

Decomposing demographic contributions to the effective population size with moose as a case study

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Abstract

Levels of random genetic drift are influenced by demographic factors, such as mating system, sex ratio and age structure. The effective population size (N_e) is a useful measure for quantifying genetic drift. Evaluating relative contributions of different demographic factors to N_e is therefore important to identify what makes a population vulnerable to loss of genetic variation. Until recently, models for estimating N_e have required many simplifying assumptions, making them unsuitable for this task. Here, using data from a small, harvested moose population, we demonstrate the use of a stochastic demographic framework allowing for fluctuations in both population size and age distribution to estimate and decompose the total demographic variance and hence the ratio of effective to total population size (N_e/N) into components originating from sex, age, survival and reproduction. We not only show which components contribute most to N_e/N currently, but also which components have the greatest potential for changing N_e/N . In this relatively long-lived polygynous system we show that N_e/N is most sensitive to the demographic variance of older males, and that both reproductive autocorrelations (i.e., a tendency for the same individuals to be successful several years in a row) and covariance between survival and reproduction contribute to decreasing N_e/N (increasing genetic drift). These conditions are common in nature and can be caused by common hunting strategies. Thus, the framework presented here has great potential to increase our understanding of the demographic processes that contribute to genetic drift and viability of populations, and to inform management decisions.

KEYWORDS

age structure, demographic variance, genetic drift, individual heterogeneity, individual reproductive value; life history

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1 | INTRODUCTION

Effective population size (N_e) is a central concept in evolutionary theory and conservation biology that is crucial for understanding changes in gene frequencies in finite populations. N_e quantifies the rate of random genetic drift and interacts with natural selection to influence the probability of fixation of advantageous and deleterious mutations (Caballero, 1994; Charlesworth, 2009; Crow & Kimura, 1970; Wright, 1931). Therefore, estimating N_e and examining how different underlying demographic factors contribute to the observed N_e is important in predicting evolutionary trajectories of finite populations and in evaluating population viability, especially for small or harvested populations (Allendorf, England, Luikart, Ritchie, & Ryman, 2008; Frankham, Bradshaw, & Brook, 2014; Sæther, Engen, & Solberg, 2009).

N_e is most commonly defined as the size of a diploid population that produces the same rate of random genetic drift (variance effective population size), or amount of inbreeding (inbreeding effective size) as a Wright-Fisher (WF) ideal population. A WF ideal population is a population of constant size that reproduces by random sampling of gametes, and has nonoverlapping generations and a Poisson distributed family size (Wright, 1931). In natural populations, deviations from a WF ideal population cause N_e to differ from the actual population size, N , usually by being smaller (e.g., Nunney, 1991, 1993, 1996; Palstra & Ruzzante, 2008). Therefore, the ratio N_e/N is a useful metric for studying genetic drift in natural populations (Frankham, 1995; Luikart, Ryman, Tallmon, Schwartz, & Allendorf, 2010). This ratio can be estimated using a demographic approach without having to estimate N_e directly (Engen, Lande, & Sæther, 2005), and can then be combined with an estimate of N , which is generally easier to estimate than N_e , if one wishes an estimate of N_e alone.

A central task in conservation genetics is to identify population traits that cause vulnerability to genetic issues that may threaten population viability. Loss of genetic variation through genetic drift is one important such issue (Allendorf, Hohenlohe, & Luikart, 2010; Frankham et al., 2014). Thus, understanding how life history and other population traits influence N_e , and developing methods for taking these traits into account in estimates of N_e , are of central importance for conservation (Waples, 2002, 2006; Waples, Luikart, Faulkner, & Tallmon, 2013).

From previous studies we know that fluctuations in population size, N , and age structure, caused partially by environmental and demographic stochasticity (Lande, Engen, & Sæther, 2003) can affect N_e in complex ways (Waples, 2006, 2010). It is therefore essential to use models that can account for population structure when estimating N_e , particularly in long-lived species. In species with two sexes, survival rates and their variance (Engen, Lande, & Sæther, 2003; Loison, Festa-Bianchet, Gaillard, Jorgenson, & Jullien, 1999), and distributions of reproductive success (Clutton-Brock, 1988; Sæther & Engen, 2019; Sæther et al., 2004) may differ between the sexes, resulting in sex-specific demographic stochasticity (Engen et al., 2003; Sæther et al., 2004). The magnitude of these sex-specific differences is closely related to mating system (Legendre, Clobert,

Møller, & Sorci, 1999; Myhre, Engen, & Sæther, 2017; Sæther et al., 2004). For instance, in polygynous populations, between-male reproductive variance is high (Clutton-Brock, 1988; Emlen & Oring, 1977), resulting in high demographic variance and reduced N_e (Lee, Engen, & Sæther, 2011; Lee, Sæther, & Engen, 2011; Lee, Sæther, Markussen, & Engen, 2017; Nunney, 1993). The demographic variance ($\sigma_{d_g}^2$) is a measure of demographic stochasticity based on quantifying the temporal mean of the within-year variance in individual genetic contributions to the future population (see Engen, Lande, Sæther, & Gienapp, 2010). High variance in reproductive success is expected from theory to be a dominant factor reducing N_e (Crow & Morton, 1955; Hill, 1972, 1979; Kimura & Crow, 1963; Wright, 1938). Accordingly, this has been found in species from a wide range of taxa, ranging from fishes (e.g., steelhead trout, *Oncorhynchus mykiss*; Araki, Waples, Ardren, Cooper, & Blouin, 2007) to amphibians (e.g., Italian agile frog, *Rana latastei*; Ficetola, Padoa-Schioppa, Wang, & Garner, 2010), birds (e.g., Gunnison sage-grouse, *Centrocercus minimus*; Stiver, Apa, Remington, & Gibson, 2008) and mammals (e.g., woodrats, *Neotoma macrotis*; Matocq, 2004).

Another factor that could influence N_e is demographic autocorrelation, as individual vital rates are not necessarily independent from year to year. Covariation in individual reproductive success from one year (or time step) to the next (hereafter 'reproductive autocorrelations') are widespread in nature (e.g., Hamel et al., 2010; Rivalan et al., 2005; Veran & Beissinger, 2009). If reproduction is costly (Stearns, 1992), we might expect negative reproductive autocorrelation due to the principle of allocation (Williams, 1966) with current reproductive output leading to reduced future reproduction. However, positive autocorrelation might be observed if some individuals consistently produce more offspring than others resulting in individual heterogeneity in fitness and increased variance in lifetime reproductive success (Hamel, Côté, Gaillard, & Festa-Bianchet, 2009; Markussen et al., 2019, 2018; Weladji et al., 2008). Theoretical studies have shown that positive reproductive autocorrelations can increase the demographic variance and thus decrease time to extinction (Lee et al., 2017; Vindenes, Engen, & Sæther, 2008), as well as decreasing N_e (Lee, Engen, et al., 2011; Nunney, 1996).

Although a number of demographic factors are known to influence N_e , it is challenging to evaluate the relative contributions from each of them, and to identify the demographic parameters, processes, and groups of individuals to which N_e is the most sensitive (Stubberud et al., 2017). Given the importance of genetic drift for population viability and management, evaluating contributions to N_e in this way is an important task that requires not only data on age, sex and individual realizations of reproduction and survival, but also appropriate modelling techniques. In this study, we use a combination of modelling approaches, combined with sensitivity analyses, to demonstrate how this task can be accomplished, estimating N_e/N and showing how the different demographic contributions presented above can be partitioned out.

We use data on individual survival and reproductive success from a long-term study of a small, harvested moose (*Alces alces*) population, and utilize the demographic framework developed by

Engen et al. (2005), Engen et al. (2010), and Engen et al. (2013) to estimate N_e/N from the generation time (T) and the demographic variance (σ_{dg}^2) of a hypothetical subpopulation of heterozygotes carrying a rare neutral allele at a diallelic locus. This method uses the knowledge that dynamics of age-structured populations can be approximated by the dynamics of the total reproductive value (Engen, Lande, Sæther, & Festa-Bianchet, 2007), and does not make biologically unrealistic assumptions about the sampled population, such as constant population size or stable age structure (cf. Hill, 1972, 1979). In order to decompose the demographic variance and the ratio N_e/N into contributions from sex, age, reproductive autocorrelations, and covariances between survival and reproduction we use three different classifications of individuals in our models. First, we develop a sex-age-structured model and a simplified sex-maturity-structured version with only two age classes (juveniles and adults). This is combined with a variance-based global sensitivity analysis to partition out contributions from reproduction and survival in different sex-age classes. Then we use a more complicated sex-age-state-structured model where individuals are additionally classified according to reproductive state (number of calves), to look at contributions from reproductive autocorrelations and covariance between survival and reproduction. Figure 1 provides an overview of the main analyses and how they relate to each other. Using this framework, we evaluate the different demographic contributions to σ_{dg}^2 and thus N_e/N in our moose case study. The moose is a relatively long-lived, polygynous species, and the studied population is harvested. Results from this case study are therefore directly relevant to many other harvested ungulates, and to our understanding of the effective population size of polygynous species. More broadly, the modelling framework we present here can be used in a wide variety of systems to estimate N_e/N and evaluate contributions to this measure from different demographic factors.

2 | MATERIALS AND METHODS

2.1 | General population genetic model

In this section, we present the theoretical modelling framework used to calculate and decompose N_e/N . This demographic framework was developed by Engen et al. (2005), Engen, Lande, Sæther, and Dobson (2009), and Engen et al. (2010), where they show that the asymptotic variance effective population size of age-structured populations can be expressed as

$$\frac{N_e}{N} = \frac{1}{\sigma_{dg}^2 T}. \quad (1)$$

Here, N is the total population size and T is the generation time, calculated as the mean age of all parents of newborns (Lande et al., 2003). Specifically, following Pollak (2000), this method derives the variance effective size of age-structured, two-sex populations from the demographic variance (σ_{dg}^2) of a hypothetical subpopulation of

individuals carrying a rare, neutral allele, that can be assumed to mate with individuals from the larger subpopulation not carrying the allele (Engen et al., 2005). The subscript g in σ_{dg}^2 signifies that the demographic variance also has a genetic component due to Mendelian segregation. The method can be used for population structure other than simple age (Lee, Engen, et al., 2011) and has been shown to give accurate approximations of the effective population size even when populations are small and alleles are not rare (Engen et al., 2005).

Let $n = (n_{f1}, n_{f2}, \dots, n_{fk}, n_{m1}, \dots, n_{mp})$ be a vector representing the number of females and males in each class carrying the rare allele. The stochastic projection matrix, L , with dimensions $(k + p) \times (k + p)$ that fulfills $n_{t+1} = Ln_t$, then contains four types of fecundities (female and male production of females and males carrying the rare allele) as well as survival of females and males (Engen et al., 2010). Within this framework, individuals can be classified in different ways. For example, the k female classes and p male classes can represent ages and/or different states. The matrix L always consists of four submatrices, representing contributions from females to females, females to males, males to females, and males to males. The construction of these submatrices depends on the classification used. In Appendix S1 we show specific matrices for the models used in our analyses.

The dominant eigenvalue of L is the asymptotic population growth rate λ of the population, while the right eigenvector u , gives the proportion of individuals in each class i (u_i) under stable population structure (scaled such that $\sum u_i = 1$). The left eigenvector v gives the reproductive values (v_i) of each class i and is scaled such that $\sum u_i v_i = 1$ to give the Fisherian age distribution (Engen et al., 2009). These are fundamental for calculating the effective population size in age-structured populations from the demographic variance.

Since the total number of offspring (of each sex) produced by the female population must equal the total number of offspring (of each sex) produced by the male population, contributions to the asymptotic population growth rate λ from females and males must be the same (Caswell, 2001; Engen et al., 2010). Due to sampling error, this is not always the case when male and female parameters are estimated separately. To assure internal consistency of the model, male reproduction is therefore scaled by a constant, such that the submatrix of males (contributions from males to males) has the same growth rate as the submatrix of females (contributions from females to females) (see Engen et al., 2010, and Appendix S1.3).

Using v and u from L , the demographic variance of the population, accounting for genetic stochasticity can be expressed as

$$\sigma_{dg}^2 = \sum \sigma_{dgi}^2 u_i, \quad (2)$$

where $\sigma_{dgi}^2 = \text{Evar}(W_i|Z)$ are the class-specific demographic variances. Here W_i is the individual reproductive value of an individual in class i , and Z represents the environment in a given year. The individual reproductive value describes the contribution of an individual in class i to the total reproductive value of the population the next year, such that

$$W_i = \sum_j J_{ij} v_j + X_i v_{f1} + Y_i v_{m1}, \quad (3)$$

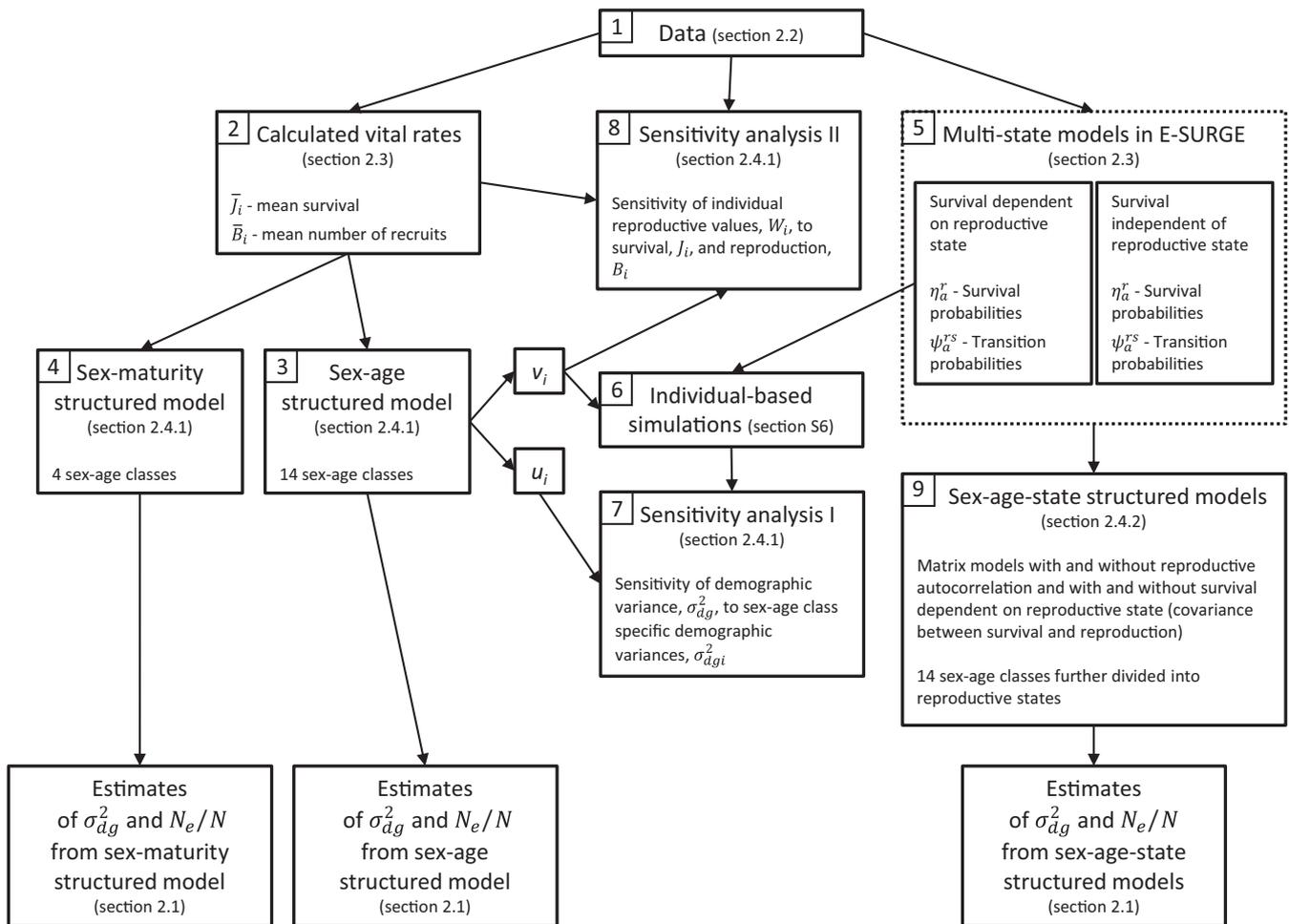


FIGURE 1 Overview of the main analyses in the paper and how they relate to each other, with references to the appropriate methods sections. The subscript i refers to sex-age class, a to age, and r and s to states. u_i and v_i are the proportion of individuals in sex-age class i under stable sex-age structure, and the reproductive value of sex-age class i , respectively

where J_{il} is an indicator variable for the individual's own survival that takes the value 1 if the individual survives and moves into class l , and zero if the individual dies prior to the next census or moves into a class other than l . X_i and Y_i are the number of female and male offspring, respectively, produced by an individual carrying the rare allele, that survive to the next census. The v_i is the reproductive value of class l that an individual in class i may move into, and v_{f1} and v_{m1} are the reproductive values of class one for females and males, respectively. Note that all individuals in class i share the same age a , and hence the summation over l in Equation 3 represents all the states an individual within that age class may move into at age $a + 1$. Thus, in a sex-age-structured model without additional states, this sum collapses to $J_i v_{i+1}$. This method, using individual reproductive values, makes it possible to filter out stochastic fluctuations due to deviations from the stable stage structure (Engen et al., 2009). Thus, it becomes possible to calculate the asymptotic N_e/N ratio even if the study population was not at its stable structure when the data were collected.

With no environmental variance, the class-specific demographic variance σ_{dgi}^2 (cf. Equation 2) is simply the variance in the W_i , which can be written as

$$\sigma_{dgi}^2 = \text{Var}(W_i) = \sum_l v_l^2 \text{Var}(J_{il}) + 2 \sum_l \sum_{y \neq l} v_l v_y \text{Cov}(J_{il}, J_{iy}) + v_{f1}^2 \text{Var}(X_i) + v_{m1}^2 \text{Var}(Y_i) + 2v_{f1} v_{m1} \text{Cov}(X_i, Y_i), \quad (4)$$

where $y \neq l$ represents classes other than l that individuals from class i may move into. The σ_{dgi}^2 can then be combined with the u_i calculated from the projection matrix L to give an estimate of the demographic variance of the population (Equation 2). In the sex-age-structured model, the σ_{dgi}^2 can also be estimated using a sum of squares method in which individual data on vital rates are used directly (Engen et al., 2009, 2010). However, when contributions to σ_{dgi}^2 of more complex structures than sex and age (like reproductive autocorrelations) are examined, the more complicated patterns of transition between states prevent the use of this method. Then σ_{dgi}^2 must be calculated using Equation 4 (see further details in Appendix S2.2).

Finally, in order to obtain an estimate of N_e/N (Equation 1), an estimate of the generation time T is needed. Using the asymptotic growth rate λ from the projection matrix L , the female-specific generation time can be calculated as $T_f = q \sum_{a=1}^{\infty} a l_a b_a \lambda^{-a}$ where l_a is the probability that a female survives until age a and b_a is the average number of offspring

produced by a female of age a (Engen et al., 2010). The parameter q is the expected sex ratio at birth, calculated as the proportion of females. The expression for the male generation time, T_m , is equivalent, calculating l_a and b_a for the male segment, and replacing q with $1 - q$. The generation time of the total population is then $T = (T_f + T_m)/2$.

2.2 | Study system

Vega (119 km², 65°40'N, 11°55'E) is an island 13 km off the coast of northern Norway. The moose population there was founded by one male and two females immigrating from the mainland in 1985, and an additional 20 immigrants have been recorded between 1986 and 2011. By 1989, the population had grown to 15 individuals and annual hunting was initiated. After 1992, the population breeding size has varied between 21 and 39 individuals, with 12–25 calves born each year (Haanes et al., 2013; Solberg, Heim, Grøtan, Sæther, & Garel, 2007; Table S1). The natural mortality is very low (5% in calves, 2% in older individuals), so hunting is the main mortality factor on the island (Solberg et al., 2010). Although the exact length and timing of the permitted hunting season has varied a bit over the study period, the vast majority of hunting has taken place in October, i.e., after the start of the rut. Hunting is based on quotas of calves, adult females and adult males. Due to varying age- and sex-biased harvesting, the sex ratio and age structure in the population has fluctuated over time (Herfindal et al., 2014). Environmental variation does not seem to affect the vital rates of the moose at Vega, as the estimated environmental variance in this population is close to zero (Sæther, Engen, Solberg, & Heim, 2007). More information about the study system can be found in for example Kvalnes et al. (2016), Solberg et al. (2007), Sæther et al. (2007), Sæther, Solberg, and Heim (2003) and Sæther et al. (2004).

Since 1992, all new calves that survived the annual hunt during autumn have been radio/GPS collared and measured annually during winter (except in 2003 and 2008). In addition, female moose have been observed around potential parturition dates and recorded with/without calves. Sex, age and tissue samples have been collected from nearly all moose harvested on the island.

With the collected tissue samples, Haanes et al. (2013) constructed a nearly complete genetic pedigree of the population based on 22 microsatellite loci. This parentage assignment enabled the number of offspring to be genetically determined for both sexes. The data include individual histories of 207 females and 240 males from 1984 to 2011, where 111 females and 137 males were alive at the start of their first potential mating season (1.5 years old). Females can start reproducing when two years old and can give birth to one or two calves during May–June each year. The oldest male recorded was 11 years old, while the oldest female was 15 years old.

2.3 | Parameter estimation

Based on the available sample size and previous knowledge about the life history of moose (Garel et al., 2009; Markussen et al., 2018,

2019; Sæther & Haagenrud, 1983), we assumed vital rates to be equal for females aged 2.5–9.5. Thus, we estimated survival and fecundity rates for four subsets of females and males (females aged 0.5–1.5 years old, 1.5–2.5, 2.5–9.5 and 9.5+, and males aged 0.5–1.5, 1.5–2.5, 2.5–3.5 and 3.5+). Because of the thorough pedigree/parentage assignment for this population (Haanes et al., 2013), these parameters were calculated directly from the data, assuming no errors in the recording of reproductive and survival status of individuals. The data were structured to conform to a prebreeding census (Caswell, 2001), with the census set to late September (right before the hunting season). Although calves are not born until May–June, males that have mated before being shot can still produce offspring in the time step that they are killed. However, this is not true for females. Therefore, females shot during the hunting season were assigned to the dead state one time step before (i.e., before census and breeding). Thus, the survival estimate for females in age class f_1 covered two consecutive hunting seasons. The probability of a new calf being female, q , was set to 0.5 based on previous research (Sæther et al., 2007) and estimates of the sex ratio at birth being very close to even.

To estimate transition probabilities between the different reproductive states used in the sex-age-state-structured model we used multi-state capture-mark-recapture models run in E-SURGE (for more information see Appendix S4; Choquet, Rouan, & Pradel, 2009). Due to the thorough pedigree/parentage assignment for this population (Haanes et al., 2013) we assumed that the reproductive and survival status of all individuals was known (no error in determination of reproductive or survival state), and the capture probability was fixed to one. Females were divided into four states: (a) No reproduction; (b) produced one calf; (c) produced two calves and (d) hunted/died naturally (Figure S1.2a). Males in age class m_1 to m_3 were also divided into four states: (a) No reproduction; (b) produced 1–2 calves; (c) produced three or more calves, and (d) hunted/died naturally. Males in age class m_4 were divided into five states: (a) No reproduction; (b) produced 1–2 calves; (c) produced 3–4 calves; (d) produced five or more calves, and (e) hunted/died naturally (Figure S1.2b). This class structure was selected to best capture the distribution of male calf production observed in the data.

2.4 | Estimation and decomposition of demographic variance and effective population size

2.4.1 | Effects of sex, age, survival and reproduction

For the sex-age-structured model, the J_i , X_i and Y_i in Equation 3 were found directly from the data. The estimated vital rates were used to construct a projection matrix, L , with 14 sex-age classes (10 age classes for females f and 4 age classes for males m), giving $i = (f_1, f_2, f_3, f_4, f_5, f_6, f_7, f_8, f_9, f_{10}, m_1, m_2, m_3, m_4)$, where f_1 represents 0.5–1.5-year-old females (calves), f_2 represents 1.5–2.5-year-old females (potential age at primiparity), f_{3-9} represents females of age 2.5–9.5 years (prime-aged females, all with equal survival and fecundity estimates),

and f_{10} represents females of age 9.5 years and above (potentially senescent females). For males, m_1 represents 0.5–1.5-year-old males (calves), m_2 represents 1.5–2.5-year-old males (potential age at first reproduction), m_3 represents 2.5–3.5-year-old males, and m_4 represents 3.5-year-old males and older. Since prime-aged females (f_{3-9}) share the same vital rates, the u_i 's and v_i 's from the projection matrix L for these females were merged into a single value of u and v , subsequently producing a single σ_{dg}^2 (see Appendix S1.1).

To assess the importance of age structure among adults for the ratio N_e/N , we also calculated the ratio using the same approach as described above, but merging all mature individuals of each sex into a single age class (sex-maturity-structured model). The projection matrix L then consisted of four sex-age classes (one class of each sex for ages 0.5–1.5 years, and one class of each sex for mature individuals older than 1.5 years).

We used a variance-based global sensitivity analysis (GSA), the Sobol' method, to evaluate the sensitivity of (i) the total demographic variance to the different sex and age-specific demographic variances (Equation 2) and (ii) the individual reproductive values to survival and reproduction (for more information about the method, see Saltelli & Annoni, 2010; Saltelli et al., 2010; Sobol', 2001; Yang, 2011). Sensitivity of the total demographic variance (i) translates directly to sensitivity of N_e/N , because the vital rates at each age are not altered in this analysis, causing the generation time, T , to be constant (see Equation 1). In (ii), we used the formula $W_i = J_i v_{i+1} + q B_i v_{f1} + (1 - q) B_i v_{m1}$, where B_i is the total number of offspring produced by an individual in sex-age class i that survive to the next census. This formula, with total offspring number and sex ratio rather than numbers of male and female offspring directly (cf. Equation 3), was used because the separation between offspring sexes is of little interest in this context.

The Sobol' method (Saltelli et al., 2010; Sobol', 1993, 2001; Yang, 2011) examines the full range of variation of each input parameter and provides quantitative measures of the importance of these by the use of sensitivity indices. Specifically, the total, unconditional variance in the output variable R , $\text{var}(R) = V$ is decomposed into conditional variances, $\text{var}(E(R|X=x)) = V_x$, where $V_x \in [0, V]$ gives the expected reduction in V if parameter x was fixed, and represents the first order effect of x on R . The associated sensitivity index (first order sensitivity coefficient) of parameter x is

$$S_x = \frac{V_x}{V}. \quad (5)$$

Parameter x may interact with the other input parameters in affecting R . This "total order" effect of x on R (including the first order effect and all interactions) is given by the total sensitivity index

$$S_{Tx} = 1 - \frac{V_{\sim x}}{V} = 1 - S_{\sim x}, \quad (6)$$

where $\sim x$ denotes all input parameters except x (Saltelli & Annoni, 2010). The difference between S_x and S_{Tx} , $\Delta S = S_{Tx} - S_x$, denotes the

degree of interaction between parameter x and the other parameters, and was in the current study considered significant if $\Delta S \geq 0.05$ (Chu-Agor, Muñoz-Carpena, Kiker, Emanuelsson, & Linkov, 2011). To estimate S_x and S_{Tx} , we used the Monte Carlo based estimator *soboljansen* in the R-package *sensitivity* (Iooss et al., 2018). To ensure convergence, the base sample size of each input parameter was 15,000 in the sensitivity analysis of the demographic variance and 10,000 in the sensitivity analyses of the individual reproductive values. In the first sensitivity analysis these were drawn from simulated estimates (see Appendix S5.1 and S5.2 for more details), while in the second analysis they were drawn directly from the moose data (see Appendix S5.3).

2.4.2 | Effects of reproductive autocorrelation and covariance between survival and reproduction

To quantify the effect of reproductive autocorrelations on N_e/N , we used an expanded population structure where males and females of each age were further classified according to the number of calves they produced (sex-age-state-structured model; see Lee et al., 2017). Transition probabilities between these different states were parameterized with the E-SURGE estimates described in Section 2.3. A scaling similar to the one described above (Section 2.1) was used to assure that the total contribution of offspring was the same from the male and female population segments (Appendix S1.3).

Equivalent models without reproductive autocorrelations, or with reproductive autocorrelations only in one sex, were constructed for comparison. Without reproductive autocorrelations the probability of an individual entering a certain reproductive class is independent of the reproductive class that individual was in the year before. To remove the reproductive autocorrelations without introducing other differences between the two models, these probabilities were set to the values that preserved the stable stage structure of the model with reproductive autocorrelations. Additionally, we ran models where these probabilities were estimated from E-SURGE.

Each model was run in two versions; one with and one without covariance between survival and reproduction. Survival estimates were obtained from E-SURGE models with separate survival estimates for the different reproductive classes (i.e., with covariance) and without separate survival estimates for the different reproductive classes (i.e., without covariance; survival only depends on age) (Appendix S4).

Using these models, we calculated σ_{dg}^2 and N_e/N from Equations 1 and 2 above (details in Appendix S2.2) for the different model combinations. The influence of uncertainty in the parameter estimates on calculated σ_{dg}^2 and N_e/N was investigated by drawing new values from the distributions around the parameter estimates provided by E-SURGE (see Appendix S6). Combinations of parameter estimates were drawn 50,000 times, and σ_{dg}^2 recalculated for each set of parameters.

All calculations and analyses in this paper were carried out in R (R Core Team, 2019) unless otherwise specified.

TABLE 1 Demographic variance σ_{dg}^2 , generation time T and N_e/N for moose at Vega, 1984–2011, estimated from the sex-age-state-structured models using transition estimates from E-surge; partitioning out the contributions from covariance between survival and reproduction (i.e., when survival differs among reproductive classes) and reproductive autocorrelations

Row	Autocorrelation females	Autocorrelation males	Covariance females	Covariance males	σ_{dg}^2	T	N_e/N
1	X	X	X	X	0.669	5.371	0.278
2	X		X	X	0.601	5.362	0.310
3		X	X	X	0.665	5.371	0.280
4			X	X	0.598	5.362	0.312
5	X	X	X		0.591	5.360	0.316
6			X		0.543	5.352	0.344
7	X	X		X	0.664	5.523	0.273
8				X	0.592	5.511	0.307
9	X	X			0.584	5.509	0.311
10	X				0.540	5.499	0.337
11		X			0.581	5.509	0.313
12					0.537	5.499	0.339

Note: For more information about the models, see methods (Sections 2.1, 2.4.2 and Appendix S1.2 and S2.2).

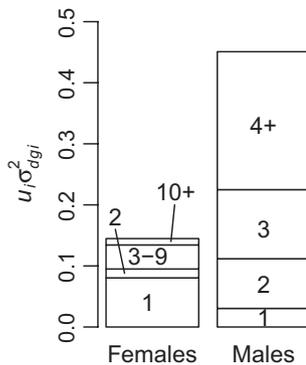


FIGURE 2 Older males contributed most to the demographic variance. Bars show cumulative sum of the sex-age class specific demographic variances weighted by the proportion of individuals in each sex-age class at stable stage structure ($u_i \sigma_{dgi}^2$). Numbers on bars indicate age classes

3 | RESULTS

Depending on the model used and its associated assumptions, the σ_{dg}^2 estimates ranged from 0.54 to 0.76, T ranged from 4.81 to 5.52 and the estimated N_e/N ranged between 0.27 and 0.34. For the moose population at Vega, which is known to both have reproductive autocorrelation and covariance between survival and reproduction in both sexes (Lee et al., 2017; Markussen et al., 2018, 2019), we consider the most accurate estimates to arise from the fully sex-age-state-structured model (Table 1, first row), in which σ_{dg}^2 is estimated to 0.67, T is estimated to 5.37 and hence N_e/N is estimated to 0.28.

3.1 | Effects of sex, age, survival and reproduction

The sex-age-structured model (Equations 1 and 2 in Section 2.1, and equations 1, 3 and 4 in Appendix S2.1) gave a ratio of effective to total

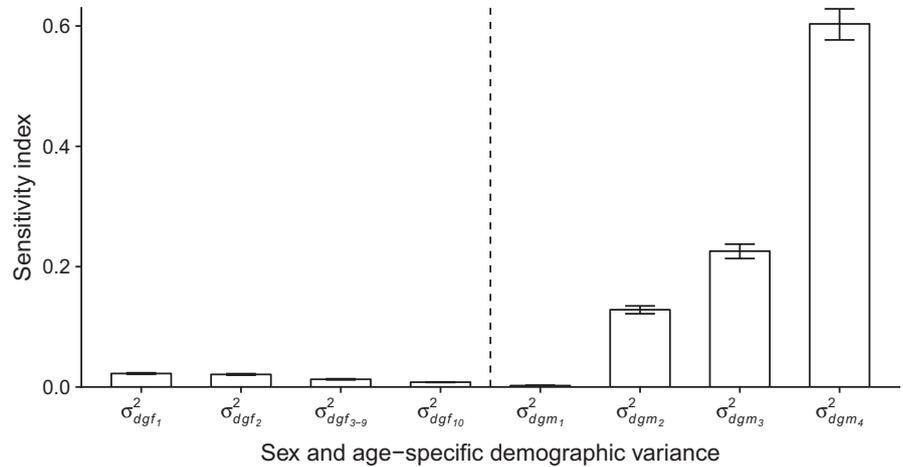
population size, N_e/N , estimate of 0.31 ($\sigma_{dg}^2 = 0.60$, $T = 5.49$ years). Males contributed more to σ_{dg}^2 than females ($\sigma_{dgm}^2 = 0.45$, $\sigma_{dgf}^2 = 0.15$; Figure 2, Table S7). When partitioned into sex- and age-specific demographic variances, σ_{dgi}^2 , males in age class m_4 contributed most, followed by males in age class m_3 (Figure 2, Table S7). The weighted demographic variance in male age class m_2 ($u_{m2} \sigma_{dgm2}^2 = 0.08$) was approximately equal to that of female calves ($u_{f1} \sigma_{dgf1}^2 = 0.08$), while for male calves, the weighted demographic variance was quite low ($u_{m1} \sigma_{dgm1}^2 = 0.03$). For females, the pattern of age-specific variances differed from that of males, being highest in calves (Figure 2, Table S7).

In the sex-maturity-structured model (with no age structure among mature individuals), the estimate of total demographic variance σ_{dg}^2 was 1.28 times higher than in the sex-age-structured model (Table S7 vs. Table S8), and the estimated generation time T was 1.14 times lower than in the sex-age-structured model ($T = 4.81$ years). As a result, the estimated N_e/N from this model was slightly smaller than that from the sex-age-structured model (0.27; Table S8). As for the sex-age-structured model, the demographic variance of the males constituted the largest part of the total demographic variance, and adult males contributed the most, while male calves contributed the least (Table S8). In contrast to the results from the sex-age-structured model, the adult female class was estimated to be the class with the second highest contributions (Table S8).

In the sensitivity analyses, none of the interaction effects, ΔS , were significant and the first order indices, S_x , and the total order indices, S_{Tx} , were accordant. Results are therefore only shown for S_{Tx} , which were used to rank the parameters (see Appendix S9, Table S9.1.1 and S9.1.2 for both indices and the ΔS).

In the sensitivity analysis of the demographic variance, σ_{dg}^2 (Equation 2), the most important input parameter was the demographic variance of males in age class m_4 , followed by the demographic variance of males in age class m_3 , and age class m_2 (Figure 3). As seen by their 95% confidence intervals, these three were all significantly

FIGURE 3 The demographic variance (σ_{dg}^2) was most sensitive to the sex-age class specific demographic variances (σ_{dg}^2) of males in age class 2, 3 and 4. The total order (S_{Tx}) sensitivity indices are shown with their 95% confidence intervals. Female age classes are to the left of the dotted line, male age classes are to the right. The sensitivity indices are scaled and sum to one (cf. Equations 5 and 6)



more important for the demographic variance than the remaining parameters, which all had S_{Tx} close to zero (Figure 3). Nevertheless, the total order indices show that the younger female age classes were more important than the older, and that male calves was the least important sex-age group (Figure 3, Table S9.1.1).

In the sensitivity analysis of the individual reproductive values, W_i , the sensitivity to reproduction B_i increased gradually with age for both sexes, while the sensitivity to survival J_i decreased with age for both sexes (Figure 4). Since calves do not reproduce, all variation in W_{f1} and W_{m1} originated from survival (i.e., cf. Equation 5: $S_j = V_j/V = 1$, Figure 4). For adults of both sexes, W_i 's of f_2 and m_2 were significantly more sensitive to survival compared to reproduction, while for female age classes f_{3-9} and f_{10} , the W_i 's had become significantly more sensitive to reproduction than to survival (Figure 4e,g, Table S9.1.2). Although the sensitivity to reproduction also increased with male age class, the individual reproductive values of males in all age classes were more sensitive to survival (right column in Figure 4, Table S9.1.2).

3.2 | Effects of reproductive autocorrelation and covariance between survival and reproduction

Estimates of transition and survival probabilities from E-SURGE showed evidence of positive reproductive autocorrelations and covariance between survival and reproduction in the moose population. Both males and females were more likely to have a high reproductive output one year if they already had a high reproductive output the year before (Appendix S10). Additionally, males and females with high reproductive output had higher survival probability than those that produced few or no offspring (Appendix S10).

Estimation of σ_{dg}^2 and N_e/N from the sex-age-state-structured model with covariance between survival and reproduction but without reproductive autocorrelation (i.e., the version of this model that is most equivalent to the simpler sex-age-structured model) gave a σ_{dg}^2 of 0.60, and N_e/N of 0.31 (Table 1), which matches the estimates found from the sex-age-structured model. Adding reproductive autocorrelation in both males and females caused σ_{dg}^2 to increase to 0.67, and N_e/N to decrease

to 0.28. Thus, the demographic contribution of reproductive autocorrelations to σ_{dg}^2 was 10.6% (compare row one with row four in Table 1). This contribution was mainly due to reproductive autocorrelation in males, while the effect of female reproductive autocorrelation was small (compare row one with rows two and three in Table 1). The observed positive covariance between survival and fecundity influenced σ_{dg}^2 the most in the presence of reproductive autocorrelations (compare rows one and nine with rows four and 12 in Table 1), giving a contribution of 12.7% at the most. The covariance between survival and fecundity in males affected σ_{dg}^2 more than the covariance in females, both in the presence and absence of reproductive autocorrelations (Rows 5–8 in Table 1). Results from the model where transition probabilities without reproductive autocorrelations were estimated from E-SURGE gave very similar results (Table S11.1). Drawing parameter values from the distributions provided by E-SURGE gave distributions of σ_{dg}^2 around the mean values presented in Table 1 (Appendix S11.2).

4 | DISCUSSION

In this paper, we have demonstrated how a combination of models from a common framework can be used to decompose the demographic variance, σ_{dg}^2 , and N_e/N into contributions from different demographic sources, including sex, age, survival and multiple aspects of reproduction. In this way, we can improve our understanding of which aspects of a population's demography have the greatest influence on loss of genetic variation, with implications for population viability and management.

The most complete model in the current study (i.e., accounting for age structure, covariance between survival and reproduction, and reproductive autocorrelations) estimated the N_e/N ratio of the moose population on Vega to be 0.28. This is at the lower end of the range suggested in a previous simulation study of moose (0.24–0.36) (Ryman, Baccus, Reuterwall, & Smith, 1981) and the range typically seen for demographic N_e/N over all species (0.25–0.75; Nunney, 2000). Polygynous species such as the moose are expected to have a lower N_e/N ratio than species with a more even distribution of reproductive success among individuals (Frankham, 1995; Nunney, 1993).

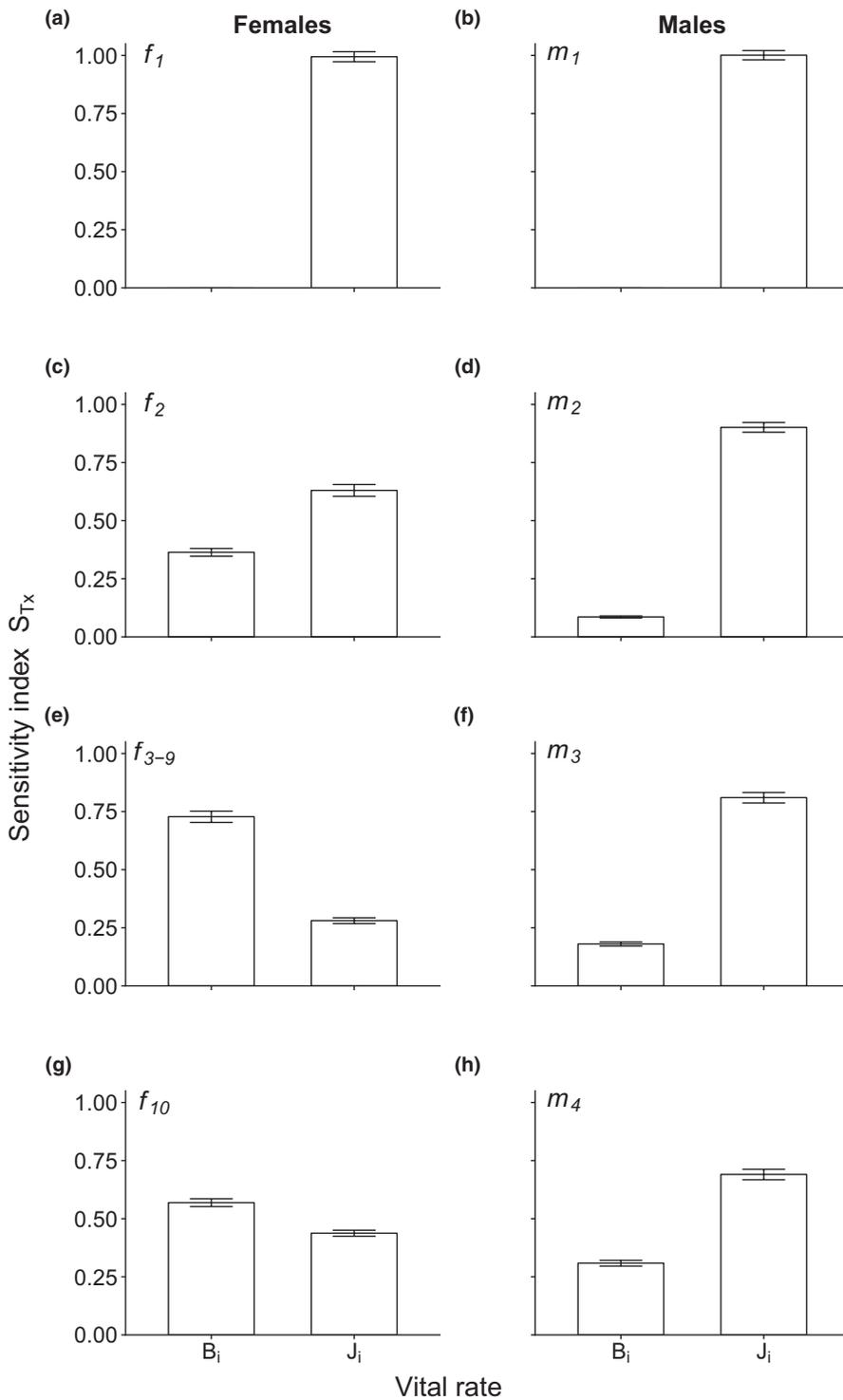


FIGURE 4 The sensitivity of individual reproductive values (W_i) to reproduction (B_i) generally increased with age class, while that to survival (J_i) decreased, in both females (left column) and males (right column). Sex-age classes i are labelled on the individual panels, from calves at the top to the final sex-age classes at the bottom; (a) f_1 , (b) m_1 , (c) f_2 , (d) m_2 , (e) f_{3-9} , (f) m_3 , (g) f_{10} , (h) m_4 . The total order sensitivity indices (S_{Tx}) of the W_i are given with their 95% confidence intervals. Sensitivity indices are scaled to sum to one (cf. Equations 5 and 6)

In addition, our model incorporates more sources of demographic variation than previously used models (Nunney, 1993, 1996; Nunney & Elam, 1994), and we have shown that several of these sources contribute to lowering the N_e/N ratio. It is therefore not surprising that our estimates are comparatively low.

Nonrandom distribution of offspring among individuals is one of the major factors contributing to the effective population size being lower than the actual population size in many species (Frankham, 1995). Large variation in reproductive success among

individuals of one sex is common in many systems (Shuster & Wade, 2003), particularly those with mating systems in which some individuals have the possibility of obtaining many mates through competition (Emlen & Oring, 1977). In polygynous species, such as the moose, males' reproductive success typically depends on their ability to outcompete rival males and fertilize as many females as possible (Clutton-Brock, 2017; Emlen & Oring, 1977; Komers, Messier, & Gates, 1994), leading to large variation in male reproductive success. We therefore generally expect the N_e/N

ratio to be lower in these species than in monogamous ones where reproductive success is typically more evenly distributed among individuals (Myhre et al., 2017; Nomura, 2002; Nunney, 1993). Reproductive success in the moose study population follows this pattern, with high variance in reproductive success among males and many males failing to sire any calves during their lifetime (Markussen et al., 2019). Accordingly, we found that the demographic variance, and thus the levels of genetic drift expected, in the moose population were driven more by variation in male reproduction than female reproduction (Figure 2). In contrast, previous studies that have split σ_{dg}^2 into separate components for males and females have been looking at socially monogamous bird species and have found the male and female components to be very similar (Engen et al., 2010; Stubberud et al., 2017; Trask, Bignal, McCracken, Piertney, & Reid, 2017). It is worth noting that it is the variation in reproductive success among individuals of each sex that drives this difference, not the (social) mating system per se. High variation in reproductive success can be caused by the mating system, such as in various types of polygyny (Emlen & Oring, 1977; Shuster & Wade, 2003) or by high variation in offspring survival (Bose, Borowiec, Scott, & Balshine, 2019; Breuer et al., 2010).

Lee et al. (2017) have previously shown that positive reproductive autocorrelations in female moose have only small effects on the demographic variance, σ_d^2 (excluding genetic components). Here, we found that the positive reproductive autocorrelations and covariance between survival and reproduction in males had a greater role in decreasing N_e/N than the equivalent effects in females (Table 1), and in combination they contributed to decreasing N_e/N from 0.34 to 0.28. This change would for example mean a decrease in the asymptotic (harmonic mean) N_e from 17 to 14 when using the harmonic mean of the population sizes experienced between 1992 (when the population growth leveled off) and 2011 ($N=50$), which is quite a large change for such a small population.

The effect of positive reproductive autocorrelations was the greatest when combined with positive covariance between survival and reproduction (as was observed in the moose population). This combination means that individuals with high reproductive success have higher probability to survive as well as higher probability to breed in the future, thus causing increased variance in lifetime reproductive success. It has previously been shown theoretically that persistent individual differences in reproductive success tend to reduce N_e/N (Lee, Engen, et al., 2011; Nunney, 1996), and that the effect of such persistent individual differences (i.e., positive reproductive autocorrelation) in males is greater in more polygynous mating systems with greater variance in annual male mating success (Lee, Engen, et al., 2011). Here, in the moose population, we found that this effect can be further amplified by a positive covariance between survival and reproduction, which increases individual differences in lifetime reproductive success even more. Positive covariance between survival and reproduction in females is common in hunted ungulates, due either to regulations and prohibition or simply to a reluctance among hunters to shoot females with offspring at heel (Ericsson, 2001; Markussen

et al., 2018; Mysterud, Yoccoz, & Langvatn, 2009; Weladji et al., 2008; Table S2), and has also been reported in a number of other systems from a variety of taxa (e.g., Beauplet, Barbraud, Dabin, Küssener, & Guinet, 2006; Cam, Link, Cooch, Monnat, & Danchin, 2002; Hassall, Sherratt, Watts, & Thompson, 2015; Kenamer, Hepp, & Alexander, 2016). We also found a strong positive covariation between reproduction and survival of males (Markussen et al., 2019; Table S10.2). The specific mechanism behind this is uncertain, but probably due to informal agreements among hunters and managers not to shoot the largest males if other males are available in the hunting district during the hunting season (Kvalnes et al., 2016). Interestingly, our results suggest that this hunting strategy has a negative effect on the ratio N_e/N , as the ratio would be higher if male moose of all sizes were shot with the same probability; all else being equal (compare line eight with line 12 in Table 1).

In age-structured populations, the contribution to σ_{dg}^2 may show large age-specific variation (Sæther et al., 2013), for instance due to age-specific responses to density or environmental conditions (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000). Genetic drift may then largely depend on processes occurring in specific sex-age classes (Engen et al., 2010). For the moose population on Vega, we found that the largest age-specific contributions to σ_{dg}^2 were from the three adult male age classes, and female calves (Figure 2). In other words, the demographic processes occurring in these four sex-age classes are main drivers of the rate of genetic drift in this population. However, it does not necessarily follow that the demographic variance and ratio N_e/N are the most sensitive to demographic changes in these sex-age classes. Establishing these sensitivities, which are of high relevance for management and conservation, requires a separate sensitivity analysis, such as the one performed in Section 2.4.1. For male moose, the results of the sensitivity analysis confirmed the patterns indicated by the $u_i \sigma_{dg_i}^2$. Thus, a change in the vital rates of older males has the greatest potential to decrease or increase the ratio N_e/N . On the other hand, the large contribution from female calves to σ_{dg}^2 was not reflected by the sensitivity analysis (Figure 3). Since all variation in this parameter arises from survival (and the binomial distribution), the variability of the demographic variance of calves from which the sensitivity is evaluated, was small (Figure S5.2). Thus, although calves have important contributions to σ_{dg}^2 , there is little potential to reduce σ_{dg}^2 by altering the demographic variance (i.e., variance in survival) of this age class.

In addition to evaluating the sensitivity of different sex-age classes to demographic changes, the combination of evaluating the sex-age specific contributions to σ_{dg}^2 (and N_e/N) and performing a sensitivity analysis allows us to more fully understand the demographic drivers of genetic drift in a population. For example, in a previous study that looked at the sensitivity of σ_{dg}^2 to changes in different sex-age classes in a population of house sparrows, *Passer domesticus*, the sensitivity was also found to increase with male age (Stubberud et al., 2017). However, in the sparrows, individual reproductive values were much more sensitive to reproduction than to

survival, whereas in male moose we found the sensitivity to survival to be much greater (Figure 4). Also, the sensitivity of individual reproductive value towards reproduction in male moose increased with age (Figure 4, second column). This makes sense in light of the different life history and mating system of the two species. In sparrows, individuals are short-lived and reproduction early in life has a higher potential to create individual differences in lifetime reproductive success than increased survival. In male moose, on the other hand, individuals with high survival have the possibility to build up their reproductive output over time. Thus, the future potential for reproduction is high even for older males (as seen by the reproductive value; Table S7), and even as reproduction becomes more important with age, survival continues to be the most important vital rate in all age classes (Figure 4).

For female moose, reproductive success is not as dependent on gaining size (increasing in age), but is restricted to a maximum of two offspring per year for mature females in all age classes. This, combined with a hunting strategy in which young, nonreproductive females are at greater risk, can explain the observed decrease of the female age-specific demographic variances with age (Figure 2, Table S7). The youngest age class has a relatively high variance due to the survival component, whereas the variability in success in older individuals is quite low due to high survival and a life history in which between individual differences in reproductive output are limited. This differs greatly from the house sparrow study discussed above (Stubberud et al., 2017), in which the sensitivity of σ_{dg}^2 to changes in female age classes increased with age. Harvesting that targets young animals and adult males is common in many ungulate populations (Lavsund, Nygrén, & Solberg, 2003; Solberg, Loison, Ringsby, Sæther, & Heim, 2002; Solberg et al., 2006), and natural mortality is also high in the youngest age classes of many long-lived species (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Gaillard et al., 2000), which could mean that the results found for females in this study (Figures 2–4) reflect a common pattern in long-lived species in nature. This also confirms previous suggestions that common hunting strategies that result in female-biased sex ratios and skewed age distributions (Sæther et al., 2004; Solberg, Grøtan, Rolandsen, Brøseth, & Brainerd, 2005; Solberg et al., 2002, 2006) leading to harvest-induced changes in demographic structure and age composition can affect N_e and N_e/N (Ryman et al., 1981; Sæther et al., 2009).

Our results demonstrate that we can learn a lot about age-specific contributions to the demographic variance and genetic drift by using an age-structured model. We also fitted a model without adult age structure to see how this would influence estimates in this population where such structure is present. This resulted in an upwardly biased demographic variance (due to less variation being explained by the model structure), mainly driven by the female segment (Table S7 vs. Table S8), and a downwardly biased generation time. The estimated N_e/N was almost unchanged due to the opposing effects on σ_{dg}^2 and T , which at first glance could seem to indicate that accounting for age structure was superfluous. However, estimates of the generation time and the demographic variance would not be reliable from this model, and it is difficult to know whether the overall

small change in N_e/N in this system is a general rule or more of a coincidence.

The modelling framework presented in this paper could be useful for estimating and partitioning N_e/N in a wide range of systems. Here, we have run a series of different models to evaluate the importance of different demographic factors on N_e/N . However, the individual models can also be used separately to estimate N_e/N in various systems. For example, in systems without reproductive autocorrelation but with age-structured vital rates the sex-age-structured model would be the most relevant, whereas N_e/N in systems without age structure beyond the juvenile stage could be estimated using the sex-maturity-structured model. However, comparisons of estimates from the different models, in combination with sensitivity analyses, are particularly powerful in understanding how different demographic factors influence N_e/N .

The two main models used in this paper both have strengths and weaknesses. The sex-age-structured model calculates σ_{dg}^2 and N_e/N directly from individual demographic data, but does not account for the positive reproductive autocorrelation that has been observed in this population (Markussen et al., 2018, 2019). The sex-age-state-structured model incorporates reproductive autocorrelations, but requires estimation of a number of transition estimates calculated in a separate mark-recapture model, which can be difficult to obtain when data are scarce. These estimates also contain estimation uncertainty. We demonstrated how the influence of uncertainty in estimates of vital rates on the uncertainty in estimates of σ_{dg}^2 can be evaluated by drawing parameter values from their estimated distributions. In our case, the relative differences between estimates incorporating different factors stayed consistent across analyses, and the distributions were relatively similar in their width (see example shown in Figure S11.2), giving us good reason to believe that the uncertainty in parameter estimates is not driving or obscuring our results.

Both models rely on the same demographic framework to estimate σ_{dg}^2 and N_e/N (developed by Engen et al., 2009; Engen, Lande, et al., 2007; Engen et al., 2010; Engen, Ringsby, et al., 2007; Lee et al., 2017) a framework that has few strict assumptions compared to other models for N_e (typically assuming constant population size, discrete generations, stable environment and/or no or stable age structure; see Caballero (1994), Crow and Denniston (1988) and Wang, Santiago, and Caballero (2016) for excellent reviews of different models). For example, the pioneering models of Felsenstein (1971) and Hill (1972, 1979) (further modified by for example, Nunney, 1991, 1993, 1996; Waples, Do, & Choquet, 2011), that allowed for overlapping generations and age structure, still assumed a constant environment, constant population size (or constant growth; Felsenstein, 1971), stable age distribution and no autocorrelation in vital rates. The widely used model of Hill (1972, 1979) also requires knowledge of the lifetime variance in reproductive success, which is particularly difficult to obtain for long-lived species. Introducing simplifying (and equivalent) assumptions to the model framework underlying this paper has shown that it agrees with models by Felsenstein (1971), Hill (1979) and Engen et al. (2005).

Although requiring fewer strict assumptions than the above mentioned models, the model used in the current study assumes an isolated population with density independent dynamics, where all variation in the observed individual reproductive values (Equation 3) originates from demographic stochasticity (i.e., there is no sampling error, and none of the variation in vital rates originates from selection pressure). The moose population at Vega is not completely isolated, but has received 20 immigrants (five females, 15 males) during the study period (Herfindal et al., 2014). This could potentially have biased our estimates somewhat if there are fitness differences between residents and immigrants (Baalsrud et al., 2014). In addition, the moose population may show hunting-induced density regulation, as the harvesting strategy keeps the population at a moderate, approximately constant size (Markussen et al., 2018, 2019). However, the majority of the harvested individuals are calves (Solberg et al., 2010), and our results show that the demographic variance and hence the ratio N_e/N is robust to changes in this age class (Figure 4). It is therefore unlikely that hunting-induced density dependence has had much influence on our results for the moose population.

Overall, the framework used in this paper has the potential to teach us a lot about the relative contributions of different demographic processes to genetic drift and effective population size, and how sensitive they are to changes induced by for instance management or conservation action. Such knowledge is valuable as loss of genetic variation increases a population's vulnerability to extinction (Gilpin & Soulé, 1986; Newman & Pilson, 1997) and may lower its ability to evolve in response to a changing environment (Lai et al., 2019; Nunney & Campbell, 1993). From the moose case study we have seen that both sex, age structure and patterns of reproduction and survival can be important in this context. Performing similar analyses on a range of species with different life histories may uncover general patterns that will improve our understanding of the processes that drive genetic drift in natural populations, as well as informing management decisions in specific systems.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare

AUTHOR CONTRIBUTIONS

S.S.M., and B.E.S. developed the idea. A.M.L. developed the state-dependent model. S.S.M., and A.M.M. wrote the script for the age-structured model developed by S.E. A.M.M. parameterized and ran sensitivity analysis. S.S.M. parameterized the models and ran E-surge. H.H. performed genetic analyses and constructed the

pedigree in collaboration with K.H.R. M.H. was in charge of the field-work, tissue sampling and the life history databases. A.M.L., A.M.M., and S.S.M. wrote the paper with input from the other coauthors.

DATA AVAILABILITY STATEMENT

Data will be uploaded to DRYAD data repository when accepted. The data file will contain information needed to estimate N_e and carry out the sensitivity analyses: year, sex, survival and recruit production, as well as the moose pedigree. R code for running the analyses presented here are available from the authors on request, and the authors can assist in adapting this code to other systems. The data that support the findings of this study are openly available in DRYAD at <https://doi.org/10.5061/dryad.d7wm37pxj>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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