

ORIGINAL ARTICLE

Life-history traits and effective population size in species with overlapping generations revisited: the importance of adult mortality

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The relationship between life-history traits and the key eco-evolutionary parameters effective population size (N_e) and N_e/N is revisited for iteroparous species with overlapping generations, with a focus on the annual rate of adult mortality (d). Analytical methods based on populations with arbitrarily long adult lifespans are used to evaluate the influence of d on N_e , N_e/N and the factors that determine these parameters: adult abundance (N), generation length (T), age at maturity (α), the ratio of variance to mean reproductive success in one season by individuals of the same age (ϕ) and lifetime variance in reproductive success of individuals in a cohort ($V_{k\bullet}$). Although the resulting estimators of N , T and $V_{k\bullet}$ are upwardly biased for species with short adult lifespans, the estimate of N_e/N is largely unbiased because biases in T are compensated for by biases in $V_{k\bullet}$ and N . For the first time, the contrasting effects of T and $V_{k\bullet}$ on N_e and N_e/N are jointly considered with respect to d and ϕ . A simple function of d and α based on the assumption of constant vital rates is shown to be a robust predictor ($R^2=0.78$) of N_e/N in an empirical data set of life tables for 63 animal and plant species with diverse life histories. Results presented here should provide important context for interpreting the surge of genetically based estimates of N_e that has been fueled by the genomics revolution. *Heredity* (2016) 117, 241–250; doi:10.1038/hdy.2016.29; published online 8 June 2016

INTRODUCTION

Virtually all evolutionary processes depend to some extent on effective population size (N_e) that directly determines the rates of stochastic processes such as genetic drift and loss of neutral genetic variability and also influences the effectiveness and predictability of selection and migration. Effective population size is an elegantly simple concept that rapidly becomes complex when simplistic assumptions are confronted with practical realities. Because obtaining the demographic data to calculate N_e directly is challenging in natural populations, effective size is often estimated using indirect genetic methods that quantify a genetic index that is theoretically linked to N_e (Wang, 2005; Luikart *et al.*, 2010).

N_e accounts for disparities among individuals in lifetime reproductive success. This is particularly difficult to measure in iteroparous species with overlapping generations because it is necessary to integrate information on production of offspring across multiple years or seasons. The most general and widely used method for calculating N_e in species with overlapping generations was developed by Hill (1972):

$$N_e = \frac{4N_1T}{V_{k\bullet} + 2} \quad (1)$$

In this formulation, N_1 is the number of offspring produced each time period, T is generation length and $V_{k\bullet}$ is lifetime variance in reproductive success (production of offspring) among the N_1 individuals in a cohort. Although generation length is straightforward to calculate from basic life-history information, $V_{k\bullet}$ is more challenging

because it requires integrating reproductive contributions across entire lifetimes of individuals with variable lifespans and expected fecundities.

Much of what we know about how life-history traits influence N_e and the ratio of effective size to census size (N) when generations overlap is because of a body of work by Len Nunney during the 1990s (Nunney, 1991, 1993; Nunney and Elam, 1994; Nunney, 1996). These studies evaluated the influence of a variety of factors, including primary and secondary sex ratio, mating system, variation in fecundity, generation length and the way N is defined in computing the N_e/N ratio. However, most of these evaluations involved simplifying assumptions and approximations that considered the effects of varying one factor while holding others constant. In reality, however, a variety of life-history traits that can change over the course of an individual's lifetime jointly affect recruitment, generation length, variance in reproductive success and hence both N_e and N_e/N .

This study adopts a three-pronged approach to revisit the general question of how life-history traits influence N_e and the N_e/N ratio when generations overlap. First, 'true' N_e is calculated using a recently developed method (AgeNe; Waples *et al.*, 2011) based on the population's vital rates (age-specific patterns of survival, fecundity and variance in reproductive success). This allows one to directly calculate the elusive parameter $V_{k\bullet}$ in Hill's equation.

Next, analytical methods explore how a single parameter (annual rate of adult mortality) affects the other factors that determine N_e and N_e/N . This produces some simple relationships that allow one to predict the N_e/N ratio that has been the subject of much controversy

in the literature (Husband and Barrett, 1992; Hedgecock, 1994; Frankham, 1995; Nunney, 1995; Vucetich *et al.*, 1997; Kalinowski and Waples, 2002). Finally, performance of these analytical relationships is evaluated using artificial life tables and a large published data set of vital rates for 63 species of vertebrates, invertebrates and plants. Results provide heuristic insights into the factors that determine N_e/N and show that a simple function of adult mortality can be a robust predictor of that key ratio.

MATERIALS AND METHODS

Notation and the AgeNe model

AgeNe is a discrete-time, age-structured model with separate sexes that requires one to specify a finite number of time steps that represent a maximum lifespan. Here we assume that the time steps are years, but periods such as days, weeks or months can also be used and might be appropriate for some species (see Waples *et al.*, 2013 for examples of each). Following Felsenstein (1971) and Hill (1972), the underlying model used here assumes that population size is constant, age structure is stable and probabilities of survival and reproduction are independent across time.

Table 1 summarizes the notation used. Following Nunney and Elam (1994), N is defined as the adult population size (all mature individuals, including those that might not breed in a given year). In the model, x is used as an index of age, and hence N_x represents the number of individuals alive at any given time that are age x . Age-specific vital rates that we will be concerned with include m_x = mean number of offspring per year produced by an individual of age x ; s_x = probability of survival from age x to age $x+1$; $d_x = 1 - s_x$ = probability of dying between age x and age $x+1$; and l_x = cumulative survival through age x (with $l_1 = 1$ and $l_x = \prod_{x>1} s_{x-1}$). This formulation of cumulative survivals

corresponds to a prebreeding census in which individuals are counted just before breeding and age-one individuals ('newborns') are actually almost 1-year old (Caswell, 2001, equation 2.40). When survival varies with age, it can be useful to calculate the geometric mean survival rate (\bar{s}), the constant adult survival rate that would produce the observed value of l_x at age ω : $(\bar{s})^{\omega-x} = l_x$,

so $\bar{s} = l_x^{1/(\omega-x)}$, assuming l_x is set to 1.0. The analogous term $\bar{d} = 1 - \bar{s}$ is a useful way to approximate the annual rate of adult mortality when it varies by age.

Finally, to calculate $V_{k\bullet}$, AgeNe requires age-specific information on variance in reproductive success. If V_x is the variance in number of offspring produced in one time period among all individuals of age x , then $\phi_x = V_x/m_x$ = the ratio of the variance to mean reproductive success in one time period for individuals of age x . In the AgeNe model, each of these vital rates and reproductive parameters can take different values for males and females, but for simplicity in the notation below and in Table 1, sex-specific indices are not used. Although AgeNe can accommodate any primary sex ratio, it is assumed here that the sex ratio of recruits is 1:1, but the adult sex ratio can depart from unity because of different survival rates and/or different rates of maturation between sexes.

In the default AgeNe model, age at maturity (α) is the youngest age at which reproduction can occur, and ω is the maximum realistic age. Adult lifespan (AL) is then defined as the maximum number of seasons in which an individual can reproduce and is given by $AL = \omega - \alpha + 1$ (the '+1' term accounts for the fact that an individual could potentially reproduce in years α and ω and every year in between). As discussed below, a better definition of age at maturity would be the first age at which at least 50% of the survivors of a cohort have matured, and hence that definition is used here.

Hill (1972) used N_1 to represent the number of individuals in a newborn cohort. In practice, N_1 can be defined in terms of any life stage up to age at maturity, provided that $V_{k\bullet}$ is measured for these same cohorts of recruits. Because of the interest in adult census size, focus here instead is on N_α = the number of recruits in a cohort that survive to age at maturity. The underlying model assumes a constant N , and hence relative fecundities are scaled to produce a constant number of N_α recruits each year. Random mortality before age at maturity of course will reduce the number of recruits that survive to become adults, but it has no effect on the N_e/N ratio that is the primary interest here.

Analytical explorations

The core analyses here involve analytical exploration of how changes in vital rates and reproductive parameters affect N , T , $V_{k\bullet}$ and hence N_e and N_e/N .

Table 1 Notation used in this paper

N	Adult population size (all mature individuals)
N_x	Number of individuals alive at any given time that are age x
N_1	Number of offspring produced each year
N_α	Number of offspring produced each year that survive to age at maturity and hence are considered recruits
N_e	Effective population size per generation
α	Age at maturity (first age at which at least 50% of the individuals are mature)
ω	Maximum age
s_x	Probability of survival from age x to age $x + 1$
d_x	$= 1 - s_x$ = probability of dying between age x and age $x + 1$
l_x	Cumulative survival through age x
\bar{s}	Constant survival that would produce the observed value of l_x at age ω ; $\bar{s} = l_x^{1/(\omega-x)}$, with l_x set to 1.0
\bar{d}	Constant probability of dying associated with \bar{s} ; $\bar{d} = 1 - \bar{s}$
m_x	Mean number of offspring that survive to age of recruitment produced per time period by an individual of age x
T	Generation length; $T = \sum x l_x m_x / \sum l_x m_x$ = average age of parents at birth of a cohort
$V_{k\bullet}$	Lifetime variance in reproductive success among individuals in a single cohort
\bar{k}_\bullet	Mean lifetime reproductive success of individuals in a single cohort; $\bar{k}_\bullet = 2$ in a stable population
~	Indicates an estimate based on analytical results for populations with arbitrarily long adult lifespans (\bar{T} , \bar{N} , $\bar{V}_{k\bullet}$, \bar{N}_e)
SS_x	The sum of squared numbers of offspring produced in one time period by individuals of age x
V_x	Variance in number of offspring produced in one time period by individuals of age x ; $V_x = SS_x/N_x - m_x^2$
ϕ_x	Ratio of the variance to the mean reproductive success in one time period of individuals of age x ; $\phi_x = V_x/m_x$
$\bar{k}_{(z)\bullet}$	Mean lifetime reproductive success of individuals that die at age z
D_z	Number of individuals that die after reproducing at age z
SS_z	The sum of squared numbers of lifetime offspring produced by individuals that die at age z
$V_{k(z)\bullet}$	Lifetime variance in reproductive success of individuals that die at age z ; $V_{k(z)\bullet} = SS_z/D_z - \bar{k}_{(z)\bullet}^2$
ϕ_z	Ratio of the variance to the mean lifetime reproductive success of individuals that die at age z ; $\phi_z = V_{k(z)\bullet}/\bar{k}_{(z)\bullet}$

Most of these are based on a model that assumes adult lifespan can be arbitrarily long and hence involve sums of infinite series. Proofs for the solutions to these infinite series can be found in the Supplementary Information. Because all real populations have finite longevity, the degree of bias that results when these relationships are applied to finite life tables was evaluated.

Sensitivity analysis with empirical data

Although the analytical evaluations considered a range of age-specific patterns of vital rates, real populations have complex mixtures of life-history traits that often do not correspond to assumptions of simple models. Therefore, robustness of the analytical results was evaluated by applying them to a large data set of published life tables for a diverse group of species, from seaweed and polychaetes to chimpanzees and pine trees. Original sources, full life tables and notes for each of the 63 species are given in the online appendices to Waples *et al.* (2013). A summary of the data for each species that were used in this study can be found in Supplementary Table S1. The modified life table produced by Waples and Antao (2014) was used for the loggerhead turtle. To deal with diverse types of data reported for these species, Waples *et al.* (2013) adopted a simple rule to define age at maturity: the first age that has a non-zero probability of producing offspring. But this can be misleading in literal conversion of stage-based matrices (as in the case of the loggerhead turtle), or if a small fraction of individuals mature early. Accordingly, each species was reviewed according to the conceptual definition (see above) that age at maturity is the first age for which at least half of the survivors are adults. Information on age-specific probability of maturity was available for some species; if not, for species in which fecundity increased with age, age at maturity was increased until the ratio m_x/m_{x+1} was approximately 0.5 or higher. If males and females had different age-specific fecundity, this was done separately for each sex and an average taken across males and females. Because N represents the number of adults alive at any given time in the population, changes in α also required adjustments to adult census size. The net result was changes to α and N for several species (see Supplementary Table S1). In addition, \bar{s} and \bar{d} were calculated for each species as described above.

RESULTS

Analytical results

Population size. If N_1 newborns each year survive to age 1, the number of individuals alive at each age $x > 1$ is $N_x = N_1 l_x$, and the total census size is

$$N_T = \sum_{x=1,\omega} N_x = \sum_{x=1,\omega} N_1 l_x = N_1 \sum_{x=1,\omega} l_x.$$

With N_α recruits reaching age at maturity each year, the adult census size is

$$N = N_\alpha \sum_{x=\alpha,\omega} l_x, \tag{2}$$

where l_α (survivorship to age at maturity) is defined to be 1.

Constant vital rates. Consider a simple model in which annual survival is constant (all $s_x = s$ and all $d_x = d$) and maximum age can be arbitrarily large. Under these conditions, the survivorship function $l_x = (1 - d)^{x-1} = 1, 1 - d, (1 - d)^2, \dots$ for $x = 1, 2, 3, \dots$. As x can be arbitrarily large, $\sum l_x$ is an infinite sum that can be shown to equal $1/d$ (see Supplementary Material online). Therefore, the adult census size is given by

$$N = N_\alpha \sum_{x=\alpha,\omega} l_x = \frac{N_\alpha}{d}. \tag{3}$$

That is, adult census size is simply the number of recruits per year divided by the annual mortality rate. Although this result is exact for an infinite series, all natural populations have a finite number of age

classes, and hence an ‘ \sim ’ is used to denote an estimate for practical applications.

$$\tilde{N} = N_\alpha \sum_{x=\alpha,\omega} l_x = \frac{N_\alpha}{d}. \tag{3a}$$

Survival declines with age. In many species, including humans and many large mammals with Type I survivorship, adult mortality increases with age. This can be modeled with a type of Gompertz function where mortality increases each year by a constant factor $\lambda > 1$ according to the compound interest principle. If d_α is annual mortality at age of maturity, then $d_{x,x>\alpha} = d_\alpha \lambda^{x-\alpha}$, $s_x = 1 - d_\alpha \lambda^{x-\alpha}$, and $l_x = \prod s_{x-1}$.

Figure 1 shows some typical patterns of Type I survival for different adult lifespans. These curves all used $d_\alpha = 0.05$ and solved for λ as the value that would produce $l_x = 0.01$ at the end of the adult lifespan (when $x = \omega$). Applying this criterion produced $\lambda = 2.695, 1.43, 1.137$ and 1.038 for adult lifespans of 5, 10, 20 and 40 years, respectively. The Gompertz function does not lend itself to the infinite series analysis because eventually the mortality rate will exceed 1, which is biologically impossible. Therefore, numerical methods were used to generate results for the scenarios shown in Figure 1, as well as comparable scenarios with different levels of initial mortality (d_α). These results are shown in Supplementary Table S2. For each scenario, it is possible to calculate $\bar{d} = 1 - \bar{s}$ that, using an analog of Equation (3), can be used to produce estimates of adult census size as

$$\tilde{N}_\bullet = \frac{N_\alpha}{\bar{d}}. \tag{4}$$

As shown later, Equation (4) will underestimate adult census size when mortality increases with age.

Another simple way to model increasing adult mortality is to have annual survival be inversely proportional to age: $s_x = 1 - d_x = f(1/x)$. As an example, consider a population with $s_x = 1/x$. In this case $\sum l_x = 1 + 1/x + 1/x^2 \dots$, and hence $\sum_{x=1}^{\infty} l_x = \sum_{x=1}^{\infty} \frac{1}{x!} = e = 2.718$. Thus, overall

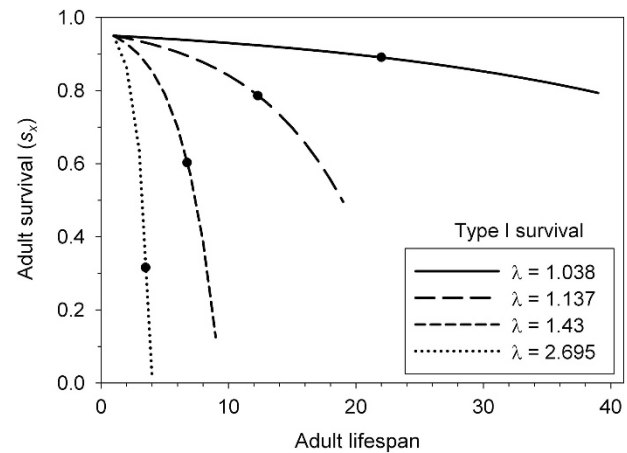


Figure 1 Typical patterns of Type I survival in species with adult lifespans of 5, 10, 20 and 40 years. Annual mortality at age of maturity was $d_\alpha = 0.05$; d_x increased each year by the proportion λ that was chosen to produce cumulative survivorship of $l_x = 0.01$ at the maximum age. The filled circles are $\bar{d} = 1 - \bar{s}$, the constant mortality rate that would produce the same cumulative survivorship over the adult lifespan.

population size is $N_T = 2.718N_1$, the same result expected in a population with constant mortality at level $\bar{d} = 1/(2.718) = 0.368$.

Generation length. Generation length does not depend on population size or the number of recruits—only on age-specific vital rates. A general definition (see, for example, Charlesworth, 2009) is the mean age of parents of a cohort of newborn offspring:

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x} \quad (5)$$

with the term in the denominator accounting for population growth rate. We are interested in stable populations, in which case $\sum l_x m_x = 2$. (Note that if we were only counting production of females by females, we would use $\sum l_x m_x = 1$, as is common in ecology. However, N_e requires considering reproduction in terms of genetic contributions by both sexes, and hence in a stable diploid population $\sum l_x m_x = 2$ as each parent on average contributes half the genes to two offspring.)

Constant vital rates. If fecundity is constant, all $m_x = m$ and the fecundity terms cancel, producing this general result:

$$T = \frac{\sum x l_x}{\sum l_x} \text{ (assumes constant fecundity)} \quad (6)$$

As $\sum l_x m_x = m \sum l_x = 2$ when fecundity is constant, $m = 2/\sum l_x$. If adult mortality is also constant, then $\sum l_x = 1/d$ (from above), implying that $m = 2d$. That is, in a stable population with constant vital rates, the mean number of offspring produced each year by an individual is twice the annual mortality rate, d .

As $\sum l_x m_x = 2$ in our stable population, $T = \sum x l_x m_x / 2 = 2d \sum x l_x / 2 = d \sum x l_x$. It can be shown (see Supplementary Information online) that $\sum x l_x = (1/d)^2$. Therefore,

$$\begin{aligned} T &= d \sum x l_x = d \left(\frac{1}{d} \right)^2 \\ &= \frac{1}{d}. \text{ (assumes constant vital rates and } \alpha = 1) \end{aligned} \quad (7)$$

That is, with constant survival and fecundity, the generation length is simply the inverse of the annual mortality rate. Nunney (1991) obtained a similar result. Note that in this model of constant vital rates, T is also the multiplier by which one expands N_1 to get total population size N_T , as in Felsenstein (1971).

Delayed age at maturity. Equation (7) equals $1/d$ if the summation begins from $x=1$, which in effect assumes that age at maturity is $\alpha=1$. More generally, assume that age at first maturity is α , and from that age on the demographics follow the patterns described above in terms of annual changes (or not) in vital rates. Delayed maturity can be accommodated by simply resetting the age index to 1 at age α , as in Equation (2). For generation length, we also have to account for the fact that each individual is $\alpha-1$ years older when it reproduces than is the case when $\alpha=1$. Therefore, a general expression for generation length in our constant vital rate model is

$$T = 1/d + \alpha - 1 \text{ (assumes constant vital rates)}. \quad (8)$$

Survival declines with age. Under Type I survivorship with constant fecundity, it is still the case that $T = \sum x l_x / \sum l_x$ (Equation (6)), but Equation (7) no longer applies. Supplementary Table S2 records the values of $\sum x l_x$, $\sum l_x$ and T that apply to the Type I survival scenarios described above. As expected, generation length increases with adult lifespan and declines when initial adult mortality is higher. We also see

from Supplementary Table S2 that $\tilde{T}_\bullet = 1/\bar{d}$, which is a naive estimate of generation length computed by replacing constant d in Equation (7) with \bar{d} , underestimates true T for short adult lifespans.

For a model in which fecundity is constant but adult survival declines with age such that $s_x = 1/x$, we showed above that $\sum l_x = 2.718$ and census size is the same as would be found in a population with constant mortality at level $d = 1/(2.718) = 0.368$. This model also produces $\sum x l_x = 5.437$, and hence generation length is $T = \sum x l_x / \sum l_x = 5.437/2.718 = 2.0$ as compared with $T = 1/d = 2.718$ if mortality were constant and $\alpha = 1$.

Fecundity increases with age. Although constant fecundity with age might be approximately true for many species (for example, birds, many mammals), in species with indeterminate growth (as in many plants or ectotherms with indeterminate growth) fecundity commonly increases with size and age. For illustration, we evaluate a single scenario of this type, where fecundity is proportional to age: $m_x = x\beta$. We want to find the value of β that will produce a stable population, in which case $\sum l_x m_x = 2$. Substituting for m_x leads to $\sum x l_x \beta = 2 = \beta \sum x l_x$. From above we know that $\sum x l_x = (1/d)^2$, so $\beta = 2d^2$ and $m_x = 2xd^2$. From above we also have $T = \sum x l_x m_x / 2$, and substituting for m_x produces $T = d^2 \sum x^2 l_x$. It can be shown (see Supplementary Information) that $\sum x^2 l_x = (2-d)/d^3$, so

$$\begin{aligned} T &= (2-d)d^2/d^3 + \alpha - 1 \\ &= (2-d)/d + \alpha - 1 \text{ (assumes } m_x \propto x). \end{aligned} \quad (9)$$

Figure 2 shows how generation length varies as a function of patterns of adult survival and fecundity. Because T is a function of $1/d$, generation length increases very rapidly when adult mortality drops below ~ 0.2 .

Variance in reproductive success. AgeNe calculates lifetime variance in reproductive success among individuals in a cohort ($V_{k\bullet}$) in a three-

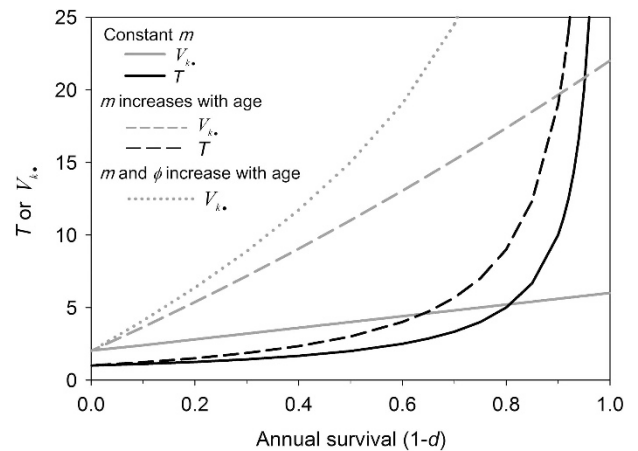


Figure 2 Relationship between adult survival (assumed to be constant at annual rate $1-d$) and generation length (T) and lifetime variance in reproductive success ($V_{k\bullet}$). These are analytical and numerical results based on relationships in Equations (8, 9, 11 and 12). Three scenarios are considered: constant fecundity (m) with $\phi=1$; fecundity that is proportional to age ($m_x = \beta x$) with $\phi=1$; and m_x and ϕ both proportional to age. Changes in ϕ do not affect generation length, and hence in the last scenario the curve for T vs $1-d$ is also given by the black dashed line. When survival is constant with age, the rate of increase of adult N with increasing survival is identical to the rate of increase in T with constant vital rates (solid black curve).

step process that takes advantage of fact that a variance is the mean of the squares minus the square of the mean: $V = SS/n - \bar{k}^2$, where SS is the sum of squares of n observations and \bar{k} is the mean. A simple rearrangement gives $SS = n(V + \bar{k}^2)$. AgeNe sequentially builds the overall SS in this three-step process and then uses the above relationship to calculate the overall variance. The first step is the user-input values for $\phi_x = V_x/m_x$, the ratio of the variance to the mean reproductive success of individuals at age x . This means that $V_x = \phi_x m_x$, which is just a scalar times the mean fecundity for age x , and $n = N_x$, which is the number of potential parents of age x over which the variance is computed, and hence $SS_x = N_x(\phi_x m_x + m_x^2)$.

The next step is to group the individuals within a cohort by age at death (for example, all those that die at age z). The number of individuals that die after reproducing at age z but before reaching age $z+1$ is $D_z = N_z - N_{z+1} = N_l(l_z - l_{z+1})$. These D_z individuals have the same expected lifetime reproductive success $\bar{k}_{(z)\bullet} = \Sigma m_x$, with the summation from age at maturity through age z . The lifetime variance in reproductive success among individuals that die at age z ($V_k(z)\bullet$) and the value of $\phi_z = V_k(z)\bullet/\bar{k}_{(z)\bullet}$ depend on age-specific patterns of vital rates as described below. Once ϕ_z and $V_k(z)\bullet$ are calculated, then $SS_z =$ the sum of squared lifetime offspring numbers for all individuals dying at age z is obtained as $SS_z = D_z(V_{k(z)\bullet} + (\Sigma m_x)^2)$.

Finally, the overall ΣSS_z for lifetime reproductive success of all N_1 individuals in a cohort is obtained by summing across all ages at death, and that is used to compute $V_{k\bullet} = \Sigma SS_z / N_1 - \bar{k}_\bullet^2$. Because the mean lifetime number of offspring per individual must be $\bar{k}_\bullet = 2$ in a stable population,

$$V_{k\bullet} = \sum SS_z / N_1 - 4.$$

Constant vital rates. If we assume constant survival and fecundity, then $D_z = N_1[(1-d)^{z-1} - (1-d)^z]$. At each age up to and including age z , this group of individuals has produced a mean of $m = 2d$ offspring/individual, and hence the mean lifetime production through age of death is $\bar{k}_{(z)\bullet} = \Sigma m_x = 2dz$. For the moment, we assume that ϕ does not vary by sex or age, in which case $\phi_z = \phi$ and $V_k(z)\bullet$ is just the product of ϕ and the lifetime mean reproductive success of individuals that die at age z : $V_k(z)\bullet = \phi \bar{k}_{(z)\bullet} = 2\phi dz$, and hence $SS_z = D_z[2\phi dz + (2dz)^2]$. Substituting from above produces the following for overall lifetime reproductive success:

$$\begin{aligned} V_{k\bullet} &= \sum_{z=x}^{\omega} SS_z / N_1 - 4 \\ &= \sum_{z=x}^{\omega} [D_z[2\phi dz + (2dz)^2]] / N_1 - 4 \\ &= \sum_{z=x}^{\omega} [N_1[(1-d)^{z-1} - (1-d)^z][2\phi dz + (2dz)^2]] / N_1 - 4 \\ &= \sum_{z=x}^{\omega} [(1-d)^{z-1} - (1-d)^z][2\phi dz + (2dz)^2] - 4. \end{aligned} \tag{10}$$

This equation is not very tractable analytically, but numerical methods show that the relationship is actually very simple and perfectly linear (see Figure 2). Equation (10) produces a family of relationships between $V_{k\bullet}$ and annual survival $(1-d)$ that are parallel to that for $\phi = 1$ but have intercepts that are higher by the

amount $2\phi_x$ (Supplementary Figure S1). The general relationship therefore can be expressed as

$$V_{k\bullet} = 4(1-d) + 2\phi \text{ (assumes } s_x, m_x, \text{ and } \phi \text{ are constant with age).} \tag{11}$$

The intercept (2ϕ) gives the value of $V_{k\bullet}$ when annual survival is 0, corresponding to a semelparous population with discrete generations. In this case, and (assuming $\phi = 1$), the entire population behaves like an ideal population with variance in reproductive success equal to the mean (More precisely, an ideal population has random variance in reproductive success, in which case V_k is the binomial variance: $V_k = \bar{k}(N-1)/N$. This is very close to the Poisson variance (where the variance equals the mean) unless N is very small.)

Survival declines with age. For the model above with constant fecundity and survival the inverse of age ($s_x = 1 - d_x = 1/x$), we can numerically solve for $V_{k\bullet}$ by modifying the formula for D_z and account for the different age structure. For this scenario, the result is $V_{k\bullet} = 2.414$, compared with the value expected (4.528) for a constant mortality scenario with $d = 0.368$ (from Equation (10) with $\phi = 1$).

Fecundity increases with age. We can accommodate effects of changes in fecundity on $V_{k\bullet}$ as follows. When fecundity is constant, mean lifetime production of offspring for individuals that die at age z is $2zd$. When fecundity is proportional to age, $m_x = 2xd^2$, and hence mean lifetime reproductive success of individuals that die at age z is $\Sigma 2xd^2 = 2d^2 \Sigma x$, where the summation is taken through age z . Implementing this modification and summing across ages at death produces the following result for lifetime variance in reproductive success of an entire cohort:

$$\begin{aligned} V_{k\bullet} &= \sum_{z=x}^{\omega} \left[[(1-d)^{z-1} - (1-d)^z] \left[2\phi d^2 \sum_{x=z}^{\omega} x + \left(2\phi d^2 \sum_{x=z}^{\omega} x \right)^2 \right] \right] \\ &\quad - 4 \text{ (assumes } m_x \propto x). \end{aligned} \tag{12}$$

Results are plotted in Figure 2. A polynomial of the form $V_{k\bullet} = 16(1-d) + 4(1-d)^2 + 2\phi$ that accommodates the quadratic effect of mortality on fecundity provides an essentially perfect fit to the numerical results ($R^2 \sim 1.0$). Note that when fecundity increases with age, $V_{k\bullet}$ rises very sharply with increases in adult survival, because in that case more individuals live to older ages and make disproportionate contributions to overall production of offspring.

Variance in reproductive success increases with age. Equations (10–12) assume that ϕ can take different values but does not vary with age. If we assume that ϕ and m_x are both proportional to age ($\phi_x = \beta x$), the result gets complicated because the overall ratio $\phi_z = V_{k(z)\bullet}/\bar{k}_{(z)\bullet}$ for individuals that die at age z is a function of the ϕ_x values for each age. It can be shown that ϕ_z is the weighted mean of the ϕ_x values, with the weights being proportional to the cumulative mean reproductive success of individuals that die at age z ; results are depicted in Figure 2. Supplementary Table S3 summarizes the general patterns of change in key life-history parameters described above.

Effective size and the effective to census size ratio. The above information can be integrated as follows to develop estimators of N_e and N_e/N for a couple of common scenarios.

Constant vital rates:

$$\tilde{N}_e \approx \frac{4N_x(1/d + \alpha - 1)}{4(1-d) + 2\phi + 2} = \frac{N_x(1/d + \alpha - 1)}{(3 + \phi)/2 - d}; \quad (13)$$

$$\tilde{N}_e/\tilde{N} \approx \frac{1 + d(\alpha - 1)}{(3 + \phi)/2 - d} \quad (14)$$

If $\phi = 1$, this reduces to

$$\tilde{N}_e/\tilde{N} \approx \frac{1 + d(\alpha - 1)}{2 - d}. \quad (15)$$

If $\alpha = 1$, this further simplifies to

$$\tilde{N}_e/\tilde{N} \approx \frac{1}{2 - d}. \quad (16)$$

Fecundity proportional to age:

$$\tilde{N}_e \approx \frac{4N_x[(2-d)/d + \alpha - 1]}{16(1-d) + 4(1-d)^2 + 2\phi + 2}; \quad (17)$$

$$\tilde{N}_e/\tilde{N} \approx \frac{4d[(2-d)/d + \alpha - 1]}{16(1-d) + 4(1-d)^2 + 2\phi + 2}. \quad (18)$$

If $\alpha = 1$, this reduces to

$$\tilde{N}_e/\tilde{N} \approx \frac{2(2-d)}{8(1-d) + 2(1-d)^2 + \phi + 1}. \quad (19)$$

If in addition $\phi = 1$, this further simplifies to

$$\tilde{N}_e/\tilde{N} \approx \frac{2-d}{d^2 - 6d + 6}. \quad (20)$$

Bias assessment. Biases associated with model misspecification were evaluated in two ways. First, all results based on solutions to infinite time series are subject to bias when applied to populations with finite lifespans. Second, results based on simple assumptions such as constant vital rates are subject to bias when age-specific patterns of survival, fecundity and variance in reproductive success do not correspond to assumptions. The first issue was evaluated numerically using computer-generated data for adult lifespans of varying lengths, and the second issue was evaluated using published life tables for over 60 species (see next section).

Figure 3 addresses the first issue for the three key parameters that determine the N_e/N ratio: N , T and $V_{k\bullet}$. These scenarios all had constant adult mortality at a rate of either $d=0.1$ or 0.4 , constant $\phi=1$ and either constant fecundity (top) or fecundity proportional to age (bottom). Several points can be made from results shown in this figure. First, as adult lifespan increases, the estimates converge on the theoretical values predicted from the solutions to infinite series. This demonstrates that those solutions are asymptotically correct. Second, the rates of convergence for all parameters are faster when mortality is higher. This is logical, as high adult mortality ensures that few individuals live very long, and hence short life tables capture most of the biologically relevant information. Third, the rates of convergence are slower (and hence typical biases more severe) when fecundity increases with age. This is also logical, as the consequences of truncating life tables will be more severe when the oldest individuals have the highest reproductive output. Finally, using the estimators based on the infinite series leads to overestimates of all of these parameters.

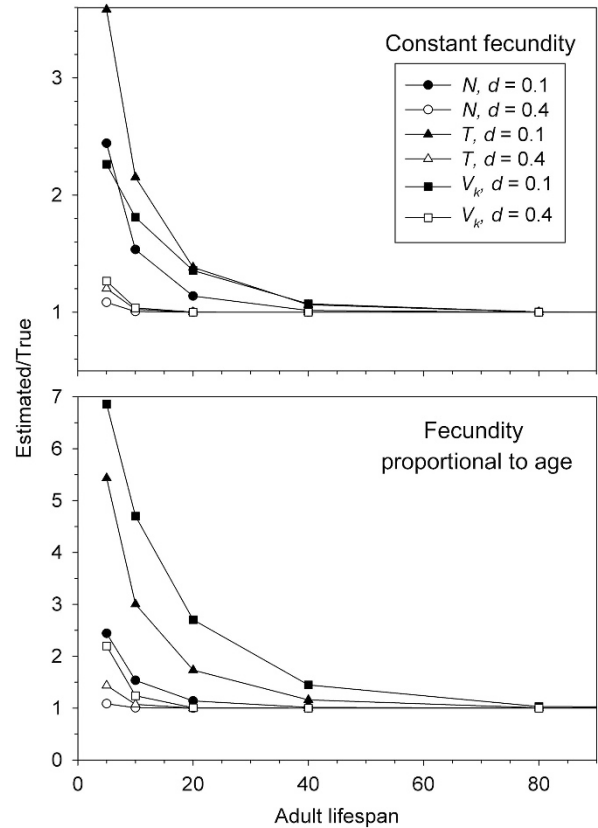


Figure 3 Bias in estimates of key demographic parameters when applying analytical results based on infinite series to populations with finite adult lifespan. These scenarios used constant adult mortality at the levels indicated, constant $\phi=1$ and either constant fecundity (top) or fecundity proportional to age (bottom). ‘Estimated’ parameters were based on the expectations from infinite series analysis and ‘True’ values were calculated for the actual time series using the AgeNe method described by Waples *et al.* (2011).

When fecundity is constant (Figure 3, top), relatively little bias occurs for any of the parameters when $d=0.4$, but all three (and especially T) have a strong upward bias for $d=0.1$ unless adult lifespan is ≥ 20 years. The pattern is similar when fecundity is proportional to age (Figure 3, bottom), except the upward bias is generally higher and the strongest bias occurs with $V_{k\bullet}$. Qualitatively similar patterns of bias are seen when ϕ is held constant at 5 (Supplementary Figure S2), with one difference. Because N and T do not depend on ϕ , increasing ϕ only affects $V_{k\bullet}$, and the bias in at short lifespan is actually reduced when ϕ is larger. This occurs because the effects of large and constant ϕ are influential for young ages, even if few individuals live very long.

The consequences for estimates of N_e and N_e/N of these biases in \tilde{T} , \tilde{N} and $\tilde{V}_{k\bullet}$ are seen in Figure 4. When fecundity is constant and $d=0.1$, \tilde{N}_e has a strong upward bias for adult lifespans < 20 years, reflecting an even stronger upward bias in \tilde{T} (Figure 3 top). However, this strong bias in N_e does not lead to appreciable bias in N_e/N , presumably because the upward bias in T is offset by the combined upward biases of $V_{k\bullet}$ and N , both of which reduce the ratio N_e/N . When fecundity is proportional to age and $d=0.4$, both N_e and N_e/N are effectively unbiased if $AL \geq 20$ years. When mortality is low, N_e/N has a persistent downward bias until AL is well over 40 years.

Figure 5 shows biases associated with estimating T and N for species with Type I survivorship, based on the scenarios shown in Supplementary Table S2. It is apparent that using \bar{d} in Equations (4)

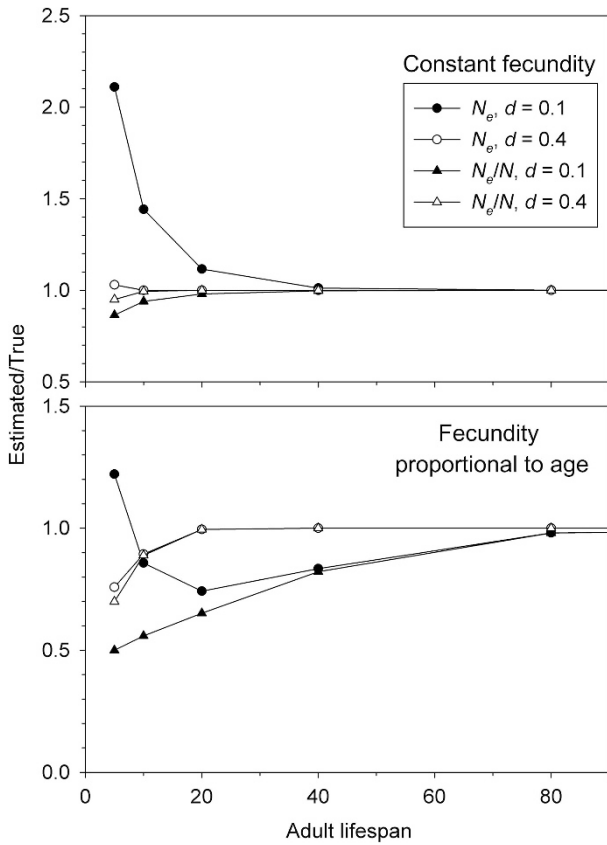


Figure 4 Bias in estimates of N_e and N_e/N when applying analytical results based on infinite series to populations with finite adult lifespan. These scenarios used constant adult mortality at the levels indicated, constant $\phi=1$ and either constant fecundity (top) or fecundity proportional to age (bottom). ‘Estimated’ parameters were based on the expectations from infinite series analysis and ‘True’ values were calculated for the actual time series using the AgeNe method described by Waples *et al.* (2011).

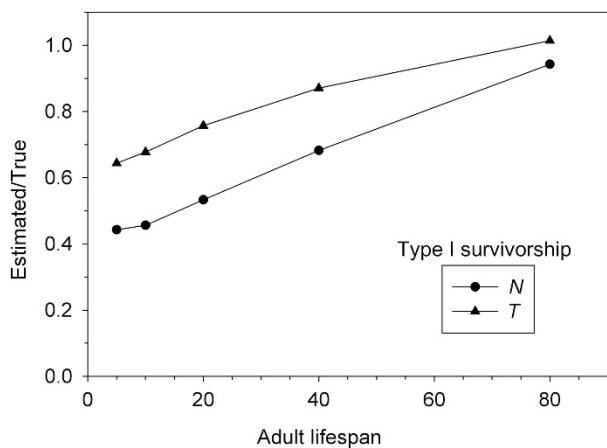


Figure 5 Bias in estimates of adult census size and generation length when assuming constant survival for species with Type I survivorship. These scenarios used constant fecundity and survivorship followed the Gompertz functions depicted in Figure 1. True parameters were calculated for the observed data using the AgeNe method described by Waples *et al.* (2011) and the estimates were calculated using the \bar{d} values in Supplementary Table S2 to represent mortality in Equations (4) and (7), assuming $\alpha=1$.

and (7) can be expected to substantially underestimate both T and N in all but the longest-lived species, with the downward bias in \tilde{N} being stronger. These underestimates occur because the survivorship curve is consistently higher for Type I survival than it is assuming constant mortality to produce the same end point, and T and N are both functions of Σl_x .

Figure 6 integrates results obtained in this paper for all key parameters into an overall assessment of the expected value of the N_e/N ratio as a function of adult mortality. These results assume constant survival and either constant fecundity or fecundity proportional to age. Results are presented for two ages at maturity (1 and 5) and two values of ϕ (1 and 4). Although these results are only asymptotically correct for populations with long adult lifespan, they are useful heuristically to illustrate the relative importance of some key variables. With age at maturity fixed at one year (top panel) and ϕ fixed at 1, expected N_e/N varies from > 0.9 to ~ 0.5 when fecundity is constant and from ~ 0.8 to 0.33 when fecundity is proportional to age. These results are consistent with the conclusion by Nunney (1993) that N_e/N should generally be > 0.5 and only rarely as low as 0.25; they are also generally consistent with empirical estimates of single-generation N_e/N reviewed by Frankham (1995).

However, two other factors can substantially reduce or increase the N_e/N ratio. First, even if all individuals mature at age 1, N_e/N is lower if reproductive success of same-age individuals is overdispersed ($\phi > 1$). In that case, whether fecundity is constant or increases with age has little effect, as the N_e/N ratio is driven by ϕ that is only mildly sensitive to adult mortality and hence adult lifespan. Because lifetime $V_{k\bullet}$ increases in direct proportion to ϕ (Figure 2), the N_e/N ratio approaches 0 as ϕ becomes arbitrarily large. As discussed below, this has relevance to the hypothesis of Hedgcock (1994) of sweepstakes reproductive success. $V_{k\bullet}$ can also become very large in species with low adult mortality if ϕ increases with age (Figure 2). Second, every year of delayed maturity increases generation length by 1 year (equation (8)) but by itself has no effect on the other parameters. Because N_e is proportional to T (equation (1)), increasing age at maturity increases both N_e and N_e/N , as others have reported (Nunney, 1993; Waite and Parker, 1996; Lee *et al.*, 2011). It is easy to show that the N_e/N ratio can considerably exceed 1 when the age at maturity is substantially > 1 (Figure 6, bottom; see also Waples *et al.* 2013).

An interesting observation from Figure 6 is that, quite consistently, the expected N_e/N ratio declines with increasing adult survival and hence longer adult lifespan. This occurs in spite of the fact that reduced mortality increases generation length that (all else being equal) should increase N_e . However, unlike the situation with delayed maturity, T does change independently of the other parameters when survival increases—that same phenomenon also increases both N and $V_{k\bullet}$. The combined effects of these increases more than offset the increases in T , with the result that increases in survival generally are associated with a net reduction in N_e/N .

Empirical data

Supplementary Table S1 reproduces key data for the 63 life tables compiled by Waples *et al.* (2013), with modifications to age at maturity and adult census size as described in Methods. Waples *et al.* (2013) reported a multiple R^2 value of 0.5 for the correlation between N_e/N and the log of the ratio AL/α ; with the modifications here, the correlation has strengthened to $R^2 = 0.61$, indicating that this ratio of simple life-history traits explains just over 60% of the variation in N_e/N across these diverse species. The improvement in this association suggests that the adjustments to age at maturity and hence adult N made here are biologically reasonable.

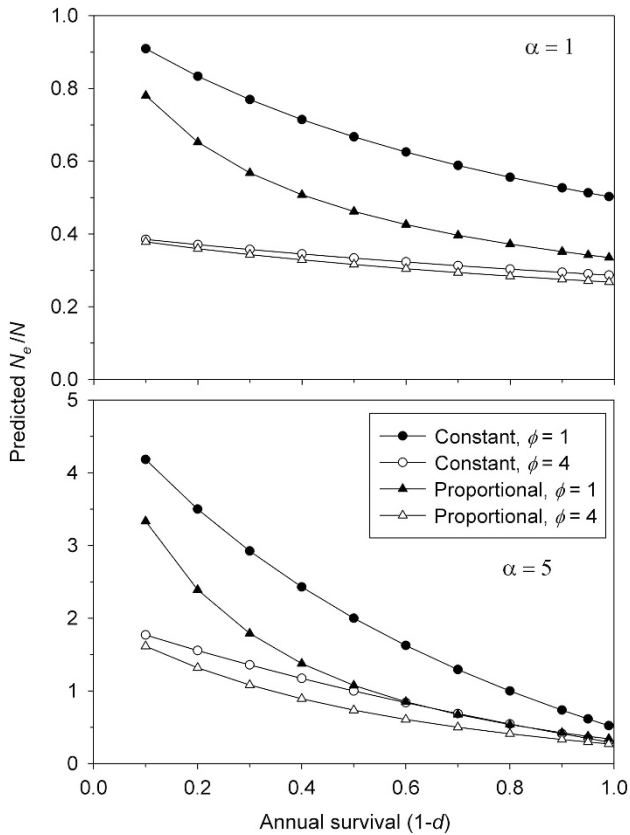


Figure 6 Relationship between annual survival ($s=1-d$, assumed to be constant) and predicted N_e/N , for scenarios involving different combinations of age at maturity, ϕ and fecundity (constant or proportional to age). Predictions for constant fecundity use Equation (14) and those for fecundity proportional to age use Equation (18).

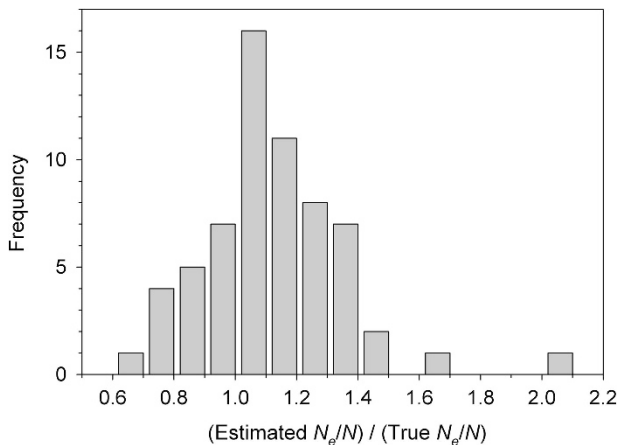


Figure 7 Estimates of N_e/N compared with the true ratio for 63 species with diverse life histories. True parameters were calculated using the life tables compiled by Waples *et al.* (2013), with modifications as described in Methods and shown in Supplementary Table S1. Estimates of N_e/N were calculated from Equation (14) using the actual age at maturity and the values of \bar{d} shown in Supplementary Table S1.

For the simplest general model considered in this paper that incorporates age at maturity (constant vital rates; Equation (14)), the correlation between the estimated \hat{N}_e/N and the predictor $[d(1-d + \alpha - 1)/(2-d)]$ is very strong ($R^2=0.78$). That is, this

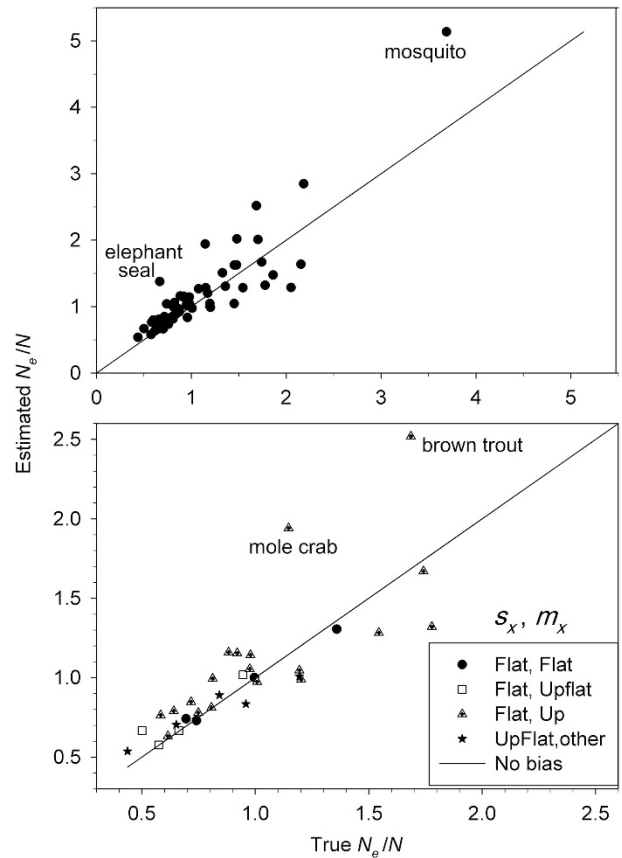


Figure 8 Relationship between estimated and true N_e/N for individual species, using data from Figure 7. The top panel shows results for all 63 species; the bottom panel shows results only for species with survival that is constant with age, or nearly so. Some outlier species are identified. The legend indicates general patterns of age-specific survival and fecundity. 'Flat'=constant with age; 'UpFlat'=increasing in the first few years after maturity before leveling off; 'Up'=increasing with age; 'other'=decreasing with age, complex patterns or different patterns in males and females.

simple function of adult mortality and age at maturity explains over three-fourths of the empirical variation in N_e/N , which spans a >8-fold range, from 0.44 to 3.69 (Supplementary Table S1). Figure 7 shows the distribution of the ratio estimated/true N_e/N for the 63 species. The median ratio is 1.08 and the range is 0.6–2.1, indicating a slight upward bias. A comparison of estimated and true N_e/N for all species reveals a couple of outliers with unusual life-history features and estimates of N_e that are well above the true value (Figure 8, top). The mosquito (Chubachi, 1979) has sharply declining patterns of both adult survival and fecundity that departs strongly from the assumed simple model of constant vital rates. The elephant seal has strongly asymmetric maturity and fecundity schedules between males and females (LeBoeuf and Reiter, 1988) that reduces N_e in ways not considered here.

If we restrict attention to only those species with constant (or nearly constant) adult survival (Figure 8, bottom), for all species that also have constant fecundity (filled circles) the true N_e/N is very similar to the estimate based on Equation (14). The estimator is also fairly accurate for most other species with constant survival but varying patterns of fecundity. The simple model considerably overestimates N_e/N for brown trout (presumably because of divergent vital rates in males and females; see Jorde and Ryman, 1996) and the mole crab (perhaps because fecundity increases sharply with age; see Diaz, 1980).

For species with constant survival but increasing fecundity with age, the estimator of N_e/N from Equation (18) was also evaluated. This estimator consistently underestimated true N_e/N (data not shown). This is consistent with results in Figure 4, which show that when fecundity is proportional to age, N_e/N is substantially underestimated using Equation (18) unless adult lifespan is very long. This result, in turn, can be traced to the pronounced upward bias in T , N and especially $V_{k\bullet}$ for this model (Figure 3), with the latter having a strong effect of reducing N_e .

DISCUSSION

The influence of generation length and variance in reproductive success

It is useful to review the factors that can influence the key parameters N , T and $V_{k\bullet}$, and hence N_e and N_e/N in iteroparous species (Equation (1)). Adult abundance depends on only two parameters (Equation (2)): the number of recruits that reach age at maturity (N_α) and Σl_x . Because survivorship does not depend on patterns of fecundity or variance in reproductive success, the age-specific pattern of adult mortality directly determines N .

Generation length (Equation (5)) depends entirely on (1) age at maturity and (2) functions of age-specific survival and fecundity; as a consequence, T is also unaffected by variance in reproductive success among individuals. In contrast, lifetime $V_{k\bullet}$ is sensitive to three parameters (Equations (10–12)): age-specific patterns of survival, fecundity and variance in reproductive success by individuals of the same age (ϕ_x).

Like census size, N_e is a linear function of N_α , and hence the level of recruitment does not affect the N_e/N ratio. Because generation length appears in the numerator of Equation (1) and variance in reproductive success appears in the denominator, the two parameters have contrasting effects on N_e . All else being equal, increases in T increase N_e , whereas increases in $V_{k\bullet}$ reduce N_e and vice versa. But these parameters are not independent; life-history traits that increase one generally increase the other, although they typically change at different rates with changes in the population's vital rates. Therefore, a key determinant of N_e/N is how the ratio $T/V_{k\bullet}$ changes with the species' life history. Because ϕ_x affects $V_{k\bullet}$ (but not T or N), and α affects T (but not N or $V_{k\bullet}$), these parameters can also have an important influence on both N_e and N_e/N .

Lifetime $V_{k\bullet}$ is a complicated parameter that has been little studied, no doubt in part because it is not very tractable analytically. Waples *et al.* (2011) showed how to calculate $V_{k\bullet}$ using a species' vital rates but did not conduct a sensitivity analysis. To the best of my knowledge, Figure 2 represents the first attempt to jointly evaluate the effects of life-history parameters on $V_{k\bullet}$ and T . This figure provides several important insights. First, when vital rates are constant, $V_{k\bullet}$ is a linear function of d . As d drops and survival increases, $V_{k\bullet}$ also increases because more individuals live to ages at which they can amass large numbers of lifetime offspring. Second, regardless of the value of d , $V_{k\bullet}$ is increased by exactly 2 units for every unit increase in ϕ . This makes it easy to account for the consequences of over-dispersed variance in reproductive success of individuals of the same age. Third, the slope of the regression of $V_{k\bullet}$ on $1-d$ is shallow, and hence (regardless of the value of d) different levels of mortality do not lead to dramatically different values of $V_{k\bullet}$, provided survival and fecundity do not vary with age. In contrast, generation length is a simple inverse function of d , and hence as adult mortality becomes very low T increases sharply. This means that when adult survival is high, the relationship between T and $V_{k\bullet}$ (and consequently the N_e/N ratio) can be very sensitive to small changes in (or errors in

estimating) mortality. Finally, when ϕ and fecundity both increase with age, $V_{k\bullet}$ increases very rapidly and nonlinearly with reductions in mortality. A caveat is that the relationships shown in this figure are based on analytical results for populations with arbitrarily long lifetimes. As shown in Figure 3, these relationships can substantially overestimate both T and $V_{k\bullet}$ in scenarios in which fecundity increases with age, mortality is low and adult lifespan is short.

Estimating N_e/N

Surprisingly, the simplest model with constant vital rates (Equation (14)) proved to be a very robust estimator of N_e/N in the 63 species for which empirical life-history data are available. Furthermore, this simple estimator appears to perform about as well for species with strongly age-specific patterns of survival and fecundity as it does for species with constant vital rates. Some of the outliers are species (such as the elephant seal and brown trout) that have strongly asymmetric vital rates in males and females. This scenario was not formally evaluated here, but its effects on N_e are well understood (and for example are fully incorporated into AgeNe calculations of N_e and N_e/N), and hence separate adjustments could be made to the estimate of N_e/N in these cases.

It should be noted that the general results shown in Figure 6 are based on the assumption that \bar{d} and α can be estimated accurately. Estimating geometric mean mortality is perhaps not unreasonable, as its calculation depends only on the adult lifespan and the (somewhat arbitrary) decision as to what value of l_x to assign to age ω ($l_\omega = 0.01$ was used here). An accurate determination of age at maturity is important because that directly affects generation length; achieving this is straightforward for some species but can be complicated when maturation occurs across a variety of ages. This topic merits careful attention. Finally, as information on age-specific values of ϕ are rare for natural populations, these analyses followed Waples *et al.* (2013) in using the default assumption that ϕ is constant at 1 (equivalent to assuming, for example, that reproductive success of all age-6 females corresponds to a mini Wright–Fisher ideal population). Values of ϕ almost certainly vary among species, meaning that the strength of the relationship between N_e/N and d shown in Figure 6 ($R^2 = 0.78$) is probably optimistic. Nevertheless, integration of all the key factors affecting the N_e/N ratio into a single analysis expressed as a function of adult mortality should help advance our understanding of this key eco-evolutionary parameter.

Some additional factors that can affect N_e and N_e/N also were not considered here. The Felsenstein–Hill model that AgeNe is based upon assumes that (1) N is constant and age structure is stable, and (2) probabilities of survival and reproduction are independent and not affected by previous timesteps. Felsenstein (1971) showed that his model accurately calculated N_e for populations that are increasing or declining at a constant rate, and Waples *et al.* (2011, 2014) showed that AgeNe results are robust for dynamically stable populations with random demographic stochasticity. However, caution should be used in applying these results to species that are characterized by large or chaotic changes in abundance.

In many species, females (and sometimes males) generally skip one or more years after breeding. Waples and Antao (2014) showed that although this reduces the effective number of breeders each year (N_b), particularly for species with Type III survivorship, this life-history feature has only a slight (<10%) positive effect on N_e . Constraints on litter size that can result in $\phi_x < 1$ also lead to only small increases in N_e (Waples and Antao, 2014). On the other hand, if some individuals consistently are either good or bad at producing offspring across their

lifetime, this will increase lifetime variance in reproductive success and reduce N_e (Lee *et al.*, 2011). This is difficult to track in natural populations but for some species it could significantly reduce the N_e/N ratio.

Hedgcock (1994) proposed that a pattern of 'sweepstakes' reproductive success, in which only a small fraction of families leave offspring that survive to reproduce, could produce tiny N_e/N ratios in marine species with high fecundity and high mortality in early life stages. The framework discussed here can evaluate that scenario, but it requires that ϕ be very high ($\geq 10^3$) for most or all ages, which in turn can only occur if the fraction of parents of a given age that successfully produce offspring in a given year is as small as $1/\phi$.

Genomic estimates of N_e

Although this paper considered only demographic data, genetically based estimates of effective size have skyrocketed in recent years (Palstra and Fraser, 2012), and this trend is only likely to increase with the ability to use next-generation DNA sequencing techniques to generate thousands of markers for nonmodel species (for example, see Hollenbeck *et al.*, 2016; Jones *et al.*, 2016). To provide context for interpreting these estimates, most of these new studies will have to consider the N_e/N ratio, and hence results presented here will be relevant. Furthermore, for the majority of the earth's species that do not have discrete generations, it will be necessary to consider the effects of age structure on the genetic estimates. In these cases, careful attention must be paid to sampling design to evaluate whether the resulting estimates are more relevant to effective size in one reproductive cycle (N_b) or to N_e for an entire generation. Researchers interested in applying the two-sample (temporal) method to age-structured species can find useful guidance in Waples (1990), Jorde and Ryman (1996) and Waples and Yokota (2007). The single-sample sibship method can be applied to species with overlapping generations using an approach suggested by Wang *et al.* (2010). Robinson and Moyer (2013) and Waples *et al.* (2014) have evaluated performance of the single-sample method based on linkage disequilibrium with iteroparous species.

DATA ACCESSIBILITY

The empirical data used in this study are all published and freely available elsewhere.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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Supplementary Information accompanies this paper on Heredity website (<http://www.nature.com/hdy>)