on age-specific trajectories in both survival probability and reproduction (Williams 1957; Partridge & Barton 1996). As well as facilitating a deeper evolutionary understanding of senescence, measuring senescence in several life-history traits can allow researchers to discount 'terminal investment' explanations for late-life declines in survival probability. As discussed above, a decrease in survival probability alone could be ascribed to either physiological deterioration of the soma (senescence) or to trade-offs associated with increased reproductive investment in late life (Pianka & Parker 1975; Blarer *et al*. 1995). Studies demonstrating simultaneous declines in both reproduction and survival in wild populations argue strongly for the effect being due to senescence (Bonduriansky & Brassil 2002; Jones *et al*. in press). Although research into senescence has increasingly incor-
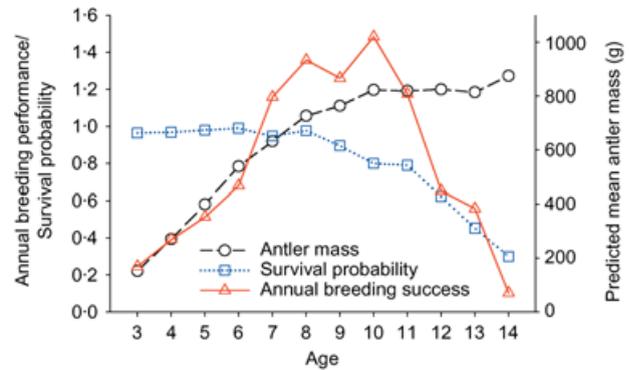

Fig. 2. Ageing patterns differ between traits in male red deer in the North Block study area, Isle of Rum, Scotland. The graph shows age-specific predicted values for survival probability (squares); annual breeding performance (triangles) and antler mass (circles). Age-specific survival probabilities were estimated using Capture–Mark–Recapture analysis (in Catchpole *et al*. 2004). Age-specific predictions for the other two traits were from generalized linear mixed-effects models including individual as a random effect, measurement year as a fixed-effect factor and age at last reproduction as a fixed covariate using data from males born between 1970 and 1996.

porated analyses of both survival and annual fecundity, it is also very important to note that fecundity alone may represent a relatively poor predictor of an individual's realized fitness. Parental condition and parental care are likely to vary with age in the wild, and thus influence the survival prospects or later performance of their offspring (Nussey *et al*. 2007a; Pavard, Sibert & Heyer 2007). Empirical and indeed theoretical investigation of the evolutionary and ecological consequences of such parental age effects on the evolution of senescence remains limited.

To assess the evolutionary and ecological effects of senescence in free-living populations, it is important to measure age-specific survival probabilities and reproductive performance simultaneously. Table 1 clearly shows that senescence can be detected across a wide range of life-history traits in wild animals. To illustrate that senescence may vary among traits, we will consider phenotypic ageing patterns from a long-term study of red deer on the Isle of Rum, Scotland (Fig. 2; see also Kruuk *et al*. 2002; Catchpole *et al*. 2004). Male red deer on Rum show declines in both survival probability and annual breeding performance (number of offspring sired) in older age but these declines commence at different ages (around 8 and 11 respectively; Fig. 2). At the same time, although male red deer cast and re-grow their antlers each year and average adult antler mass is an important determinant of lifetime fitness, mean antler mass shows no evidence of senescence (Fig. 2; Kruuk *et al*. 2002). In contrast, a recent study of wild roe deer did reveal declines in both absolute and relative antler size in old age classes, (Vanpé *et al*. 2007). This raises the question of why trait-specific ageing trajectories vary between populations or species. Life-history differences are likely to be important here, and the male mating tactics of red deer compared to roe deer may explain this particular

difference. A key challenge in the study of senescence in the wild is to understand when and why ageing trajectories vary between life-history traits within study populations, as well as within focal traits between different species.

MODELLING SENESCENCE RATES

There is considerable debate in the demographic literature about the functional form of senescent declines in survival probability with age. Research on free-living populations has yet to yield strong conclusions regarding which functions best describe senescence in different life-history traits (Table 1; see also Ricklefs (this issue)). Human demographers, and evolutionary biologists working on laboratory organisms, have modelled actuarial senescence using either Gompertz or Weibull functions of age, following well-established demographic theory (Zens & Peart 2003). Both models assume an increase in mortality risk from maturity onwards, but the rate of this increase and its relationship with initial mortality risk differ (Ricklefs 1998; Ricklefs & Scheuerlein 2002). The relative power of these two models to explain mortality data has been used to test hypotheses about senescence (see Ricklefs this issue). A few longitudinal studies of free-living animal populations have compared these models to models of constant mortality risk across ages (McDonald *et al*. 1996; Bonduriansky & Brassil 2002; Gaillard *et al*. 2004; Morbey, Brassil & Hendry 2005; Fox *et al*. 2006; Toïgo *et al*. 2007). Whilst these results clearly show that mortality risk increases with age, they provide no compelling support for either model. Indeed, a study of survival across the breeding period in semelparous salmon suggested that the best fitting model of senescence may vary across years or populations (Morbey *et al*. 2005). It is also worth noting that whilst Gompertz and Weibull models of actuarial senescence are widely used, they are not based on any fundamental biological theory and any biological interpretation placed on the shape of a best-fitting mortality curve cannot exclude other possible mechanisms or explanations (Partridge & Mangel 1999).

Human demographers and evolutionary biologists working on model laboratory systems can follow very large cohorts of individuals continuously from birth to death (Vaupel *et al*. 1979; Carey *et al*. 1992). Field studies of survival, as discussed above, often have re-sighting or re-capture probabilities of less than one and use CMR models (Lebreton *et al*. 1992), that can encompass a wide range of functions relating age to survival probability (Gaillard *et al*. 1993; Loison *et al*. 1999). Multi-state CMR models can also incorporate age-dependent transition probabilities between reproductive states (Nichols & Kendall 1995; McElligott, Altwegg & Hayden 2002; Tavecchia *et al*. 2005). In the simplest case, age class models have been used to show significant declines in average survival probability amongst the oldest age group (Gaillard *et al*. 1993; Catchpole *et al*. 2000). Alternatively, log- or logit-linear functions have been used to describe declining survival with age (Loison *et al*. 1999; Moyes *et al*. 2006). Recent studies have fitted Gompertz and Weibull functions (Gaillard *et al*.

2004; Toïgo *et al*. 2007) and nonparametric smoothing functions (Gimenez *et al*. 2006) within CMR frameworks. The main differences in log- or logit-linear, Gompertz and Weibull functions, however, will be manifest amongst the very oldest ages, when sample sizes are usually low in wild populations and the power to compare model fits to the data is most limited (Gaillard *et al*. 2004).

Although CMR-based studies of wild animals almost always involve the comparison of different models of age-dependence in survival (Lebreton *et al*. 1992; Loison *et al*. 1999; Bowen *et al*. 2006), there remains little consensus regarding specific models to describe senescent declines in survival (Gaillard *et al*. 2004). The same can be said of studies of ageing in life-history traits other than survival, which have typically utilized analysis of variance or GLMs to compare age groups or model linear or polynomial functions of trait changes with age (e.g. Moller & De Lope 1999; Charmantier *et al*. 2006a; Balbontin *et al*. 2007). Ultimately, environmental and genetic variation between populations could result in differences between the onset, rate and shape of senescence in free-living populations (Bryant & Reznick 2004; Morbey *et al*. 2005; Charmantier *et al*. 2006b; Nussey *et al*. 2007a; Wilson *et al*. 2007). Furthermore, no long-lived individual is likely to experience constant environmental conditions throughout its lifetime in the wild. Yet, our understanding of how environmental conditions experienced at different stages of life may influence senescence patterns is very limited (Nussey *et al*. 2007a; Wilson *et al*. this issue). Free-living populations require a flexible approach towards modelling the age at which senescent declines begins, as well as their shape and rate of decline. Nonparametric smoothing functions are a promising analytical tool to this end. These functions model age-dependent changes in life-history traits without making restrictive assumptions about the form of senescence, and can be readily implemented within GLM (through generalized additive models, Wood 2006) or CMR frameworks (Gimenez *et al*. 2006). These models can then be used to test which functions provided an adequate fit to age-dependent patterns of life-history traits (e.g. Loe *et al*. 2003; Gimenez *et al*. 2006).

DEALING WITH INDIVIDUAL HETEROGENEITY

Survival senescence: heterogeneity in frailty and within-individual patterns

An organism can only die once. Because an individual can only provide one datum on age at death, separating the between- and within-individual processes contributing to actuarial senescence is technically impossible. Whilst this means that 'individual frailty' (Vaupel *et al*. 1979) is a conceptual construct that can never be physically measured, it is certainly possible to account for sources of heterogeneity in mortality risk (e.g. early life conditions, sex, body size, social group, habitat quality or type) when assessing actuarial senescence (Vaupel & Yashin 1985; Fox *et al*. 2006). This can be achieved either by separating individuals into homogeneous groups with respect to frailty (McDonald *et al*. 1996) or
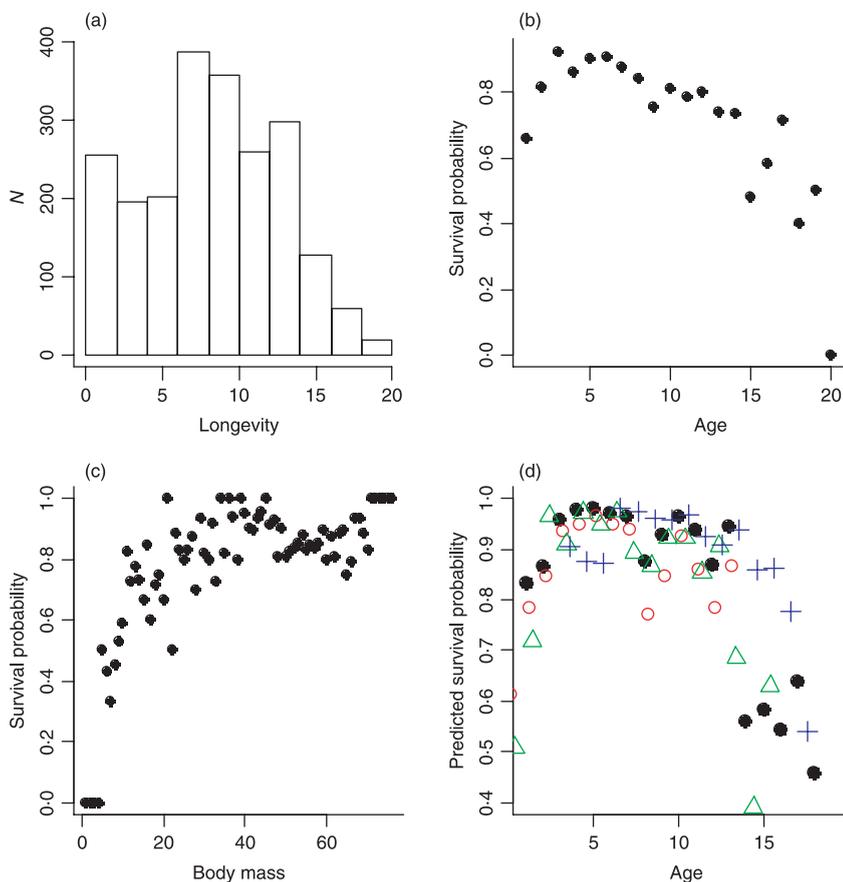
Fig. 3. Patterns of longevity and survival in female bighorn sheep at Ram Mountain, Canada as a function of age and weight. (a) The frequency distribution of longevity, (b) mean probability of survival as a function of age, (c) distribution of estimated body mass on 15 September with age, and (d) predicted individual age-specific survival probabilities with age for four females, based on estimates from a GLM with each female removed from the data set.

including these sources as covariates in survival analyses or CMR models (Loison *et al.* 1999; Morbey *et al.* 2005; Fox *et al.* 2006). 'Shared frailty' survival models allow variance in initial mortality risk between grouping levels to be assessed within accelerated failure time and proportional hazards models (e.g. Fox *et al.* 2006). These models can be used to test and account for heterogeneity in frailty associated with factors with repeated measures at each level such as parental, nest or group identity or birth cohort (Fox *et al.* 2006).

A key aim of any evolutionary analysis of senescence is to estimate within-individual ageing patterns and, ultimately, explain between-individual, between-population or between-species level variation in those patterns. An individual's somatic 'state' will be reflected in a wide range of phenotypic traits, many of which can be measured longitudinally and therefore change with age. These may include phenotypic traits such as body size or condition, immune response, bone density and dental attributes, which themselves often deteriorate with age. An estimate of individual age-specific mortality risk, and thereby individual rates of actuarial senescence, could be predicted from such phenotypic data for well characterized populations where survival patterns and numerous longitudinal phenotypic traits are measured.

We illustrate such an approach by generating predictions of age-specific survival probability for individuals using longitudinal recapture data collected between 1975 and 2004 from female bighorn sheep (*O. canadensis*) living at Ram Mountain, Alberta, Canada (Festa-Bianchet 1989). This population is closed and all living adults are uniquely marked. Data consisted of 2172 annual recaptures of 803 females. Individuals are caught and weighed repeatedly each summer. Annual body mass was standardized to reflect predicted mass on 15 September each year (following Festa-Bianchet *et al.* 1996). For simplicity of illustration, we considered only individual data for age, year of birth and annual body mass. The adult female recapture rate at Ram Mountain is 0·99 (Jorgenson *et al.* 1997), so recapture rates do not need to be modelled. We consequently modelled survival using a GLM with a binomial error structure and included age (as a factor), year of birth (factor) and body mass (covariate). Our starting GLM included these three main effects and all two-way interactions, and the most parsimonious model was selected by backwards deletion of terms using likelihood ratio test statistics to compare models. No second order interactions were statistically significant, but main effects of age ($\chi^2_{16} = 118\cdot15$, $P < 0\cdot001$), birth year ($\chi^2_{29} = 99\cdot41$, $P < 0\cdot001$) and body mass ($\chi^2_1 = 18\cdot82$, $P < 0\cdot001$) were all significant. The distribution of female longevity was bimodal, suggesting a change in survival as a function of age (Fig. 3a). A plot of age-specific survival probability confirmed this, revealing an inverted 'U' shaped pattern characteristic of ungulates (Fig. 3b; Gaillard *et al.* 2000b). The GLM also showed that survival probability increased with body mass (Fig. 3c), and showed significant variation between cohorts.

Naturally, the better the fit of a model to data and the better the behaviour of residuals, the greater confidence that these predicted survival rates are realistic. A large proportion of this data set was comprised of young females (lambs and yearlings), and it is important to stress that biological conclusions should not be drawn from this model in light of the distribution of ages. Our intention is to illustrate how a model of annual survival which incorporates age and some other longitudinally measured covariates (body mass in this case) can be used to predict within-individual age-specific survival probabilities. The predictions are based on individual-level data, but the estimates (and hence the model) are describing population level processes. The inclusion of age in the model means that an individual's age-specific probability of survival having corrected for known sources of variation (e.g. environment in birth year, body mass) can be predicted.

The model used to predict age-specific survival rates of individual x should be parameterized from a data set with individual x removed (e.g. by jack-knifing the data). This is to avoid the circularity of making predictions for an individual using data collected from that individual. This does assume that individuals are independent and that the presence of one individual does not (substantially) impact directly on other members of the population (Coulson *et al.* 2006). To illustrate this approach, we predicted survival probabilities for four bighorn females from the data set for each age at which they were alive, based on their actual annual body mass measures, birth year and age. We used estimated parameters for each female from a GLM of survival probability from which the focal female was excluded.

The age-specific predicted survival probabilities for each of the four females are shown in Fig. 3d. There was substantial variation in both the predicted survival rates across individuals, and in their predicted rates of decline in survival probability in old age (Fig. 3d). In the GLM used to predict these individual patterns, mean survival rates vary with age, and year of birth effects will be constant across a female's life. This means that the variation in predicted age-specific survival patterns in Fig. 3d must be due to different patterns of within-individual changes across percentiles of the population's body mass distribution over ontogeny, possibly as a consequence of recent reproductive effort or environmental conditions. We offer this simple example as a first step towards predicting within-individual age-specific survival trajectories in wild populations. Similar models could readily be fit using CMR techniques when re-capture probabilities are less than one, or survival analyses such as proportional hazards models. Predictions from such models can (cautiously) be treated as describing an individual's pattern of actuarial senescence, and could be used to make comparisons between species, populations living in different environments, sexes and genotypes.

Longitudinal traits: a mixed-effects model approach

Although the jack-knifing approach discussed above can be used to predict individual age-specific trajectories for any life-history trait, linear mixed-effects models (LMMs) represent a powerful alternative analytical tool to control for between-individual heterogeneity when analysing ageing patterns in longitudinally-measured life-history traits (Nussey *et al.* 2006; van de Pol & Verhulst 2006; Balbontin *et al.* 2007). Longitudinal data allow us to disentangle the effects of between-individual phenotypic heterogeneity between age classes from the within-individual changes across age that may actually reflect senescence (Cam *et al.* 2002; van de Pol & Verhulst 2006). A standard approach has been to model age-dependent changes in a longitudinally measured trait with individual identity fitted as a random effect in a LMM (e.g. Ericsson *et al.* 2001; Reid *et al.* 2003). This approach ensures that the significance of the variance in the trait of interest explained by age differences is tested at the appropriate within-individual level (Pinheiro & Bates 2000). However, a recent study of wild oystercatchers (*Haematopus ostralegus*) has shown that within-individual age-related changes in reproductive traits may be poorly estimated by simply including a random effect for individual (van de Pol & Verhulst 2006). This is because this approach does not control for between-individual 'selective disappearance' effects (van de Pol & Verhulst 2006). If individual age at maturity or last reproduction is associated with an individuals average performance in the focal life-history trait, then the average within-individual ageing pattern across the population is likely to be under- or over-estimated (e.g. Fig. 1 and 'Individual heterogeneity' section).

Previous studies have attempted to deal with this problem by analysing ageing rates within groups of individuals with similar ages at first or last reproduction (Laaksonen, Korpimaki & Hakkarainen 2002; Reid *et al.* 2003). van de Pol & Verhulst's (2006) suggested simply incorporating individual age at first and last reproduction (or trait measurement for non-reproductive traits) within a LMM framework to deal with this problem. They proposed the following basic model:

$$r_{ij} = \beta_0 + \beta_1 \cdot \text{age}_{ij} + \beta_2 \cdot \alpha_i + \beta_3 \cdot \omega_i + u_{0i} + e_{0i}$$

where r is the focal, longitudinally measured trait expressed in individual (i) at time point (j). Here, β_0 is the population-level intercept for the trait, age_{ij} refers to individual age at each measurement, and α_i and ω_i to individual age at first and last reproduction, respectively. β_1, β_2 and β_3 are slope parameters relating r with age, α and ω, respectively. u_{0i} is a random effect modelling between-individual variation in trait intercept (assumed to have a mean of zero and variance of σ_u^2) and e_{0i} is the residual variance terms (assumed to have mean of zero, variance of σ_e^2). The approach is highly flexible. The parameters for age, α and ω can easily be substituted for age classes or the model can be extended to incorporate higher order polynomial terms. Other known causes of variation in the focal trait (e.g. sex, body size, environmental conditions) can be readily incorporated as additional fixed or random effects. The approach can also model non-normally distributed traits, through the selection of a non-normal error structure and an appropriate link function and could also be applied within a GAM framework. The model described above assumes
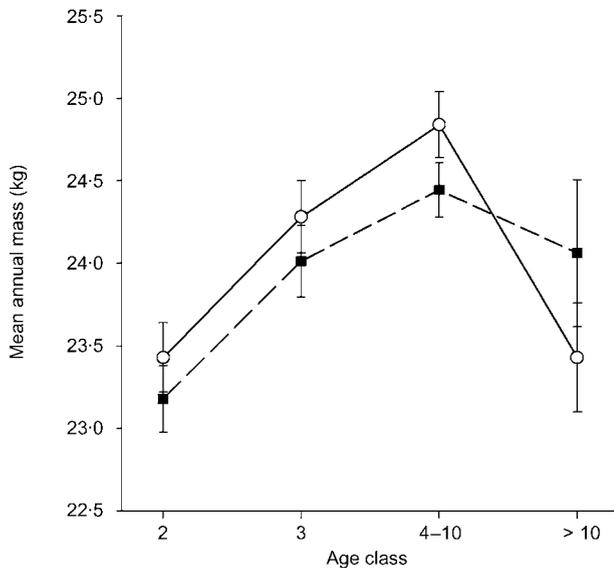
Fig. 4. Ageing patterns in body mass in female roe deer in Trois Fontaines, France, estimated using a cross-sectional (same as Fig. 1b, filled squares) and a linear mixed-model (LMM) approach (open circles). The open circles show the predicted mean body mass (with SEs) for each age class from a LMM including individual as a random effect and age class and age class at last measurement as fixed factors. This LMM approach reveals a highly significant decline in body mass between 4–10 years and > 10 year age classes, which are masked by individual heterogeneity in the cross-sectional analyses (see text).

that the relationship between ω_i (or α_i) and r_i is both linear and independent of age, however both assumptions can be readily tested and incorporated within the model by including polynomial functions of ω_i or interactions between ω_i and the age term.

We applied this LMM approach to the roe deer mass data in Fig. 1 ('Individual heterogeneity' section). The model included individual as a random effect (variance component = 2·477 ± 0·322 SE, accounting for 57% of total variance) and age at last weighing (ω_i; fitted as a four-level factor, $F_{(3,217)} = 5·40$, $P = 0·001$) and age class (age$_{ij}$; five-level factor, $F_{(4,387)} = 590·19$, $P < 0·001$). From a statistical perspective, α_i and ω_i refer specifically to the age (or age class) at which an individual first and last appears in the data set, although they can be interpreted as correlates of maturity and longevity. In analyses of senescence, controlling for effects of ω_i (between individual variance associated with age at last appearance in the data set) is likely to be much more important than α_i because most individuals will have begun breeding (or have first been measured) before the effects of senescence are manifest. Furthermore, in the Trois Fontaines roe deer populations virtually all individuals begin breeding at 2 years of age (Gaillard et al. 1998). We therefore did not fit α_i in our LMM. Predicted mean body mass at each age class from the LMM declined by 1·41 kg between the 4–10 and > 10 year-old age classes (Fig. 4), with significant differences between the predicted means in the two age classes ($t_{92} = 4·55$, $P < 0·001$). The LMM approach controls for the heavier average mass

of longer-lived females (Fig. 1a), and reveals the pattern of senescence in body mass that was evident in the within-individual analysis (Fig. 1b), but undetectable in a cross-sectional analysis (Fig. 4). The estimated change in mass between the 4–10 year-old age group and the > 10 year-old group in the LMM (open circles, Fig. 4) is very close to that estimated by an analysis of average within-individual changes between females across these age groups (LMM estimate: 1·41 kg decline; average within-individual change: 1·56 kg decline).

The LMM method has recently been used to measure senescence in several wild vertebrate populations (Nussey et al. 2006, 2007a; Balbontin et al. 2007). A recent study of wild guillemots (*Uria algae*) has shown that even where the exact age at first capture of individuals is not known, this approach can be applied by assessing reproductive traits relative to time until death of individuals (Reed et al. 2008). The approach can readily be extended to incorporate between-individual variation in ageing rates within a random regression framework (Brommer et al. 2007; Wilson et al. 2007; Nussey, Wilson & Brommer 2007b), allowing separation of genetic and environmental causes of variation in senescence (see Wilson et al. (this issue) for further discussion). Furthermore, specific environmental factors or individual properties that might be expected to influence individual senescence rates can be incorporated in these models as fixed effects and their interactions with the age terms tested (Nussey et al. 2006). Using this approach, recent studies have uncovered evidence that early life investment in reproduction is associated with increased reproductive ageing rates as predicted by life-history theories of senescence (Nussey et al. 2006; Reed et al. 2008). Modelling effects of early life history on within-individual ageing rates in this way may reduce the masking effect of between-individual variation in average performance when testing for early-late trade-offs ('Life-history trade-offs' section).

Discussion and synthesis

Studies of senescence in free-living populations need to accurately describe the average pattern of ageing within individuals, then to try to explain variation in ageing patterns between individuals. We have argued that longitudinal studies of individuals provide the only reliable data source to achieve either aim. Although cross-sectional life-history and life-table data have been frequently used in comparative studies of senescence (e.g. Promislow 1991; Ricklefs 1998), the reliability of conclusions drawn from such data is currently unclear (Gaillard et al. 1994). New statistical analyses of existing life-table data (e.g. Skalski, Millspaugh & Spencer 2005) and comparisons with longitudinal data sets are required to evaluate the conditions under which such data sets may be reliable sources of information for comparative studies of ageing in the wild.

We have presented two promising analytical approaches to estimate within-individual ageing patterns using longitudinal data. Jack-knifing to model predicted individual age-specific

trait values may prove to be a useful approach, particularly for understanding variation in actuarial senescence patterns where longitudinal data on non-survival traits are available. The mixed-effects model suggested by van de Pol & Verhulst (2006) is clearly promising. However, a simulation-based assessment of how well this approach recovers within-individual ageing patterns is definitely required, particularly where trait distributions are non-Gaussian or when the trait in question is not expressed at each age. It would also be interesting to investigate how inclusion of individual performance indicators (e.g. body mass) or shared frailty terms (e.g. nest site) within CMR or survival analyses influence estimates of actuarial senescence rates, and to further assess the utility of the predictive jack-knifing approach to modelling individual survival patterns.

Re-sighting probabilities of recognisable individuals are frequently less than one in longitudinal field studies. However, CMR and multi-state models are powerful statistical tools to account for this potential source of bias (Lebreton *et al.* 1992; Nichols & Kendall 1995), and are readily implemented using several free software packages (e.g. MARK; M-SURGE, E-SURGE). Regardless of the trait in question, there is currently little consensus about the form of senescence in survival or in other life-history traits in wild animal systems. In light of this, statistical comparison of different models of age-dependence is clearly to be favoured over the use of a model selected *a priori* (e.g. Gompertz or Weibull models). Such an approach is very well-established within the CMR literature, and is often used for GLMs (Lebreton *et al.* 1992; Burnham, White & Anderson 1995; Crawley 2002). Models of age-dependence should be tested against null models that are either fully age-dependent (e.g. Loison *et al.* 1999) or make no strong assumptions about the form of the ageing pattern (e.g. nonparametric smoothers; Bowen *et al.* 2006; Gimenez *et al.* 2006). Simulation studies to determine whether and when data sets of the type collected in the field can differentiate between ageing functions would be useful (Ricklefs & Scheuerlein 2002; Gaillard *et al.* 2004), and more studies comparing a wide array of models of age-dependence, including Gompertz and Weibull models of actuarial senescence, are warranted (e.g. Morbey *et al.* 2005; Bowen *et al.* 2006; Toïgo *et al.* 2007).

Senescence rates in free-living animals do not just vary between individuals, populations and species. There are clearly differences in the onset, rate and shape of senescence between different life-history traits (Fig. 2; Moller & De Lope 1999; Bowen *et al.* 2006). Research aimed at determining when and why senescence patterns vary between life-history traits is required. Multi-state models and multivariate mixed-effects models are extremely promising approaches that should allow to explicitly estimate patterns of covariance across ages between different life-history traits (Orrell & Belda 2002; Wintrebert *et al.* 2005; Nussey *et al.* 2008). Wider application of these techniques will undoubtedly provide new insight into how age-dependent changes in late life are associated across different traits, and what role trade-offs with early-life reproductive investment play in these differences.

The challenges involved in measuring senescence in the wild are numerous, and for some systems may be insurmountable. Rigorous analyses of longitudinal data from wild populations that reveal no age-related declines in demographic rates or life-history traits would suggest that senescence has negligible impact on the evolutionary and ecological dynamics of those populations (e.g. Slade 1995; Sparkman, Arnold & Bronikowski 2007). However, given the evidence that age-related declines in demographic rates do occur in wild populations (Table 1), studies addressing the ecological consequences of ageing in free-living systems are notably lacking in the ecological literature. Population age structure and the age of onset and rate of decline in demographic rates with age will clearly be crucial in determining the population dynamic consequences of senescence. Senescent individuals may contribute little to population growth relative to prime-age adults but consume a similar amount of resources per capita, and may be more sensitive to environmental conditions than prime-age adults. Furthermore, recent studies have suggested that environmental conditions experienced in early life may influence senescence rates in wild vertebrates (Nussey *et al.* 2007a; Reed *et al.* 2008). Clearly, senescence could have subtle but important effects on population dynamics, but very few studies have considered these to date (although see Boonstra 1994; Gaillard *et al.* 2000b).

We have shown that an array of powerful statistical tools is available to measure patterns of ageing and their ultimate causes using longitudinal phenotypic data from wild populations. Coupled with the increasing availability of physiological and molecular assays of oxidative stress, immune function and physiological state (Cichon, Sendecka & Gustafsson 2003; Angelier *et al.* 2007; Münch, Amdam & Wolschin 2008), the opportunity to develop and understand both ultimate and proximate causes of variation in ageing rates in wild organisms in their natural habitats has never been greater. We hope this review will stimulate further study of ageing patterns in wild populations at the appropriate, within-individual level.

Acknowledgements

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