RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Fluctuations in age structure and their variable influence on population growth

Sarah R. Hoy[1] | Daniel R. MacNulty[2] | Douglas W. Smith[3] | Daniel R. Stahler[3] | Xavier Lambin[4] | Rolf O. Peterson[1] | Joel S. Ruprecht[5] | John A. Vucetich[1]

[1]School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, USA

[2]Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT, USA

[3]Yellowstone Centre for Resources, Yellowstone National Park, WY, USA

[4]School of Biological Sciences, University of Aberdeen, Aberdeen, UK

[5]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

Correspondence
Sarah R. Hoy
Email: sarah.r.hoy@gmail.com

Abstract

1. Temporal fluctuations in growth rates can arise from both variation in age-specific vital rates and temporal fluctuations in age structure (i.e. the relative abundance of individuals in each age-class). However, empirical assessments of temporal fluctuations in age structure and their effects on population growth rate are relatively rare. Most research has focused on understanding the contribution of changing vital rates to population growth rates and these analyses routinely assume that: (a) populations have stable age distributions, (b) environmental influences on vital rates and age structure are stationary (i.e. the mean and/or variance of these processes does not change over time), and (c) dynamics are independent of density.

2. Here we quantified fluctuations in age structure and assessed whether they were stationary for four populations of free-ranging vertebrates: moose (observed for 48 years), elk (15 years), tawny owls (15 years) and grey wolves (17 years). We also assessed the extent that fluctuations in age structure were useful for predicting annual population growth rates using models which account for density dependence.

3. Fluctuations in age structure were of a similar magnitude to fluctuations in abundance. For three populations (moose, elk, owls), the mean and the skew of the age distribution fluctuated without stabilizing over the observed time periods. More precisely, the sample variance (interannual variance) of age structure indices increased with the length of the study period, which suggests that fluctuations in age structure were non-stationary for these populations – at least over the 15- to 48-year periods analysed.

4. Fluctuations in age structure were associated with population growth rate for two populations. In particular, population growth varied from positive to negative for moose and from near zero to negative for elk as the average age of adults increased over its observed range.

5. Non-stationarity in age structure may represent an important mechanism by which abundance becomes non-stationary – and therefore difficult to forecast – over time-scales of concern to wildlife managers. Overall, our results emphasize the need for vertebrate populations to be modelled using approaches that consider transient dynamics and density dependence and that do not rely on the assumption that environmental processes are stationary.

1 | INTRODUCTION

Much empirical research on age- or stage-structured populations has focused on understanding which age- or stage-specific vital rates have the greatest influence on fluctuations in population growth (Ezard, Becker, & Coulson, 2006; Gaillard & Yoccoz, 2003). A common technique to assess fluctuations in population growth is perturbation analyses, which account for both temporal fluctuations of age-specific vital rates and elasticities – a relative measure of how changes in a vital rate affect population growth (Caswell, 2000). In these analyses, growth rate (defined as the asymptotic λ) for year t is expressed as a function of a transition matrix (A_t) representing the age-specific vital rates, and a column vector (N_t) representing abundances for each age-class. More specifically, $N_{t+1} = A_t(N_t)$ and $\lambda_t = n_{t+1}/n_t$, where n_t is total abundance. However, because the relative abundances of individuals in each age-class may also vary across time, N_{t+1} may be expressed as $A_t(S_t n_t)$, where S_t represents the population's standing age structure or the relative abundance of individuals in each age-class. These simple expressions lead to a long known result: For a given A_t and n_t, λ_t also depends on S_t. In other words, temporal fluctuations in growth rate may arise from both fluctuations in A_t (due perhaps to density dependence or environmental stochasticity) as well as the resulting fluctuations in S_t. A population's age structure, S_t, may fluctuate considerably in response to environmental stressors, such as severe weather, predation and intraspecific competition, because those processes tend to have less adverse impacts on prime-aged individuals, compared to juveniles and senescent adults (Coulson et al., 2001; Hoy et al., 2015; Wright, Peterson, Smith, & Lemke, 2006). However, until recently, most analyses assessing population growth for vertebrate species assumed that populations are fixed at a stable age distribution (but see Gamelon et al., 2016; Haridas, Tuljapurkar, & Coulson, 2009).

When the age structure of a population deviates from the hypothetical stable age distribution, perturbation analyses – which are routinely used to inform management decisions – may not reliably indicate which vital rates contribute the most to temporal variation in population growth (Koons, Grand, Zinner, & Rockwell, 2005; Yearsley, 2004). However, relatively little is known about the extent to which the age structure of populations fluctuates under natural conditions, particularly for terrestrial vertebrates, because it is often logistically infeasible to collect the data needed to estimate age structure for free-ranging populations (but see Coulson, Gaillard, & Festa-Bianchet, 2005; Coulson, Guinness, Pemberton, & Clutton-Brock, 2004; Gerber & Kendall, 2016; Margalida, Oro, Cortés-Avizanda, Heredia, & Donázar, 2011; Payo-Payo et al., 2018; Regehr, Amstrup, & Stirling, 2006). Furthermore, direct empirical assessments of the influence of fluctuations in age structure on population

growth rate are rare (but see Coulson et al., 2005; Koons et al., 2005; Koons, Iles, Schaub, Caswell, & Hodgson, 2016). Consequently, there is value in empirically assessing temporal fluctuations in S_t and the extent to which such fluctuations explain temporal fluctuations in population growth rates.

In recent years, there has been increasing interest in developing stochastic models of growth rate that account for both fluctuations in vital rates and age structure (Caswell, 2010; Davison et al., 2010; Ezard et al., 2010; Koons et al., 2016). Nevertheless, these models have typically made two important assumptions. The first assumption is that growth is independent of density (Stott, Townley, & Hodgson, 2011); however, density dependence is a ubiquitous phenomenon in the dynamics of free-ranging populations (Bonenfant et al., 2009). The second assumption is that environments are stationary (Haridas et al., 2009), meaning that the mean and variance of environmental processes remains constant over time. Although non-stationarity and autocorrelation are not entirely independent ideas, they are distinct, insomuch as autocorrelation measures the similarity between two observations as a function of the time-lag, whereas non-stationarity indicates that properties of the time series, such as the mean and/or variance, change over time. Many species are exposed to non-stationary environments over ecologically relevant time frames (Vasseur & Yodzis, 2004). Some examples of processes that can result in environments being non-stationary are anthropogenic changes in climate and landscape use (Wolkovich, Cook, McLauchlan, & Davies, 2014).

Non-stationary environments may result in non-stationary age structure dynamics (Hastings, 2004; Koons et al., 2016; Wolkovich et al., 2014). For example, several consecutive years of stressful environmental conditions may result in low recruitment for several years running, which in turn would lead to an increase in the proportion of older individuals in the population. Such shifts in age structure are likely to affect future dynamics, especially for mammal and bird populations, because older individuals tend to have lower reproductive rates (Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013) and their survival rates are more sensitive to environmental stress compared to prime-aged individuals. Therefore, the influence of non-stationary environments on age structure and its subsequent influence on growth rates may occur with some time-lag. Nevertheless, the extent to which populations exhibit non-stationary age structure dynamics remains largely unknown, particularly for terrestrial vertebrates. Yet, non-stationarity has important implications for understanding population dynamics (Kaitala, Ylikarjula, Ranta, & Lundberg, 1997; Ranta, Lundberg, Kaitala, & Laakso, 2000; Royle, Lindström, & Metcalfe, 2005). In particular, non-stationary processes are difficult to predict because past dynamics are a poor indicator of future dynamics (Poole, 1978).

Here, we quantify temporal fluctuations in age structure and assess whether age structure dynamics showed signs of being non-stationary for four terrestrial vertebrate populations, which have all been the focus of long-term research: grey wolves (*Canis lupus*) in Yellowstone National Park (USA), tawny owls (*Strix aluco*) in Kielder Forest (England), moose (*Alces alces*) in Isle Royale National Park (USA) and elk (*Cervus elaphus*) wintering along the northern border of Yellowstone National Park. We also assess the relationship between age structure and population growth using models which account for the potentially confounding influence of density dependence.

2 | MATERIALS AND METHODS

2.1 | Study populations

All four study species are iteroparous, with vital rates that change substantially with age (see Appendix S1; Figures S1 and S2). The grey wolf population within Yellowstone National Park, USA (44°N, 110°W), has been monitored since the population was reintroduced in 1995 (Smith, Drummer, Murphy, Guernsey, & Evans, 2004). Tawny owls have been monitored in a 70-km² subsection of Kielder Forest, England (55°13′N, 2°33′W) since 1979 (Petty, 1992b). The moose population in Isle Royale National Park (47°N, 88°W) has been studied continuously since 1958 (Vucetich & Peterson, 2004). The elk population, which winters along Yellowstone National Park's northern border and adjacent areas of Montana, has been monitored since the 1930s (Houston, 1982) and studied intensively since 1995 (White, Proffitt, & Lemke, 2012).

Wolves and elk are not hunted within Yellowstone National Park, but both species are subject to human-caused mortality when individuals leave the park, which occurs often enough to be a significant source of mortality. By contrast, the tawny owl and moose populations are not harvested. Wolves live in kin-structured social groups called packs, which aggressively defend their territories. Packs are typically comprised of one breeding pair and other subordinate non-breeding members (Mech & Boitani, 2003). Tawny owls are also territorial; however, territories are occupied by a single breeding pair, which defend their territory throughout the year (Petty, 1992b). Population dynamics are thought to be strongly density-dependent in the territorial wolf and owl populations. By contrast, moose and elk are not territorial. The moose population is limited by predation and climate (Vucetich & Peterson, 2004), whereas the elk population was strongly limited by human harvest in the past, but is increasingly impacted by predation (MacNulty, Stahler, Wyman, Ruprecht, & Smith, 2016).

2.2 | Estimating age structure

Due to differences in the type of data available for each population, we used two different methods for generating annual estimates of age structure (i.e. the number of juveniles, 1-, 2- and 3-year-olds that were present in each population, for every year of the study period).

For the wolf and tawny owl populations, we used re-sighting data of marked individuals to obtain annual estimates of age structure. For the moose and elk populations, we used reconstruction analysis based on dead-recovery data (similar to Fryxell et al., 1999; Gove, Skalski, Zager, & Townsend, 2002; Solberg, Sæther, Strand, & Loison, 1999).

2.2.1 | Grey wolves

The identity and age of a large proportion of wolves in the Yellowstone population were known because 30% to 50% of pups (surviving to 9 months of age) have been radiocollared every year since wolves were reintroduced in Yellowstone in 1995 (MacNulty et al., 2009). These radiocollared individuals were tracked and observed on a daily-to-weekly basis throughout the year (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015). We used this re-sighting data to estimate age structure each year over a 17-year period that began after reintroduction activities were completed, 1998–2014.

2.2.2 | Tawny owls

We used re-sighting data of owls, uniquely marked with metal rings, to estimate age structure for a 15-year period, 1990–1998 and 2008–2013. The gap in that time series is due to not having re-capture data for breeding males for the period, 1999–2007. Otherwise, more than 90% of the population was marked during the study period (Millon, Petty, Little, & Lambin, 2011; Petty, 1992b). The exact age of many individuals is known because they were first captured as chicks within our study site or in other sites nearby. The age of an additional 82 unmarked adults entering the population as immigrants of unknown origin could be reliably estimated from moulting patterns of primary feathers (Petty, 1992a).

2.2.3 | Moose and elk

The reconstruction analysis approach for estimating age structure uses dead-recovery data and involves the following steps: (a) creating a database of year-of-death and age-at-death for individuals in each population, (b) using this database to create a cohort matrix and (c) using the cohort matrix to calculate the minimum number of individuals alive in each age-class, every year. Each year we located the carcasses of moose and elk, which died within the past year during aerial and ground surveys in Isle Royale National Park (from 1959 onwards) and Yellowstone National Park (from 1995 onwards). We determined age-at-death for each individual moose and elk by counting cementum lines of teeth (Haagenrud, 1978; Peterson, 1977; Rolandsen et al., 2008). In total, we were able to determine age-at-death and year-of-birth for 2,779 moose dying during a known year, between 1959 and 2015. We were also able to determine age-at-death and year-of-birth for 3,078 elk dying of natural causes between 1995 and 2015 and for 10,133 elk killed by hunters between 1996 and 2009. Although young elk (<2 years old) were under-represented in the hunter-killed elk dataset, such age-specific

vulnerability to hunting is not a concern for our analyses because it is only likely to bias estimates of age structure in very recent years and we did not analyse elk age structure after 2009 (see below for details). There is no harvest data available for the Isle Royale moose population because it is not hunted.

We organized the dead-recovery data into a cohort matrix, **C**. Sample size was large enough to allow for calculating sex-specific cohort matrices for the elk population, but not the moose population. The rows in **C** represent cohorts (i.e. individuals born in the same year), whereas the columns indicate the age-at-death, such that element $C_{t,j}$ represents the number of individuals born in year t that died at j years of age. For example, $C_{1999,4} = 5$ indicates that we recovered the carcasses of five individuals that were born in 1999, and died at four years of age in 2003 (=1999 + 4). Because the **C** matrix is derived from dead-recovery data, it will contain some incomplete cohorts, insomuch as a portion of those cohorts have yet to be collected because they are still alive at the end of the data collection period. Consequently, some elements (those in the lower right corner) of the matrix **C** are necessarily zero because they represent individuals that have not yet died. For example, the element $C_{2006,15}$ represents individuals born in 2006 that will die (and be collected) at the age of 15 in the year 2021. The elements representing individuals that have not yet died are described as $C_{t,j\ X-t+1}$, where X is most recent year of carcass collection. To account for these incomplete cohorts, we adjusted the elements of **C** that were zero by following these two steps.

First, we predicted the total size of each incomplete cohort $\left(\hat{C}_t\right)$ as:

$$\hat{C}_t = \frac{\dot{C}_t}{1-l_j},\tag{1}$$

where $\dot{C}_t$ is the number of carcasses already collected from that cohort and l_j is the proportion of individuals expected to survive to age j. We estimated l_j from a survivorship curve (based on $l_{(x)}$ values in a life table) that is equal to (Caughley, 1977):

$$l_j = \prod_{k=0}^{j-l} p_k,\tag{2}$$

where p_k are estimates of annual, age-specific survival rates. We obtained age-specific survival estimates by fitting a known fate survival model (the Kaplan–Meier method) for Isle Royale moose (both sexes combined) and for male and female elk in northern Yellowstone in Program MARK (White & Burnham, 1999). See Appendix S1 for further details about age-specific survival estimates for moose and elk. From $\hat{C}_t$, we were able to estimate the number of individuals yet to be collected.

Second, we used these estimates of age-specific survival to predict the ages and years in which uncollected animals would die. One potential limitation of this method is that adjustments for incomplete cohorts will be greater for years close to the end of the data collection period (i.e. 2016) because a larger proportion of these recent cohorts will still be alive and not included in the dead-recovery database.

However, the influence of these adjustments is likely to be negligible in this study because we only assessed age structure for years when more than 75% of the cohort had already died, that is before 2007 for moose and 2009 for elk. Another limitation is that this method assumes no interannual variation in age-specific survival. However, adult survival for large mammals, such as moose and elk, is generally high and stable (Gaillard & Yoccoz, 2003). Although juvenile survival varies among years, it would only affect estimates of age-structure in the most recent years of data collection, and we did not analyse fluctuations in age structure after 2009.

The final stage of reconstruction analysis is to use **C** to calculate the minimum number of individuals alive each year in each age-class. The calculation makes use of the fact that every adult (>1 year old) alive in year t was also alive during year/t. For example, the value of $C_{1997,8} = 6$ indicates that six individuals born in 1997 all died aged eight in 2005 (=1997 + 8), as well as indicating that all of these individuals were seven years old in 2004, six years old in 2003, etc. More precisely, we used **C** to generate a new matrix **M**, where the element $M_{t,j}$ represents the minimum number of individuals alive in year t that were of age j years. The elements of **M** were calculated from the elements of **C** as:

$$M_{t,j} = \sum_{k=j}^{21} C_{t-j,k}.\tag{3}$$

The minimum number of individuals alive in year t summed across all age classes is denoted M_t and is depicted in Figure S3.

2.3 | Estimating population size

2.3.1 | Wolves and owls

We estimated total abundance (n_t) of wolves as the number of pups emerging from dens in spring plus the number of adults counted in April (Smith et al., 2015). For tawny owls, we estimated n_t as the number of owlets fledging plus twice the number of occupied territories (because territories were occupied by both male and female). These observations were made by visiting nest boxes at least three times each breeding season (i.e. between March and June, Petty, 1992a).

2.3.2 | Moose and elk

Estimates of the minimum number of individuals alive each year (M_t) may be converted into an estimate of n_t using independent estimates of moose and elk abundance obtained from aerial surveys (Appendix S2). More precisely, we estimated n_t through a regression that relates estimates of M_t to estimates of abundance based on aerial survey counts for a subset of years (i.e. years for which aerial-based estimates were available). The relationship between M_t and aerial abundance counts is depicted in Figure S4 and described by Equation 4 for moose and Equation 5 for elk:

$$n_t = M_t \times 2.12 + 91.13\tag{4}$$

$$n_t = \exp\left(0.41 \times \ln\left[M_t\right] + 5.86\right).\tag{5}$$

The resulting time series of n_t are depicted in Figure S3. Importantly, M_t is highly correlated with abundance estimates based on aerial surveys ($R^2 = .84$ for moose and $R^2 = .86$ for elk; Figures S3 and S4), which suggests that the overall trends in population size that we observed are likely to be robust.

2.4 | Analysing fluctuations in age structure

We quantified temporal variation in adult age structure (i.e. individuals > 1 year old) using three different summary statistics previously used to describe age structure. These statistics are the mean and median age of adults (Coulson et al., 2004) and the proportion of senescent individuals in the population (Festa-Bianchet, Gaillard, & Côté, 2003). The threshold for classifying individuals as senescent was based on species-specific relationships between age and survival (see Appendix S1). While senescence is a continuous process, its treatment by this statistic as discrete categories is a useful way to quantify temporal fluctuations in age structure because it contains information about an important aspect of skew. For example, whether the population is skewed more towards a young or old demographic. We excluded individuals <1 year of age (i.e. juveniles) from these three summary estimates of age structure to make our results less sensitive to fluctuations in recruitment.

Although no scalar index can convey all of the information contained in a vector (such as the abundance of individuals in every age-class) – these scalar indices still contain important information about age structure, such as the mean and an important aspect of skew. Furthermore, we used three different scalar indices of age structure to ascertain whether the results might be influenced by the way we summarized fluctuations in age structure. All three indices of age structure exhibited considerable temporal variation (see Results, Table 1; Figure 1) and were all highly correlated with each other (Appendix S3; Table S1). Additionally, our results and inferences remained consistent irrespective of which index was used in subsequent analysis. Together, those circumstances suggest that scalar indices are useful and reflect changes in age structure.
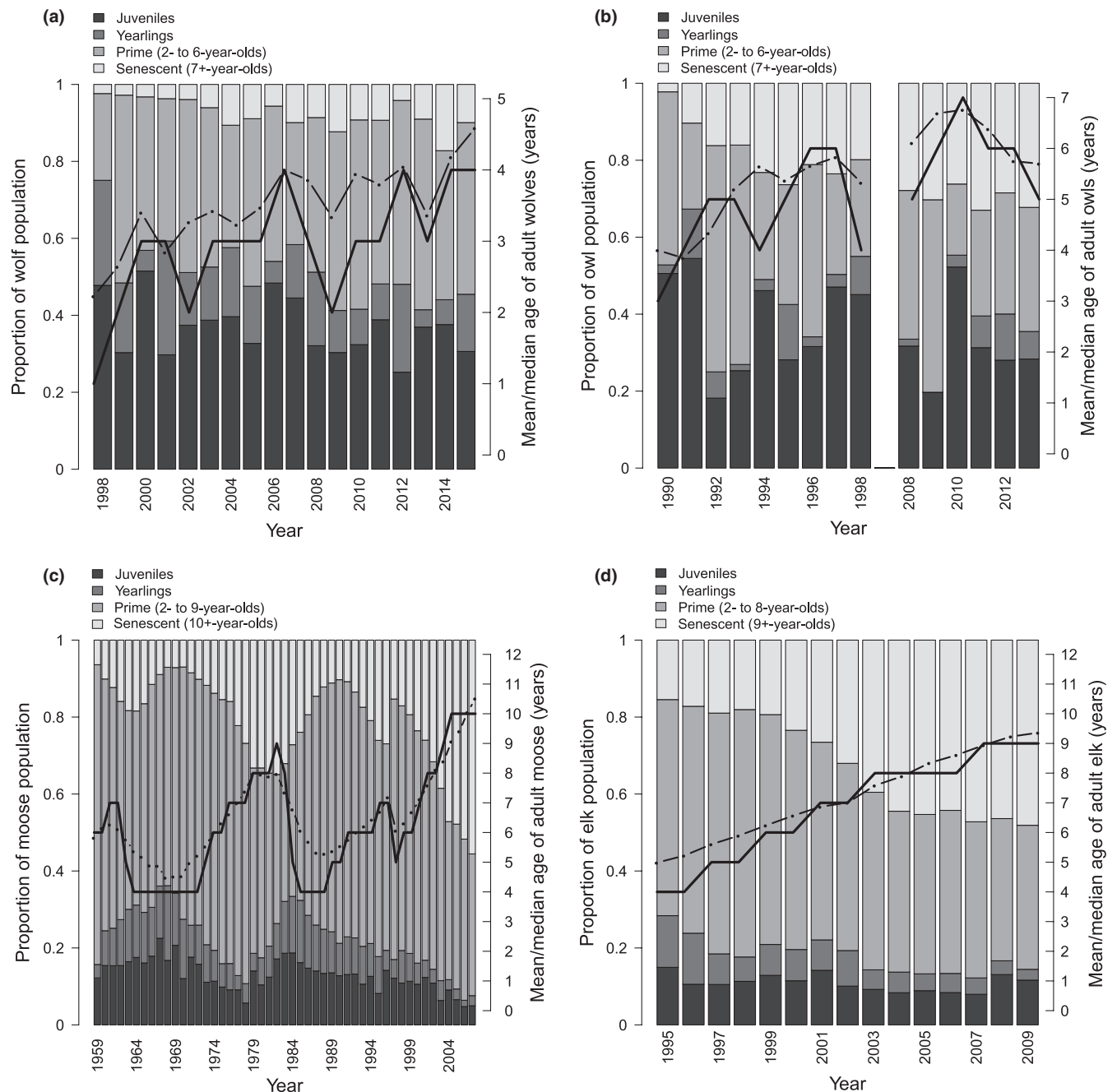
To quantify variability in the mean and the skew of the population's age structure over the study period, we calculated the coefficient of variation (CV) for each of the three age structure indices. The CV is the ratio of the standard deviation to the mean and therefore represents a standardized measure of the variability or dispersion of a variable in relation to its mean value. To provide additional context for understanding our results, we also calculated the CV for population size over the study period because variability in abundance has been assessed for many species (Pimm, 1991).

We also assessed whether age structure dynamics showed signs of being non-stationary. To reiterate, non-stationarity is a property of a time series whereby the mean and/or variance changes over time. Non-stationary dynamics are typically presumed to be externally forced – that is, the result of population dynamics being driven by exogenous processes that are themselves non-stationary (Ariño & Pimm, 1995). We follow Ariño and Pimm (1995) by assessing non-stationarity with plots showing how the sample variance (i.e. interannual variance) of the three age structure indices increases with length of time series. If the interannual variance increases to an asymptote, then dynamics are considered to be stationary; however, if the variance continues to increase (with no evidence of an asymptote), then the time series is considered non-stationary. However, any such claims about non-stationarity are always limited to the period of observation.

2.5 | Analysing population growth rate

To assess the relationship between fluctuations in age structure and population growth rate, we used Gompertz population growth models and we implemented these discrete-time, state-space models using a Bayesian approach (Buckland, Newman, Thomas, & Koesters, 2004). These models quantify density-dependent growth (Dennis, Ponciano, Lele, Taper, & Staples, 2006). Thus, they allowed us to assess the influence of age structure on population growth while also taking into account the influence of density. Additionally, these models also explicitly account for process error (variation arising from ecological processes) and observation error (noise due to imperfect observation or sampling methods)

TABLE 1 The range and coefficient of variation (CV, expressed as %) with the standard error (*SE*) in parentheses provide a simple quantitative description of the magnitude of variability in basic population-level properties, such as abundance and age structure for four free-ranging populations: grey wolves in Yellowstone National Park (USA) studied over a 17-year period; tawny owls in Kielder Forest (UK) studied over a 15-year period; moose in Isle Royale National Park (USA) studied over a 49-year period; and elk in northern Yellowstone studied over a 15-year period

Species	Grey wolves		Tawny owl		Moose		Elk	
	Range	CV (*SE*)	Range	CV (*SE*)	Range	CV (*SE*)	Range	CV (*SE*)
Mean age	2.23–4.59	17 (2.97)	3.85–6.76	16 (2.99)	4.48–10.05	21 (2.19)	4.98–9.01	19 (3.61)
Median age	1–4	28 (5.19)	3–7	21 (3.92)	4–10	30 (3.28)	4–9	26 (5.00)
Proportion senescent	0.04–0.28	53 (11.30)	0.01–0.24	58 (13.70)	0.07–0.54	53 (6.70)	0.18–0.52	37 (7.63)
Population size	99–243	27 (4.9)	120–290	28 (5.78)	448–2,058	42 (4.92)	6,009–14,263	28 (5.55)

Note: Estimates of population age structure were based on re-sighting data from marked individuals for the wolf and tawny owl populations, whereas estimates of moose and elk age structure were based on reconstruction analyses using dead-recovery data. Once age structure had been estimated for each of the four populations, we characterized temporal fluctuations in age structure using three different indices: the mean age of adults (e.g. individuals over 1 year old), the median age of adults and the proportion of adults which were senescent.

FIGURE 1 Temporal variation in the age structure of a population of: (a) grey wolves in Yellowstone National Park; (b) tawny owls in Kielder Forest; (c) moose in Isle Royale National Park; and (d) elk wintering near the northern border of Yellowstone National Park. The mean age of individuals is indicated by the dashed and dotted line. The median age of individuals is indicated by the solid line

in estimates of abundance (Buckland et al., 2004; Dennis et al., 2006).

We began with a linearized version of the Gompertz population growth model:

$$\log\left(N_t\right) = x_t = x_{t-1} + \beta_r + \beta_{den} \times x_{t-1}, \tag{6}$$

where x_t is the logarithm of the initial estimate of population size at time t, β_r is equivalent to the maximum potential growth rate when resources are not limiting (i.e. r_{max}; Dennis et al., 2006), and β_{den} is the influence of density on population growth. To estimate

the influence of changes in age structure on population growth, we modified Equation 6 to predict the median of the posterior distribution for the number of animals in year t as a function of:

$$\log\left(N_t\right) = x_t = x_{t-1} + \beta_r + \beta_{density} \times x_{t-1} + \beta_z \times z_{t-1} + \varepsilon_{t-1} = f\left(x_{t-1}\right), \tag{7}$$

where β_z is the estimated influence of some scalar indicator of age structure on growth rate. The parameter, z, was replaced with either the average age of adults (ave), median age of adults (med) or the proportion of senescent adults in the population (sen). We standardized each index of age structure to have a mean = 0 and

$SD = 1$ to facilitate model convergence and direct comparisons among the different age structure indices. The term, ε_{t-1}, is a normally distributed error with variance equal to σ_p^2, which represents environmental stochasticity (i.e. process error, the error not explained by the deterministic portion of the Gompertz model). Observation error was expressed as:

$$y_t = \text{Normal}\left(x_t, \sigma_o^2\right) = g\left(x_t\right), \tag{8}$$

where y_t is the initial estimate of population size (i.e. uncorrected for process and observation error at time t).

We used vague priors for all random variables in the state-space models for which we had no prior information. For example, age structure variables (mean and median age of adults and the proportion of senescent adults) were given a normal prior distribution for β_z ($\bar{x}=0$, $SD = 10$). Process error (σ_p^2) and observation error (σ_o^2) were also both given vague priors, but with an gamma distribution (shape = 0.001, rate = 0.001) on precision (i.e. the inverse of variance). However, using external information to inform prior distributions can result in better identifiability of other model parameters (Koons, Colchero, Hersey, & Gimenez, 2015; Lebreton & Gimenez, 2013). Consequently, for the β_{density} parameter, which estimates the strength of density dependence, we used a somewhat informative prior with a truncated normal distribution ($M = 0$, $\sigma = 2$, truncated at −2 and 2 to exclude the impossibilities). The method we used to formulate this truncated normal distribution was identical to that used in Koons et al. (2015) and Tallian et al. (2017) and is consistent with the instructions outlined in Plummer (2012). We also used informative priors for the β_r parameter, which represents the maximum intrinsic rate of population growth for each species. For the wolf population, we used a somewhat informative normal prior distribution for β_r ($\bar{x}=0.303$, $SD = 0.025$) based on the mean of three r_{max} values reported in Miller, Jensen, and Hammill (2002). For the owl population, we used a somewhat informative normal prior for β_r ($\bar{x}=0.62$, $SD = 0.316$) based on the maximum population growth rate observed for this population and the SD of growth rates across years. Because we did not have owl age structure data between 1999 and 2007, we set the missing values to the mean of the standardized age structure variables (i.e. 0) to limit the influence of these missing data values on the estimation of the β_z. For the moose population, we used the same informative normal prior distribution for β_r ($\bar{x}=0.304$, $SD = 0.08$) used in Ruprecht (2016), which was based on the mean of r_{max} values estimated in five previous studies of moose (Bergerud, 1981; Cederlund & Sand, 1991; Keith, 1983; Sinclair, 2003; Van Ballenberghe, 1983). For the elk population, we used the same informative normal prior distribution for β_r ($\bar{x}=0.263$, $SD = 0.09$) used in Tallian et al. (2017), which was based on the mean of r_{max} values estimated in five previous studies of elk (Caughley, 1977; Eberhardt, 1987; Hennemann, 1983; Houston, 1982; McCorquodale, Eberhardt, & Eberhardt, 1988).

A full description of state-space model, including the process and observation models and prior distributions, is provided in Appendix S4. We estimated posterior distributions for parameters

(i.e. β_r, β_{density}, β_{ave}, β_{med}, β_{sen}, σ_o^2, σ_p^2) using Markov Chain Monte Carlo (MCMC) simulations in JAGS (Plummer, 2012) in Program-R version 3.3.1 (R Core Team, 2016) using the JAGSUI package (version 1.4.4; Kellner, 2016). We ran three MCMC chains, each consisting of 100,000 iterations, for every model. We discarded the first 50,000 iterations as burn-in, then thinned the sample by retaining every 50th simulation. We considered a variable (i.e. β_{ave}, β_{med}, β_{sen}) to be an important predictor of growth rates if the 95% Bayesian credible interval (BCI) for that β parameter did not overlap zero.

We assessed goodness of fit using posterior predictive checks (Gelman, Carlin, Stern, & Rubin, 2004; Hobbs & Hooten, 2015; Kéry & Schaub, 2012). To do this, we generated hypothetical count data (i.e. $Y.new_t$) from the state-space model and used a squared discrepancy statistic to compare observed and expected values from the original and new hypothetical datasets at every MCMC iteration, that is $T^{\text{obs}} = \left(Y_t - N_t\right)^2$ and $T^{\text{hyp}}\left(Y.new_t - N_t\right)^2$. Calculating the proportion of iterations in which the discrepancy statistics arising from the comparison of the original and hypothetical datasets are more extreme than one another (i.e. $T^{\text{hyp}}\left(Y.new,\theta\right) \geq T^{\text{obs}}\left(Y,\theta\right)$) provides a measure of goodness of fit (Hobbs & Hooten, 2015). An average posterior predictive check score close to 0.5 indicates a good model fit, whereas scores very close to 0 or 1 suggest a lack of fit. Lastly, we assessed model convergence using trace plots and determining whether the $\hat{R}$ statistic for each parameter was < 1.1 (Gelman, 1996). Importantly, we found no evidence to suggest that there were issues with model convergence or that the models were a poor fit to the data (see Appendix S4; Figures S5 and S6).

3 | RESULTS

3.1 | Variation in age structure

All three scalar indices of age structure (the mean and median age of adults, and the proportion of senescent adults) varied considerably over time in all four populations (Table 1; Figure 1). For example, the CV for age structure indices ranged from 16% to 58%. This level of variation was comparable to levels of temporal variation in population size (with CV ranging from 27% to 42%, Table 1). Fluctuations in age structure for the tawny owl, moose and elk populations showed signs of being non-stationary as the sample variance of all three age structure indices increased across the length of the time series, without reaching an asymptote over the 15- to 48-year time periods analysed (Figure 2). By contrast, fluctuations in age structure for the wolf population appeared stationary as the variance in the mean and median age of adult wolves remained constant after the first few years of the study period (Figure 2).

3.2 | Age structure and growth rates

Population growth rate was not related to age structure for the wolf and owl populations, insomuch as the 95% BCIs for β_{ave}, β_{med}, and β_{sen}

all overlapped zero (Table 2). By contrast, all three indices of age structure (i.e. the mean and median age of adults and the proportion of senescent adults) were negatively associated with population growth in both the moose and elk populations (Table 2). For elk, the estimated coefficients representing the influence of age structure on growth rates were, coincidentally, the same for all three metrics of age structure, that is −0.03 with a SD of 0.01. For moose, the coefficients were as follows: β_{ave} = −0.07 (SD = 0.02), β_{med} = −0.06 (0.02) and β_{sen} = −0.05 (0.02). For elk and moose, none of the 95% BCIs for β_{ave}, β_{med}, and β_{sen} overlapped with zero (Table 2), which suggest the association between age structure and population growth was statistically significant.

The results depicted in Figure 3 suggest that population growth varied from positive to negative for moose, and from near zero to negative for elk as each metric of age structure increased over its observed range. For example, when average age in the moose population was relatively low (4–6 years old), the expected value of λ was approximately 1.1, which indicates a rapidly growing population. By contrast, when the moose population was comprised of more senescent individuals (i.e. when the average age of individuals was 9- to 10-year-olds), the expected λ decreased to around 0.9, which indicates a declining population. The strength of the association between age structure and population growth appeared to be similar to the strength of the relationship between density dependence and population growth given that the coefficients for β_{den} were −0.05 (0.01) for moose and −0.04 (0.01) for elk (Table 2). The posterior predictive checks that we used to assess goodness of fit indicated that the models adequately fit the data (Appendix S4; Figure S5).

4 | DISCUSSION

The main objectives of this study were to quantify temporal fluctuations in age structure, to determine whether age structure dynamics were non-stationary and to assess the extent that fluctuations in age structure are useful predictors of population growth rates for four free-ranging vertebrate populations. We found that the magnitude of temporal variation in age structure was comparable to temporal variation in population size for the four free-ranging vertebrate populations (Table 1). More generally, the CVs for age structure indices for these populations were comparable to CVs of abundance for many vertebrate populations (Pimm, 1991). Additionally, age structure fluctuated in a non-stationary manner over the observed time periods for three of the four populations (moose, elk and owls). Finally, for two of the populations (moose and elk), fluctuations in age structure were associated with population growth and the strength of the association between age structure and population growth appeared to be comparable to the effect of density dependence for these populations (Table 2; Figure 3).

While these analyses were not intended to be a comprehensive assessment of when age structure fluctuations need to be taken into account, it may be relevant that age structure was not associated with growth rates for the two populations which are strongly regulated by territoriality, wolves and tawny owls. By contrast, moose and elk are not territorial. Territoriality generally has a stabilizing influence on population dynamics (Brown, 1969; López-Sepulcre & Kokko, 2005). In particular, territorial behaviour can result in density-dependent rates of immigration and emigration, which could potentially weaken the relationships between age structure, recruitment, survival and population growth. Indeed, territorial occupancy of the owl population remained stable over the study period because increased immigration of young owls from other populations compensated for a decline in local productivity and juvenile survival (Millon et al., 2014). Alternatively, it might also be significant that the life-history strategies of tawny owls and wolves differ from moose and elk, insomuch as owls and wolves typically have shorter life spans (e.g. average life span of 4 years) and higher fecundity (e.g.
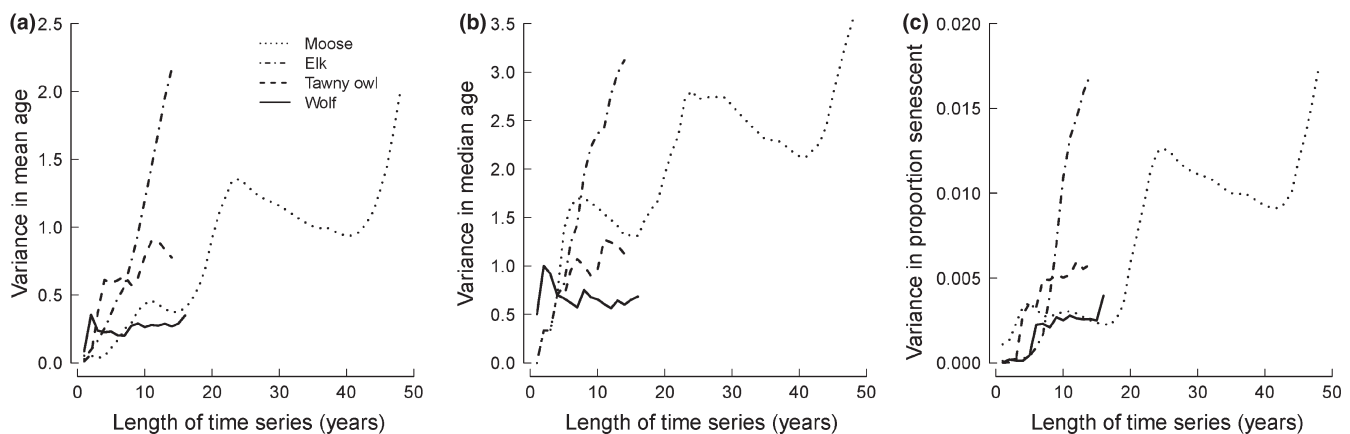

FIGURE 2 Changes in sample variance (interannual variance) as the length of the study period increased for three different indices of age structure: (a) mean age of adults, (b) median age of adults and (c) proportion of adults which were senescent, for populations of grey wolves, tawny owls, moose and elk. The relationship between the sample variance and the length of the time series indicates whether a process tends towards a stationary, or a non-stationary, process for ecological time series. Specifically, if the interannual variance quickly reaches an asymptote, then it suggests the dynamics are stationary. By contrast, if the variance does not asymptote, then the dynamics are likely non-stationary, at least for the time-scale over which observations were made

TABLE 2 Parameter estimates from Bayesian Gompertz state-space models examining the relationship between population growth, age structure and density for four different populations: wolves and elk in Yellowstone National Park (USA), tawny owls in Kielder Forest (UK) and moose in Isle Royale National Park (USA)

Species	Parameter	Mean age (β_{ave})			Median age (β_{med})			Proportion senescent (β_{sen})		
		β estimate	SD	95% BCI	β estimate	SD	95% BCI	β estimate	SD	95% BCI
Grey wolves (*Canis lupus*)	β_r	0.30	0.03	0.26, 0.35	0.3	0.03	0.26, 0.35	0.3	0.03	0.25, 0.35
	$\beta_{density}$	−0.06	0.01	−0.08, −0.04	−0.06	0.01	−0.08, −0.04	−0.06	0.01	−0.08, −0.04
	β_z	**−0.04**	**0.07**	**−0.16, 0.12**	**0.03**	**0.06**	**−0.10, 0.15**	**−0.1**	**0.06**	**−0.21, 0.03**
	σ_p^2	0.16	0.07	0.04, 0.30	0.19	0.06	0.09, 0.31	0.13	0.07	0.03, 0.27
	σ_o^2	0.11	0.07	0.03, 0.24	0.08	0.05	0.02, 0.21	0.12	0.06	0.03, 0.22
Tawny owl (*Strix aluco*)	β_r	0.78	0.3	0.18, 1.41	0.77	0.32	0.15, 1.40	0.78	0.32	0.13, 1.43
	$\beta_{density}$	−0.15	0.06	−0.27, −0.04	−0.15	0.06	−0.27, −0.03	−0.15	0.06	−0.28, −0.03
	β_z	**0.02**	**0.04**	**−0.06, 0.12**	**0.02**	**0.05**	**−0.07, 0.13**	**0.01**	**0.04**	**−0.07, 0.10**
	σ_p^2	0.12	0.09	0.02, 0.36	0.12	0.09	0.02, 0.33	0.12	0.09	0.03, 0.36
	σ_o^2	0.22	0.07	0.07, 0.36	0.23	0.07	0.08, 0.38	0.23	0.07	0.07, 0.38
Moose (*Alces alces*)	β_r	0.31	0.05	0.21, 0.41	0.31	0.05	0.21, 0.41	0.31	0.05	0.22, 0.41
	$\beta_{density}$	−0.05	0.01	−0.06, −0.03	−0.05	0.01	−0.06, −0.03	−0.05	0.01	−0.06, −0.03
	β_z	−0.07	0.02	−0.11, −0.03	−0.06	0.02	−0.10, −0.03	−0.05	0.02	−0.9, −0.04
	σ_p^2	0.12	0.02	0.10, 0.16	0.13	0.02	0.10, 0.16	0.13	0.02	0.10, 0.17
	σ_o^2	0.04	0.02	0.02, 0.07	0.04	0.02	0.02, 0.08	0.04	0.01	0.02, 0.07
Elk (*Cervus elaphus*)	β_r	0.27	0.09	0.09, 0.44	0.28	0.09	0.10, 0.45	0.27	0.09	0.09, 0.44
	$\beta_{density}$	−0.04	0.01	−0.06, −0.02	−0.04	0.01	−0.06, −0.02	−0.04	0.01	−0.06, −0.02
	β_z	−0.03	0.01	−0.05, −0.01	−0.03	0.01	−0.05, −0.01	−0.03	0.01	−0.05, −0.01
	σ_p^2	0.04	0.03	0.02, 0.05	0.04	0.02	0.02, 0.06	0.04	0.03	0.02, 0.07
	σ_o^2	0.03	0.07	0.02, 0.04	0.03	0.05	0.02, 0.05	0.03	0.07	0.02, 0.05

Note: β_r is equivalent to the maximum intrinsic growth rate of the population; $\beta_{density}$ describes the effect of density dependence on population growth; σ_p^2 represents process error, and σ_o^2 estimates observation error. Columns display the results of different versions of the model for each population where fluctuations in age structure were characterized as the mean age of adults (β_{ave}), the median age of adults (β_{med}) and the proportion of adults which were senescent (β_{sen}). Bold font indicates parameter estimates where the BCI overlap with zero (i.e. those that are not statistically significant).

Abbreviation: BCI, Bayesian credible interval.
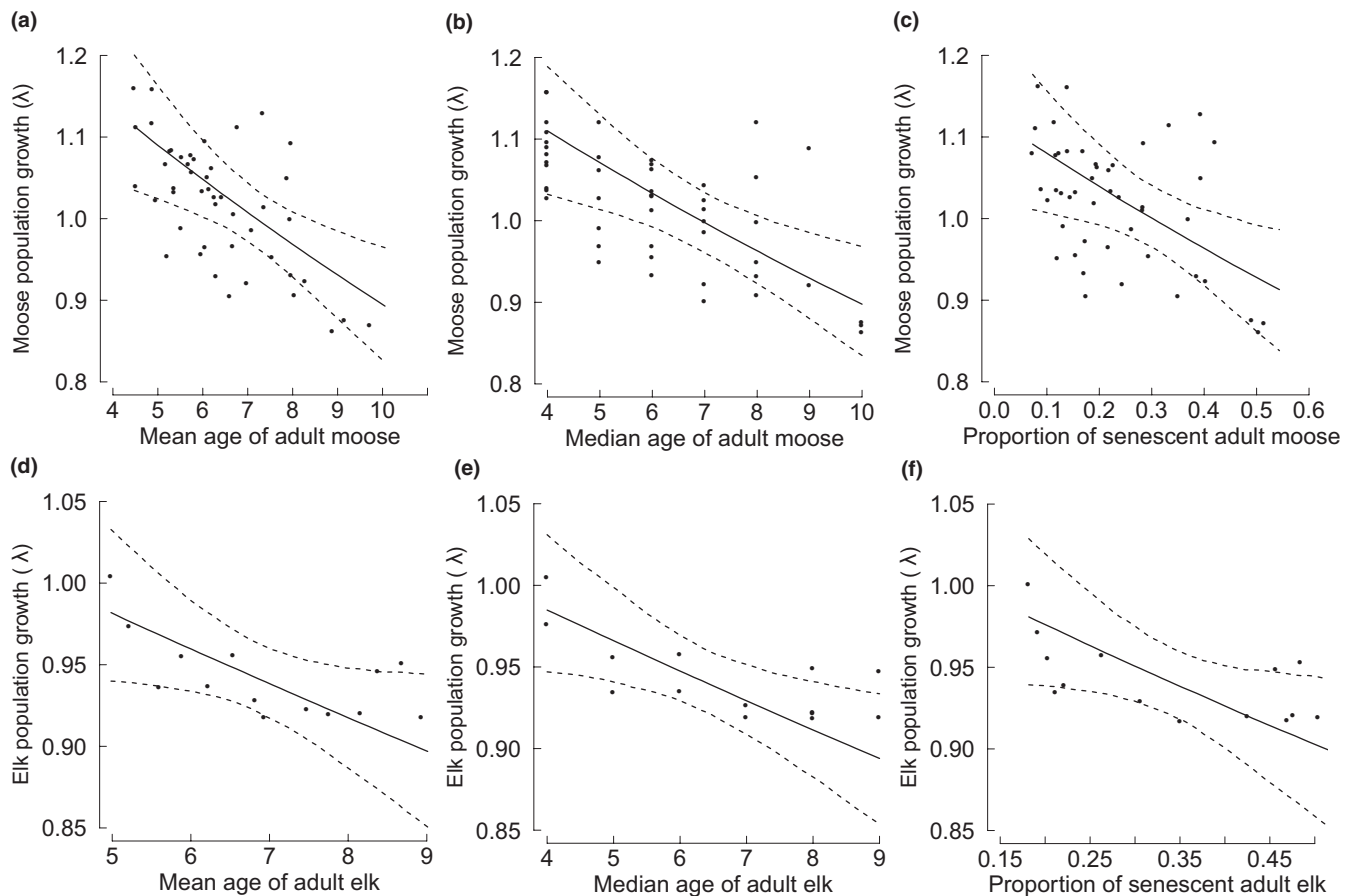
FIGURE 3 The relationship between population growth (measured as λ, the finite rate of increase) and three different measures of the population's age structure (mean and median age of adults and proportion of adults which were senescent) for a population of moose in Isle Royale National Park (a–c), and a population of elk wintering near the northern border of Yellowstone National Park (d–f). The predictions for the effect of each measure of age structure on lambda were derived from the Gompertz state-space model with population density held constant at its median value. The solid line represents the median of the posterior distribution across the range of observed values of age structure and the dashed lines represent the bounds of the 95% Bayesian credible interval. Points represent the median of the posterior distribution for each annual estimate of lambda and were derived from the abundance estimates generated by the Gompertz model as N_{t+1}/N_t. The points are displayed as a visual aid only

regularly producing four or more offspring each year) compared to moose and elk (which have an average life span of 10–20 years and are only capable of producing 1 or 2 offspring per year). Thus, owls and wolves are considered to have faster life histories than moose and elk. Life-history speed has previously been identified as one factor that can have an important mediating effect on the impact of age structure fluctuations on population growth. That is, the impact of fluctuations in age structure on population growth was greater for longer-lived species with slower life histories (Koons, Grand, & Arnold, 2006; Koons et al., 2005), but this depends on the way in which vital rates covary (Gamelon et al., 2016). Nevertheless, the finding that age structure fluctuations were more strongly associated with population growth for the two species with slower life histories (moose and elk) is consistent with earlier work (Koons et al., 2006, 2005). However, with a sample of only four populations, these considerations are only intended to be suggestive of future avenues of research. It is also worth highlighting that although this study, Koons et al. (2006) and Gamelon et al. (2016) were all focused

on vertebrates (mostly mammals), demographic senescence is a ubiquitous phenomenon that also occurs in plant and invertebrate species (Chmilar & Laird, 2019; Cooper, 1994). Therefore, we suggest that future studies focused on assessing the relationship between age structure fluctuations and population dynamics across a broader range of taxa that senesce in different ways (i.e. reproductive senescence and/or actuarial senescence) might yield important insights about the precise circumstances under which it is important to account for fluctuations in population structure.

That fluctuations in age structure showed signs of being non-stationary (i.e. the sample variance increased with the length of the time series) over the time periods analysed for three populations is significant because the future dynamics of non-stationary populations are difficult to predict (Poole, 1978). Fluctuations in abundance are known to be non-stationary over long periods of time for a wide range of taxa (Ariño & Pimm, 1995; Steele, 1985). However, the mechanisms leading to non-stationarity are not well understood. Non-stationary dynamics are typically presumed to be externally forced – that is, the

result of population dynamics being driven by exogenous processes that are themselves non-stationary (Ariño & Pimm, 1995). However, our work suggests that non-stationarity in age structure – an endogenous factor – may also play a proximate role in the non-stationarity of abundance. As such, non-stationary age structure and abundance may help explain limits in predicting future changes in abundance over timescales relevant to wildlife managers.

The extent of fluctuations (and non-stationarity) in age structure observed here (Figures 1 and 2) may also have important implications for understanding predator–prey dynamics given that many predators exhibit strong age- or stage-specific preferences for prey (e.g. for juveniles and senescent individuals Hoy et al., 2015; Wright et al., 2006). Consequently, fluctuations in the age structure of prey populations may alter the availability of preferred age classes, and thereby influence prey selection or kill rates (Sand et al., 2012), and thereby impact predator growth rates. The importance of fluctuations in the age structure of prey species may even extend to community-wide effects if predators switch to alternative prey species in response to declines in the abundance of preferred age-classes of their primary prey species. However, the relationship between prey age structure and predator demographic rates is seldom examined (but see Cubaynes et al., 2014).

In summary, we provide rare empirical evidence of how age structure dynamics can be non-stationary, which may represent an important mechanism by which fluctuations in abundance become non-stationary (Ariño & Pimm, 1995; Steele, 1985) and therefore difficult to forecast over time-scales of concern to wildlife managers (Poole, 1978). These analyses also suggest that fluctuations in age structure were sometimes significantly linked to population growth and that the strength of the relationship between age structure and population growth was of a similar magnitude to that of density dependence for the two populations of non-territorial species with slower life histories (moose and elk). The results highlighted above are significant because many analyses used to inform management decisions have traditionally assumed that populations are fixed at a stable age distribution (but see Caswell, 2007), or they have assumed that population dynamics are independent of density and that vital rates and age structure are influenced by environmental processes that are stationary (Haridas et al., 2009; Stott et al., 2011). Ignoring non-stable fluctuations in population structure may result in the failure or misevaluation of management efforts because the short-term 'transient' dynamics that occur when the population deviates from the hypothetical stable age structure can differ substantially from the expected long-term stable growth rate (Koons et al., 2005). Indeed, a recent study on a wide range of plant species revealed that >50% of the variation in observed population dynamics was attributed to 'transient' growth caused by deviation from the hypothetical stable stage structure, as opposed to the 'stable' or asymptotic growth contributed by vital rates (McDonald, Stott, Townley, & Hodgson, 2016). Lastly, our work highlights how future research might focus on using Bayesian models to more finely partition process variance into the relative contributions of stable and nonstable exogenous drivers and endogenous drivers, including environmental stochasticity, demographic stochasticity and the nonstable components determined by the difference between the actual age structure and the hypothetical stable age structure of the population. Thus, overall our work supports the view that fluctuations in age structure are important for understanding variable population dynamics (Ellis & Crone, 2013; Gamelon et al., 2016; Koons et al., 2005; McDonald et al., 2016; Pelletier, Moyes, Clutton-Brock, & Coulson, 2012) and emphasizes the need for populations to be modelled using approaches that allow for transient dynamics, density dependence and non-stationary environments.

AUTHORS' CONTRIBUTIONS

S.R.H. and J.A.V. conceived of the concept. S.R.H. led the analysis and development of the manuscript. The other co-authors led the collection of essential data and contributed to the design of the analysis and writing of the manuscript.

DATA AVAILABILITY STATEMENT

Data used in the above analyses are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.d84hg87 (Hoy et al., 2019).

ORCID

Sarah R. Hoy https://orcid.org/0000-0002-3398-6043

Daniel R. MacNulty https://orcid.org/0000-0002-9173-8910

Joel S. Ruprecht https://orcid.org/0000-0002-9443-7582

REFERENCES

Ariño, A., & Pimm, S. L. (1995). On the nature of population extremes. *Evolutionary Ecology*, 9, 429–443. https://doi.org/10.1007/BF01237765

Ballenberghe, V. (1983). The rate of increase in moose populations. *Alces*, 19, 98–117.

Bergerud, A. (1981). The decline of moose in Ontario – a different view. *Alces*, 17, 30–43.

Bonenfant, C., Gaillard, J. M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Duncan, P. (2009). Chapter 5 empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research*. https://doi.org/10.1016/S0065-2504(09)00405-X.

Brown, J. L. (1969). Territorial behavior and population regulation in birds: A review and re-evaluation. *The Wilson Bulletin*, 81, 293–329.

Buckland, S. T., Newman, K. B., Thomas, L., & Koesters, N. B. (2004). State-space models for the dynamics of wild animal populations. *Ecological Modelling*, *171*, 157–175. https://doi.org/10.1016/j.ecolmodel.2003.08.002

Cassidy, K. A., MacNulty, D. R., Stahler, D. R., Smith, D. W., & Mech, L. D. (2015). Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behavioral Ecology*, *26*, 1352–1360. https://doi.org/10.1093/beheco/arv081

Caswell, H. (2000). Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology*, *81*, 619–627. https://doi.org/10.1890/0012-9658(2000)081[0619:PARPAT]2.0.CO;2

Caswell, H. (2007). Sensitivity analysis of transient population dynamics. *Ecology Letters*, *10*(1), 1–15. https://doi.org/10.1111/j.1461-0248.2006.01001.x

Caswell, H. (2010). Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology*, *98*, 324–333. https://doi.org/10.1111/j.1365-2745.2009.01627.x

Caughley, G. (1977). *Analysis of vertebrate populations. The ecology of whales and dolphins*. London, UK: Wiley.

Cederlund, G. N., & Sand, H. K. G. (1991). Population dynamics and yield of a moose population without predators. *Alces*, *27*, 31–40.

Chmilar, S. L., & Laird, R. A. (2019). Demographic senescence in the aquatic plant *Lemna gibba* L. (Araceae). *Aquatic Botany*, *153*, 29–32. https://doi.org/10.1016/J.AQUABOT.2018.11.004

Cooper, E. L. (1994). Invertebrates can tell us something about senescence. *Aging Clinical and Experimental Research*, *6*(1), 5–23. https://doi.org/10.1007/BF03324208. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8043627

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J., Pemberton, J. M., Clutton-Brock, T. H., ... Grenfell, B. T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, *292*, 1528–1531.

Coulson, T., Gaillard, J. M., & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology*, *74*, 789–801. https://doi.org/10.1111/j.1365-2656.2005.00975.x

Coulson, T., Guinness, F., Pemberton, J., & Clutton-Brock, T. (2004). The demographic consequences of releasing a population of red deer from culling. *Ecology*, *85*, 411–422. https://doi.org/10.1890/03-0009

Cubaynes, S., MacNulty, D. R., Stahler, D. R., Quimby, K. A., Smith, D. W., & Coulson, T. (2014). Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology*, *83*, 1344–1356.

Davison, R., Jacquemyn, H., Adriaens, D., Honnay, O., de Kroon, H., & Tuljapurkar, S. (2010). Demographic effects of extreme weather events on a short-lived calcareous grassland species: Stochastic life table response experiments. *Journal of Ecology*. https://doi.org/10.1111/j.1365-2745.2009.01611.x

Dennis, B., Ponciano, J. M., Lele, S. R., Taper, M. L., & Staples, D. F. (2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*. https://doi.org/10.1890/0012-9615(2006)76[323:EDDPNA]2.0.CO;2

Eberhardt, L. L. (1987). Population projections from simple models. *Journal of Applied Ecology*. https://doi.org/10.2307/2403790

Ellis, M. M., & Crone, E. E. (2013). The role of transient dynamics in stochastic population growth for nine perennial plants. *Ecology*, *94*, 1681–1686. https://doi.org/10.1890/13-0028.1

Ezard, T. H. G., Becker, P. H., & Coulson, T. (2006). The contributions of age and sex to variation in common tern population growth rate. *Journal of Animal Ecology*, *75*, 1379–1386. https://doi.org/10.1111/j.1365-2656.2006.01162.x

Ezard, T. H. G., Bullock, J. M., Dalgleish, H. J., Millon, A., Pelletier, F., Ozgul, A., & Koons, D. N. (2010). Matrix models for a changeable world: The importance of transient dynamics in population management. *Journal of Applied Ecology*. https://doi.org/10.1111/j.1365-2664.2010.01801.x

Festa-Bianchet, M., Gaillard, J. M., & Côté, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology*, *72*, 640–649. https://doi.org/10.1046/j.1365-2656.2003.00735.x

Fryxell, J. M., Falls, J. B., Falls, E. A., Brooks, R. J., Dix, L., & Strickland, M. A. (1999). Density dependence, prey dependence, and population dynamics of martens in Ontario. *Ecology*, *80*, 1311–1321. https://doi.org/10.1890/0012-9658(1999)080[1311:DDPDAP]2.0.CO;2

Gaillard, J. M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, *84*, 3294–3306. https://doi.org/10.1890/02-0409

Gamelon, M., Gaillard, J.-M., Gimenez, O., Coulson, T., Tuljapurkar, S., & Baubet, E. (2016). Linking demographic responses and life history tactics from longitudinal data in mammals. *Oikos*, *125*, 395–404. https://doi.org/10.1111/oik.02582

Gelman, A. (1996). Inference and Monitoring Convergence. In W. R. Gilks, S. Richardson, & D. J. Spiegelhalter (Eds.), *Markov Chain Monte Carlo in practice* (pp. 131–143). Boca Raton, FL: Chapman and Hall.

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2004). *Bayesian data analysis*. London, UK: Chapman & Hall.

Gerber, B. D., & Kendall, W. L. (2016). Considering transient population dynamics in the conservation of slow life-history species: An application to the sandhill crane. *Biological Conservation*, *200*, 228–239. https://doi.org/10.1016/J.BIOCON.2016.06.014

Gove, N. E., Skalski, J. R., Zager, P., & Townsend, R. L. (2002). Statistical models for population reconstruction using age-at-harvest data. *The Journal of Wildlife Management*, *66*, 310–320. https://doi.org/10.2307/3803163. Retrieved from http://www.jstor.org/stable/3803163

Haagenrud, H. (1978). Layers of secondary dentine in incisors as age criteria in moose. *Journal of Mammalogy*, *59*, 857–858.

Haridas, C. V., Tuljapurkar, S., & Coulson, T. (2009). Estimating stochastic elasticities directly from longitudinal data. *Ecology Letters*, *12*, 806–812. https://doi.org/10.1111/j.1461-0248.2009.01330.x

Hastings, A. (2004). Transients: The key to long-term ecological understanding? *Trends in Ecology and Evolution*, *19*, 39–45. https://doi.org/10.1016/j.tree.2003.09.007

Hennemann, W. W. (1983). Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. *Oecologia*, *56*, 104–108. https://doi.org/10.1007/BF00378224

Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models: A statistical primer for ecologists*. Woodstock, UK: Princeton University Press. Retrieved from https://press.princeton.edu/titles/10523.html

Houston, D. B. (1982). *The northern Yellowstone elk herd*. New York, NY: McMillan.

Hoy, S. R., MacNulty, D. R., Smith, D. W., Stahler, D. R., Lambin, X., Peterson, R. O., ... Vucetich, J. A. (2019). Data from: Fluctuations in age structure and their variable influence on population growth. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.d84hg87

Hoy, S. R., Petty, S. J., Millon, A., Whitfield, D. P., Marquiss, M., Davison, M., & Lambin, X. (2015). Age and sex-selective predation moderate the overall impact of predators. *Journal of Animal Ecology*, *84*, 692–701.https://doi.org/10.1111/1365-2656.12310

Kaitala, V., Ylikarjula, J., Ranta, E., & Lundberg, P. (1997). Population dynamics and the colour of environmental noise. *Proceedings of the Royal Society B: Biological Sciences*, *264*, 943–948. https://doi.org/10.1098/rspb.1997.0130

Keith, L. B. (1983). Population dynamics of wolves. In L. N. Carbyn (Ed.), *Wolves in Canada and Alaska: Their status, biology and management* (pp. 66–77). Edmonton, AB: Canadian Wildlife Service.

Kellner, K. (2016). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. Retrieved from https://cran.r-project.org/package=jagsUI

Kéry, M., & Schaub, M. (2012). *Bayesian population analysis using WinBUGS: A hierarchical perspective*. San Diego, CA: Academic Press.

Koons, D. N., Colchero, F., Hersey, K., & Gimenez, O. (2015). Disentangling the effects of climate, density dependence, and harvest on an iconic large herbivore's population dynamics. *Ecological Applications*, *25*, 956–967. https://doi.org/10.1890/14-0932.1

Koons, D. N., Grand, J. B., & Arnold, J. M. (2006). Population momentum across vertebrate life histories. *Ecological Modelling*, *197*, 418–430. https://doi.org/10.1016/J.ECOLMODEL.2006.03.034

Koons, D. N., Grand, J. B., Zinner, B., & Rockwell, R. F. (2005). Transient population dynamics: Relations to life history and initial population state. *Ecological Modelling*, *185*, 283–297. https://doi.org/10.1016/J.ECOLMODEL.2004.12.011

Koons, D. N., Iles, D. T., Schaub, M., Caswell, H., & Hodgson, D. (2016). A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology Letters*, *19*, 1023–1031. https://doi.org/10.1111/ele.12628

Lebreton, J.-D., & Gimenez, O. (2013). Detecting and estimating density dependence in wildlife populations. *The Journal of Wildlife Management*, *77*(1), 12–23. https://doi.org/10.1002/jwmg.425

López-Sepulcre, A., & Kokko, H. (2005). Territorial defense, territory size, and population regulation. *The American Naturalist*, *166*, 317–329. https://doi.org/10.1086/432560

MacNulty, D. R., Smith, D. W., Vucetich, J. A., Mech, L. D., Stahler, D. R., & Packer, C. (2009). Predatory senescence in ageing wolves. *Ecology Letters*, *12*, 1347–1356. https://doi.org/10.1111/j.1461-0248.2009.01385.x

MacNulty, D. R., Stahler, D. R., Wyman, C. T., Ruprecht, J., & Smith, D. W. (2016). The challenge of understanding Northern Yellowstone elk dynamics after wolf reintroduction. *Yellowstone Science*, *24*(1), 25–33.

Margalida, A., Oro, D., Cortés-Avizanda, A., Heredia, R., & Donázar, J. A. (2011). Misleading population estimates: Biases and consistency of visual surveys and matrix modelling in the endangered bearded vulture. *PLoS ONE*, *6*(10), e26784. https://doi.org/10.1371/journal.pone.0026784

McCorquodale, S. M., Eberhardt, L. L., & Eberhardt, L. E. (1988). Dynamics of a colonizing elk population. *Journal of Wildlife Management*. https://doi.org/10.2307/3801240

McDonald, J. L., Stott, I., Townley, S., & Hodgson, D. J. (2016). Transients drive the demographic dynamics of plant populations in variable environments. *Journal of Ecology*, *104*, 306–314. https://doi.org/10.1111/1365-2745.12528

Mech, D., & L. Boitani (Eds.) (2003). *Wolves: Behavior, ecology and conservation*. Chicago, IL: The University of Chicago Press.

Miller, D. H., Jensen, A. L., & Hammill, J. H. (2002). Density dependent matrix model for gray wolf population projection. *Ecological Modelling*, *151*, 271–278. https://doi.org/10.1016/S0304-3800(01)00493-8

Millon, A., Petty, S. J., Little, B., Gimenez, O., Cornulier, T., & Lambin, X. (2014). Dampening prey cycle overrides the impact of climate change on predator population dynamics: A long-term demographic study on tawny owls. *Global Change Biology*, *20*, 1770–1781. https://doi.org/10.1111/gcb.12546

Millon, A., Petty, S. J., Little, B., & Lambin, X. (2011). Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. *Journal of Animal Ecology*, *80*, 968–975. https://doi.org/10.1111/j.1365-2656.2011.01842.x

Nussey, D. H., Froy, H., Lemaitre, J. F., Gaillard, J. M., & Austad, S. N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, *12*, 214–225. https://doi.org/10.1016/j.arr.2012.07.004

Payo-Payo, A., Sanz-Aguilar, A., Genovart, M., Bertolero, A., Piccardo, J., Camps, D., ... Oro, D. (2018). Predator arrival elicits differential dispersal, change in age structure and reproductive performance in a prey population. *Scientific Reports*, *8*, 1971. https://doi.org/10.1038/s41598-018-20333-0

Pelletier, F., Moyes, K., Clutton-Brock, T. H., & Coulson, T. (2012). Decomposing variation in population growth into contributions from environment and phenotypes in an age-structured population. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 394–401.

Peterson, R. O. (1977). *Wolf ecology and prey relationships on Isle Royale*. Scientific Monograph Series No. 11. Washington, DC: U.S. National Park Service.

Petty, S. J.(1992a). A guide to age determination of Tawny Owl Strix aluco. In C. A. Galbraith, I. R. Taylor, & S. Percival (Eds.), *The ecology and conservation of European owls* (pp. 89–91). Peterborough, UK: Joint Nature Conservation Committee (UK Nature Conservation No. 5.).

Petty, S. J. (1992b). *Ecology of the Tawny owl Strix aluco in the spruce forests of Northumberland and Argyll*. PhD thesis, Open University, Milton Keynes, UK.

Pimm, S. L. (1991). *The balance of nature?: Ecological issues in the conservation of species and communities*. Chicago, IL: University of Chicago Press.

Plummer, M. (2012). *JAGS version 3.3.0 user manual*. Retrieved from http://mcmcjags.sourceforge.net/

Poole, R. W. (1978). The statistical prediction of population fluctuations. *Annual Review of Ecology and Systematics*, *9*, 427–448. https://doi.org/10.1146/annurev.es.09.110178.002235. Retrieved from http://www.jstor.org/stable/2096756.

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/.

Ranta, E., Lundberg, P., Kaitala, V., & Laakso, J. (2000). Visibility of the environmental noise modulating population dynamics. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*, 1851–1856. https://doi.org/10.1098/rspb.2000.1220

Regehr, E. V., Amstrup, S. C., & Stirling, I. (2006). *Polar bear population status in the southern Beaufort Sea*. Reston, VA: USGS Alaska Science Center.

Rolandsen, C. M., Solberg, E. J., Heim, M., Holmstrøm, F., Solem, M. I., & Sæther, B. E. (2008). Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. *European Journal of Wildlife Research*, *54*(1), 6–14. https://doi.org/10.1007/s10344-007-0100-8

Royle, N. J., Lindström, J., & Metcalfe, N. B. (2005). A poor start in life negatively affects dominance status in adulthood independent of body size in green swordtails *Xiphophorus helleri*. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 1917–1922. https://doi.org/10.1098/rspb.2005.3190

Ruprecht, J. S. (2016). *The demography and determinants of population growth in Utah moose (Alces alces shirasi)*. Utah State University. Retrieved from http://digitalcommons.usu.edu/etd

Sand, H., Vucetich, J. A., Zimmermann, B., Wabakken, P., Wikenros, C., Pedersen, H. C., ... Liberg, O. (2012). Assessing the influence of prey-predator ratio, prey age structure and packs size on wolf kill rates. *Oikos*, *121*, 1454–1463. https://doi.org/10.1111/j.1600-0706.2012.20082.x

Sinclair, A. R. E. (2003). Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *358*, 1729–1740. https://doi.org/10.1098/rstb.2003.1359

Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S., & Evans, S. B. (2004). Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management*, *68*, 153–166. https://doi.org/10.2193/0022-541X(2004)068[0153:WPSAEO]2.0.CO;2

Smith, D., Stahler, D., Stahler, E., Metz, M., Cassidy, K., Cassidy, B., & McIntyre, R. (2015). *Yellowstone wolf project annual report 2014*. Yellowstone National Park, WY: National Park Service.

Solberg, E. J., Sæther, B.-E., Strand, O., & Loison, A. (1999). Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, *68*, 186–204. https://doi.org/10.1046/j.1365-2656.1999.00275.x

Steele, J. H. (1985). A comparison of terrestrial and marine ecological systems. *Nature*, *313*, 355–358.

Stott, I., Townley, S., & Hodgson, D. J. (2011). A framework for studying transient dynamics of population projection matrix models. *Ecology Letters*, *14*, 959–970. https://doi.org/10.1111/j.1461-0248.2011.01659.x

Tallian, A., Smith, D. W., Stahler, D. R., Metz, M. C., Wallen, R. L., Geremia, C., … MacNulty, D. R. (2017). Predator foraging response to a resurgent dangerous prey. *Functional Ecology*, *31*, 1418–1429. https://doi.org/10.1111/1365-2435.12866.

Vasseur, D. A., & Yodzis, P. (2004). The color of environmental noise. *Ecology*, *85*, 1146–1152. https://doi.org/10.1890/02-3122

Vucetich, J., & Peterson, R. O. (2004). The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 183–189.

Vucetich, J. A., & Peterson, R. O. (2004). The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. *Oikos*, *107*, 309–320. https://doi.org/10.1111/j.0030-1299.2004.13483.x

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*(Suppl. 1), S120–S139. https://doi.org/10.1080/00063659909477239

White, P. J., Proffitt, K. M., & Lemke, T. O. (2012). Changes in Elk distribution and group sizes after wolf restoration. *The American Midland Naturalist*, *167*, 174–187. https://doi.org/10.1674/0003-0031-167.1.174

Wolkovich, E. M., Cook, B. I., McLauchlan, K. K., & Davies, T. J. (2014). Temporal ecology in the Anthropocene. *Ecology Letters*, *17*, 1365–1379. https://doi.org/10.1111/ele.12353

Wright, G. J., Peterson, R. O., Smith, D. W., & Lemke, T. O. (2006). Selection of northern Yellowstone elk by gray wolves and hunters. *Journal of Wildlife Management*, *70*, 1070–1078. https://doi.org/10.2193/0022-541X(2006)70[1070:SONYEB]2.0.CO;2

Yearsley, J. M. (2004). Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling*, *177*, 245–258. https://doi.org/10.1016/J.ECOLMODEL.2003.12.053

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.