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Calculating N_e and N_e/N in age-structured populations: a hybrid Felsenstein-Hill approach

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Abstract. The concept of effective population size (N_e) was developed under a discrete-generation model, but most species have overlapping generations. In the early 1970s, J. Felsenstein and W. G. Hill independently developed methods for calculating N_e in age-structured populations; the two approaches produce the same answer under certain conditions and have contrasting advantages and disadvantages. Here, we describe a hybrid approach that combines useful features of both. Like Felsenstein's model, the new method is based on age-specific survival and fertility rates and therefore can be directly applied to any species for which life table data are available. Like Hill, we relax the restrictive assumption in Felsenstein's model regarding random variance in reproductive success, which allows more general application. The basic principle underlying the new method is that age structure stratifies a population into winners and losers in the game of life: individuals that live longer have more opportunities to reproduce and therefore have a higher mean lifetime reproductive success. This creates different classes of individuals within the population, and grouping individuals by age at death provides a simple means of calculating lifetime variance in reproductive success of a newborn cohort. The new method has the following features: (1) it can accommodate unequal sex ratio and sex-specific vital rates and overdispersed variance in reproductive success; (2) it can calculate effective size in species that change sex during their lifetime; (3) it can calculate N_e and the ratio N_e/N based on various ways of defining N; (4) it allows one to explore the relationship between N_e and the effective number of breeders per year (N_b), which is a quantity that genetic estimators of contemporary N_e commonly provide information about; and (5) it is implemented in freely available software (AgeNe).

Key words: age-structured population; effective number of breeders; Leslie matrix; overdispersed variance; overlapping generations; reproductive success; sex reversal; software.

Introduction

The concept of effective population size (N_e) is elegantly simple yet rapidly becomes complex as simplifying assumptions give way to practical realities. One major challenge (extension to age-structured populations) was addressed by Felsenstein (1971) and Hill (1972, 1979), who showed how Wright's (1938) discrete generation model could be modified to accommodate species with overlapping generations. The Felsenstein and Hill approaches are largely complementary and have contrasting advantages and disadvantages. A nice feature of Felsenstein's method is that it uses age-specific survival and fertility rates and therefore can provide information on N_e and the ratio of effective size to census size (N) for any population for which detailed demographic information is available. However, his method depends on the assumption that variance in reproductive success among same-age individuals is random, which is unlikely to occur in natural populations. Also, Felsenstein did not directly consider species with separate sexes, although he speculated that results would probably not differ substantially from those he found for haploid and monoecious species. Hill's method is more general, as it makes no particular assumptions about variance in reproductive success and can be applied to separate sexes; however, it does not provide a direct link to the population's demographic data, nor does his method provide any guidance on how to use the type of demographic information contained in a life table to calculate N_e. The two models produce the same result under Felsenstein's random-variance assumption (Johnson 1977, Charlesworth 1980).

Here, we describe a hybrid method for calculating N_e and N_e/N in age-structured populations that incorporates useful aspects of both the Felsenstein and Hill methods and includes some additional features. Like Felsenstein's (1971) model, the new method begins with demographic information for the population at hand and therefore allows one to evaluate how N_e and N_e/N vary as vital rates vary. Like Hill's (1972, 1979) model, the hybrid method provides a simple way to assess effects of overdispersed variance on effective size. The hybrid model complements the pioneering work of Len Nunney, who, in a series of papers (Nunney 1991, 1993,

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1996) derived analytical approximations for effective size in age-structured species based on some key life history parameters. The principle underlying the new method is that age structure stratifies a population into winners and losers in the game of life: individuals that live longer have more opportunities to reproduce and therefore have a higher mean lifetime reproductive success than do individuals that die at a younger age. This creates different classes of individuals within the population, based on age at death. Even if variance in reproductive success is random among all individuals that die at a specific age, the lifetime variance among individuals in the population as a whole will be greater than Poisson because of this process of stratification, and as a result N_e will be less than N. This basic idea was briefly outlined by Waples (2010); here, we provide a more rigorous quantitative treatment and extend the method to some special cases. The new method has the following features: (1) it uses demographic information of the type found in a life table or Leslie matrix; (2) it can accommodate two sexes with unequal sex ratio and/or different vital rates; (3) it can accommodate departures from Poisson variance in reproductive success; (4) it can calculate N_e and N_e/N based on various ways of defining N; (5) it can calculate the effective number of breeders per year (N_b) and the ratio N_b/N_e; (6) it can calculate effective size in species that change sex during their lifetime; and (7) it is implemented in freely available software (AgeNe; see Supplement).

Development of the Approach

Assumptions and notation

Key assumptions of our model follow those of Felsenstein and Hill: (1) there are fixed numbers of individuals at each age, (2) a constant number N_1 of newborns is produced each time period (hereafter assumed to be years), (3) individual variations in fertility are not inherited, and (4) age-specific survival and reproduction are both independent of reproductive success in previous years. With a closed population of constant size, inbreeding and variance effective sizes are the same, so the treatment that we will outline applies equally to both.

The important demographic parameters are age-specific birth rates (b_x is the mean number of newborns produced by an individual at age x) and survival rates (s_x is the probability of surviving from age x to age $x+1$). By convention, all newborns survive to the reproductive period at age 1, at which point they produce an average of b_1 newborns. Following reproduction, a fraction s_1 of the one-year-olds survive to the reproductive period at age 2. Repeated sequences of reproduction and survival or mortality continue until the remaining individuals reach the maximum age (K), at which point they reproduce and die (i,e., $s_K = 0$). These data can be assembled in a standard life table, as in Table 1. The survivorship curve (l_x is the fraction of the newborn cohort that is alive at age x) is generated by defining the function $l_1 = 1$ and $l_x = l_{x-1}s_{x-1}$ for $x > 1$. For the population to be stable in size and produce exactly N_1 offspring every year, the vectors of l_x and b_x values must satisfy the relationship $\sum b_x l_x = 1$. If this is not the case, a stable population can be generated by dividing each b_x value by $\sum b_x l_x$. This provides a handy way of rescaling estimates of age-specific, relative reproductive success to produce a stable population. In this formulation, the number of individuals in each age group is given by $N_x = N_1 l_x$, the total number of individuals alive at any given time is $N_T = \sum N_x$, the number of births by individuals of age x is given by $B_x = b_x N_x$, and the generation length (L, the average age of parents of a newborn cohort) is given by $L = \sum x B_x / N_1$.

In the example shown in Table 1, the nominal b_x values (0, 1, 2, 3 for ages 1–4 years) lead to a growing population ($\sum b_x l_x = 1.375$), so they are scaled to values in the same proportions (b_x') that lead to a stable population. In this example, the generation length is $L = 2.909$ years, the total population includes $N_T = 1875$ individuals aged 1–4 years, and the adult population includes $N_A = 875$ mature individuals aged 2–4 years.

Haploids

Our goal is to use Hill's (1972, 1979) formulas for N_e in species with overlapping generations, but to anchor the analysis to life table data, as in Felsenstein's method. We begin by considering the simple case of a haploid organism. Hill (1979) provided the following expression for N_e in an age-structured haploid species:

$$N_e \approx N_1 L / V_k \quad (1)$$

where N_1 and L are as previously defined and V_k is the lifetime variance in reproductive success among the N_1 individuals in a cohort. The "≈" sign reflects the fact that Hill ignored second-order terms in N in the derivation. To accomplish our goal, we need a means to calculate V_k from data in a life table. This can be done by partitioning the overall population into groups of individuals based on age at death. In the example in Table 1, $K = 4$ so there are four groups of individuals: those that die after reaching ages 1, 2, 3, and 4 years. Within each group, all individuals have the same expected lifetime reproductive success, given by $\bar{k}_x = \sum b_{i(i \le x)}$, where k is the number of gametes contributed by an individual to the next generation. Associated with each mean $\bar{k}_x$ will be a variance (V_x) that represents the lifetime variance in k among all individuals that die at age x. We want to relax Felsenstein's assumption that all these variances are binomial (in which case V_x is close to the Poisson variance $\bar{k}_x$). However, it is convenient to express realized V_x in terms of the Poisson variance to retain a direct connection to the ideal-population analogue that assumes random variation in reproductive success. Therefore, we specify that $V_x = \alpha_x \bar{k}_x$, where α_x is a Poisson scaling or overdispersion factor that quantifies how large V_x is compared to $\bar{k}_x$. Although in general it will be the case that $\alpha > 1$ in natural populations, this

TABLE 1. Life table data for a haploid species that produces a constant number N_1 of newborns each year, all of which survive to age 1.

Age, x (yr)	s_x	b_x	l_x	$b_x l_x$	b'_x	$b'_x l_x$	N_x	B_x	xB_x/N_1
1	0.5	0	1.000	0.000	0.000	0.000	1000	0.0	0.000
2	0.5	1	0.500	0.500	0.727	0.364	500	363.6	0.727
3	0.5	2	0.250	0.500	1.455	0.364	250	363.6	1.091
4	0	3	0.125	0.375	2.182	0.273	125	272.7	1.091
Totals				1.375		1.000	1875	1000	2.909†

Notes: The parameter b'_x is age-specific fecundity scaled to produce a constant population size, given age-specific survival rates (s_x); l_x is the fraction of the newborn cohort that is alive at age x; N_x is the number of age-x individuals in the population, and $B_x = b'_x N_x$ is the number of newborns in a single year produced by parents of age x.

† $\Sigma xB_x/N_1$ is generation length (L) in years, although the model can accommodate different time units for x and L.

treatment is general and can accommodate situations (e.g., captive breeding programs) under which extrinsic factors might constrain variance in reproductive success to be less than random (leading to $\alpha < 1$).

We use a sums-of-squares approach to obtain overall V_k from the age-at-death specific $\bar{k}_x$ and V_x values, as illustrated in Table 2. The data in Table 1 lead to mean reproductive success values that range from $\bar{k}_1 = 0$ (individuals that die at age 1 never reproduce) to $\bar{k}_4 = 4.364$ (for those that live to age 4). Because the population is haploid and stable, on average each individual must contribute exactly one gamete to the next generation; therefore, overall $\bar{k}_\cdot = 1$, which also is the weighted mean across the age-at-death groups. The numbers that die after reaching each age x are easily calculated as $D_x = N_x - N_{x+1}$. Overall $V_{k\cdot}$ is the mean squared deviation of the individual k values from the overall mean $\bar{k}_\cdot$. The total sum of squares of deviations (SSD_T) is composed of two parts: (1) deviations of the lifetime k of each individual from its age-at-death specific mean value $\bar{k}_x$, and (2) deviations of the $\bar{k}_x$ from the overall $\bar{k}_\cdot$ ($\Delta_x = \bar{k}_x - \bar{k}_\cdot$). We refer to the first component as SSD_I because it captures information about variation among individuals within groups and to the second component as SSD_G because it refers to deviations of the group means from the overall population mean. For each age-at-death group x, SSD_{Ix} is simply $D_x V_x$, SSD_{Gx} is $D_x \Delta_x^2$, and their sum is denoted by $SSD_x = SSD_{Ix} + SSD_{Gx}$. It is then straightforward to calculate SSD_T as $\sum SSD_x$ and overall $V_{k\cdot}$ as SSD_T/N_1.

When these analyses are applied to the data in the example, the result is that lifetime variance among all individuals in the population is $V_{k\cdot} = 3.107$ (Table 2A), and when this value is inserted into Eq. 1 together with $N_1 = 1000$ and $L = 2.909$ from Table 1, the result is $N_e = 936.2$. Note that this is almost exactly half the total number of individuals alive at any given time ($N_e/N_T = 936.2/1875 = 0.499$), a reduction that can be explained by the fact that $V_{k\cdot}$ for the population is over three times as large as the mean. This example assumed Poisson variance in reproductive success among individuals within an age group, so the increased variance is due to stratification of the population into groups with different mean lifetime reproductive success. For example, in this population, one-half of the individuals do not survive to age at first reproduction, and those that live until age 4 have an expected lifetime reproductive success six times as large as that for individuals that die after age 2 ($\bar{k}_4 = 4.364$; $\bar{k}_2 = 0.727$). However, only 125 individuals (one-eighth of the original cohort) live to age 4, so during any given time period more newborns are produced by two- and three-year-old parents than those age 4 (Table 1). Although in this example N_e/N_T is about 0.5 when N_T is used in the denominator, the result is quite different if N_e is compared to the number of mature adults ($N_e/N_A = 936.2/875 = 1.07$).

Table 2B shows the effect of allowing nonrandom variation in reproductive success among individuals of the same age. This example used the Poisson scaling factor $\alpha = 3$, so all $V_x = 3\bar{k}_x$. With this extra source of variability, overall variance in reproductive success is higher ($V_{k\cdot} = 5.107$; Table 2B) and effective size is considerably lower ($N_e = 569.6$, after inserting the higher $V_{k\cdot}$ into Eq. 1) than under the Poisson assumption. It is interesting to note that, with the haploid life history, for every unit increase in the Poisson scaling factor, $V_{k\cdot}$ increases by exactly 1.0. To see why this is so, note that

$$V_{k\cdot} = \frac{1}{N_1}\sum_x SSD_x = \frac{1}{N_1}\sum_x D_x(\alpha_x \bar{k}_x + \Delta_x^2).$$

Let γ be a constant. Replacing α_x in the sum above by $(\alpha_x + \gamma)$, we have

$$\frac{1}{N_1}\sum_x D_x[(\alpha_x + \gamma)\bar{k}_x + \Delta_x^2]$$

$$= \frac{1}{N_1}\sum_x D_x(\alpha_x \bar{k}_x + \Delta_x^2) + \gamma \frac{1}{N_1}\sum_x D_x \bar{k}_x$$

$$V_{k\cdot} = \frac{1}{N_1}\sum_x D_x(\alpha_x \bar{k}_x + \Delta_x^2) + \gamma \bar{k}_\cdot.$$

Thus, adding γ to the scaling factor will result in $V_{k\cdot}$ being increased by $\gamma\bar{k}_\cdot$. A similar approach can be used to show that, with separate sexes, adding a constant γ to the Poisson scaling factor will cause $V_{k\cdot}$ to be increased by $2\gamma\bar{k}_\cdot$.

Separate sexes

Now consider a population with separate sexes that still produces a constant number (N_1) of newborns each

TABLE 2. Demographic data (see Table 1) for individuals grouped by age at death, with variation in reproductive success among same-aged individuals being (A) random ($V_x = \bar{k}_x$) and (B) overdispersed (Poisson scaling factor $\alpha = 3$, so $V_x = 3\bar{k}_x$).

Age at death (yr)	$\bar{k}_x$	V_x	D_x	$\bar{k}_x D_x$	SSD_{Ix}	Δ_x	SSD_{Gx}	SSD_x
A) Random variation								
1	0.000	0.000	500	0.0	0.0	1.00	500.0	500.0
2	0.727	0.727	250	181.8	181.8	0.27	18.6	200.4
3	2.182	2.182	125	272.7	272.7	−1.18	174.6	447.3
4	4.364	4.364	125	545.5	545.5	−3.36	1414.3	1959.7
Totals	1†	3.107‡	1000	1000				3107.4
B) Overdispersed variation								
1	0.000	0.000	500	0.0	0.0	1.00	500.0	500.0
2	0.727	2.182	250	181.8	545.5	0.27	18.6	564.0
3	2.182	6.545	125	272.7	818.2	−1.18	174.6	992.8
4	4.364	13.091	125	545.5	1636.4	−3.36	1414.3	3050.6
Totals	1†	5.107‡	1000	1000				5107.4

Notes: The parameters $\bar{k}_x$ and V_x are the mean and variance of lifetime reproductive success for individuals that die at age x; D_x is the number that die at age x; $SSD_{Ix} = V_x D_x$ is the sum of squared deviations of individual (I) k values from the age-at-death mean $\bar{k}_x$; $\Delta_x = \bar{k}_x - \bar{k}_\cdot$ is the difference between the age-specific mean and the overall mean $\bar{k}_\cdot$; $SSD_{Gx} = D_x\Delta_x^2$; and $SSD_x = SSD_{Ix} + SSD_{Gx}$, where subscript G refers to deviations of the group means from the overall population mean. Although x is most commonly in years, other time units are possible.

† Overall $\bar{k}_\cdot = \sum(\bar{k}_x D_x)/N_1$.

‡ Overall $V_{k\cdot} = \sum SSD_x/N_1$.

year, of which a constant fraction m are male and $f = 1 - m$ are female. For each sex, an analogue to Table 1 can be created using sex-specific vital rates ($s_{x(s)}$, $b_{x(s)}$, where subscripted s signifies m or f). To allow for unequal sex ratio, it is necessary to scale the sex-specific b_x values so that overall population size is constant but the less numerous sex produces more offspring per capita. Each of the N_1 newborns in each time period must have exactly one male and one female parent. Therefore, during their lifetime, the mN_1 male members of a newborn cohort must father a total of N_1 offspring, and the same is true for the $(1 - m)N_1$ females in the cohort. This can be achieved by scaling $b_{x(s)}$ so that $\sum b_{x(s)}N_{x(s)} = N_1$.

In this way, analogues to Tables 1 and 2 can be constructed separately for each sex, and $V_{k\cdot}$ is then calculated across both sexes, as illustrated in Tables 3 and 4. In this example, variance in age-specific reproductive success is Poisson, but initial sex ratio is unequal (70% of newborns are male) and both b_x and s_x vectors differ between males and females (Table 3). Despite the unequal sex ratio, each sex must contribute equally to the N_1 newborns, so to maintain constant population size the nominal b_x values are scaled to ensure that $\sum B_x = \sum b'_x N_x = 1000$. This can be achieved by setting $b'_x = 1000b_x/\sum b_x N_x$. The different vital rates lead to different generation lengths in males and females, and the overall generation length (L) is simply the mean of the sex-specific values ($L = [2.240 + 3.121]/2 = 2.681$) (Charlesworth 1980).

Table 4 is based on demographic data in Table 3 and is analogous to Table 2, but with two differences: (1) separate sub-tables are presented for each sex; (2) Δ_x and SSD_x are calculated with respect to the sex-specific means ($\bar{k}_m = 1.429$; $\bar{k}_f = 3.333$), leading to sex-specific variances of reproductive success ($V_m = 2.824$; $V_f = 20.455$). Using these sex-specific means and variances, it is straightforward to calculate overall values (across both sexes) as $\bar{k}_\cdot = m\bar{k}_m + f\bar{k}_f = 2$ and $V_{k\cdot} = mV_m + fV_f + mf(\bar{k}_m - \bar{k}_f)^2 = 8.875$. Note that in our model $\bar{k}_\cdot$ will always be exactly 2 for diploids because population size is constant.

The analogue to Eq. 1 for diploids is as follows (Hill 1972: Eq. 16; Hill 1979: Eq. 8):

$$N_e \approx \frac{4N_1L}{V_{k\cdot} + 2}. \quad (2)$$

N_1, L, and $V_{k\cdot}$ as calculated here can be inserted into Eq. 2 to calculate effective size: $N_e = 4 \times 1000 \times 2.681/(8.875 + 2) = 986$. This leads to N_e/N ratios of $986/2067 = 0.48$ for the population as a whole and $986/1767 = 0.56$ when compared to the number of adults.

In this example, even though there is only random variation in reproductive success among individuals of the same age and sex each year, the combination of skewed sex ratio and age structure causes the overall $V_{k\cdot}$ to be more than four times the mean. Females are in the minority and therefore have a higher mean reproductive success; they also have a much higher variance in reproductive success than males ($V_f > 20$ compared to $V_m < 3$), in part because female fecundity increases geometrically with age while male fecundity increases only linearly (Table 3).

Hill (1972, 1979) also provided a more complicated formula for N_e with separate sexes that accounts for different pathways by which male and female gametes can be transmitted across generations. However, as the simpler formula performed well with simulated data (see Fig. 1), we use that formula here and put details of the more complicated formulation in the Appendix.

If survival rates differ between sexes, the sex ratio will vary over time even if the initial sex ratio is even. In that

TABLE 3. Life table data for a diploid species with separate sexes and an initial sex ratio that is 70% male.

Age, x (yr)	s_x	b_x	l_x	b_xN_x	b'_x	b'_xN_x	N_x	B_x	xB_x/N_1
Males									
1	0.6	1	1.000	700.0	0.399	279.3	700	279.3	0.279
2	0.5	2	0.600	840.0	0.798	335.2	420	335.2	0.670
3	0.4	3	0.300	630.0	1.197	251.4	210	251.4	0.754
4	0	4	0.120	336.0	1.596	134.1	84	134.1	0.536
Totals				2506.0		1000.0	1414	1000.0	2.240†
Females									
1	0.6	0	1.000	0.0	0.000	0.0	300	0.0	0.000
2	0.6	2	0.600	360.0	1.526	274.7	180	274.7	0.549
3	0.6	4	0.360	432.0	3.053	329.7	108	329.7	0.989
4	0	8	0.216	518.4	6.105	395.6	65	395.6	1.582
Totals				1310.4		1000.0	653	1000.0	3.121†

Notes: The parameter b'_x is age-specific fecundity scaled to ensure that each sex produces $N_1 = 1000$ offspring in each time period. Other variables are defined in Table 1. In this example, age-specific fecundity and survival both differ between sexes.

† $\sum xB_x/N_1$ is the sex-specific generation length. Overall generation length (L) = $(2.240 + 3.121)/2 = 2.681$ yr. The model can accommodate other time units.

case, it can be shown that the fraction of males in the population at age x is given by

$$m_x = \frac{l_{x\mathrm{m}} m_1}{l_{x\mathrm{f}} f_1 \; + \; l_{x\mathrm{m}} m_1} \tag{3}$$

and the fraction of females by $f_x = 1 - m_x$. Under the special case where (1) initial sex ratio is 1:1, (2) all individuals mature at age 1 but experience mortality before maturing, and (3) survival is independent of age but can vary between males and females (s_m, s_f), the fraction of males in the adult population as a whole is as follows (Nunney 1996):

$$m_\mathrm{A} = \frac{1 - s_\mathrm{f}}{2 - s_\mathrm{f} - s_\mathrm{m}}.$$

Sex change

Some species are sequential hermaphrodites, beginning life as females and changing to males (protogynous) or the reverse (protandrous). Several authors (Warner 1975, Charnov 1982, Allsop and West 2003) have proposed evolutionary mechanisms that would promote sex reversal at specific sizes or ages if, on average, it should increase individual fitness. Sex reversal creates additional layers of stratification in a population beyond those associated with separate sexes and age structure. Here, we assume that an individual can only change sex once during its lifetime (from initial sex 1 to terminal sex 2), that within the population the direction of sex change is fixed, and that the initial fraction of the N_1 newborns that are the terminal sex is y. We can expand the two-sex model discussed previously to accommodate more than two groups of individuals with similar expectations for key life history parameters. If the maximum age is K, an individual can take one of $K + 1$ different sexual-identity pathways during its lifetime. For example, with $K = 3$ the four possible ontogenetic pathways are 111, 112, 122, and 222, where (for example) pathway 122 represents individuals that begin life as sex 1, change to sex 2

TABLE 4. Demographic data for individuals grouped by sex and age at death, based on Table 3, assuming Poisson variance in reproductive success ($V_x = \bar{k}_x$ at each age).

Age at death (yr)	$\bar{k}_x$	V_x	D_x	$\bar{k}_xD_x$	$\mathrm{SS}D_{\mathrm{I}x}$	Δ_x	$\mathrm{SS}D_{\mathrm{G}x}$	$\mathrm{SS}D_x$
Males								
1	0.399	0.399	280	111.7	111.7	−1.03	296.8	408.5
2	1.197	1.197	210	251.4	251.4	−0.23	11.2	262.6
3	2.394	2.394	126	301.7	301.7	0.97	117.5	419.2
4	3.990	3.990	84	335.2	335.2	2.56	551.3	886.5
Totals	1.429	2.824	700	1000.0				1976.8
Females								
1	0.000	0.000	120	0.0	0.0	−3.33	1333.3	1333.3
2	1.526	1.526	72	109.9	109.9	−1.81	235.1	345.0
3	4.579	4.579	43	197.8	197.8	1.25	67.0	264.8
4	10.684	10.684	65	692.3	692.3	7.35	3501.1	4193.4
Totals	3.333	20.455	300	1000.0				6136.5
Overall	2†	8.875‡	1000	2000.0				

† Overall $\bar{k}_\bullet = m\bar{k}_\mathrm{m} + f\bar{k}_\mathrm{f}$.

‡ Overall $V_{k\bullet} = mV_\mathrm{m} + fV_\mathrm{f} + mf(\bar{k}_\mathrm{m} - \bar{k}_\mathrm{f})^2$.

before age 2, and remain so until they die after age 3. Individuals that follow this pathway have expected lifetime reproductive success that is a function of b_{11} for sex 1 and $b_{22} + b_{32}$ for sex 2; survival from age 1 to 2 is determined by s_{11} for sex 1 and survival from age 2 to 3 is governed by s_{22} for sex 2. That is, the sequence of events in our model is reproduction, survival (or mortality) to the next age, and sex reversal (or not). The $K + 1$ pathways define $K + 1$ groups of individuals that can be characterized by a mean and variance in lifetime reproductive success, and analogues to Tables 1 and 2 can be used to calculate overall $V_{k\cdot}$ and hence N_e using Eq. 2. For each pathway, the overall SSD_T can be calculated exactly as was done for the case of separate sexes, and the SSD_T values for all pathways can be added to get $SSD_{T\cdot}$ and hence $V_{k\cdot}$.

Note that this method provides a way to calculate lifetime variance in reproductive success of individuals that can reproduce as both males and females (albeit in different time periods). Although in principle a separate generation length could be calculated for each pathway, the result would be of uncertain biological relevance. Instead, it is simpler to calculate generation length for the population as $L = \sum xB_{x\cdot}/N_1$, where $B_{x\cdot}$ is the total number of births in a given time period by parents of age x. That is, $B_{x\cdot} = B_{xf} + B_{xm} = b_{xf}N_{xf} + b_{xm}N_{xm}$. Because individuals can change sex, the numbers of each sex at each age (N_{xm}, N_{xf}) are no longer given by $N_{xs} = N_1 l_{xs}$ but instead have to be calculated based not only on N_1 and age- and sex-specific survival rates, but also on the sex ratio of newborns (y, $1 - y$) and the age-specific probability of changing sex (p_x is the probability of changing from sex 1 at age x to sex 2 at age $x + 1$).

Effective number of breeders per year (N_b)

Our previous treatments have all focused on lifetime means and variances in reproductive success, which are the appropriate quantities for assessing N_e per generation in iteroparous, age-structured species. However, it can also be of interest to calculate the effective size of the breeding population in any given year and compare that to the annual census size. Here we use the term "effective number of breeders" (N_b; Waples 1990) to refer to the N_e analogue that reflects contributions of parents in a single year.

Only minor adjustments to the model just described are necessary to calculate N_b, which considers $\bar{k}$ and V_k for a single year among all N_T individuals in the population. In any given year, the number of individuals of age x and sex s in the population is given by N_{xs}, the mean number of offspring each produces that year is $\bar{k}_{xs} = b'_{xs}$, and the variance is $V_{xs} = \alpha_x \bar{k}_{xs}$. Each sex must contribute one-half of the genes to the N_1 newborns, so the sex-specific means (across all ages) are $\bar{k}_s = N_1/N_{Ts}$, where $N_{Ts} = \sum N_{xs}$ is the total number of individuals in the population of sex s. Overall, the $N_T = N_{Tm} + N_{Tf}$ individuals in the population contribute $2N_1$ genes to the newborns, so overall $\bar{k}_{\cdot} = 2N_1/N_T$. Then, a sums-of-squares approach similar to that in Table 2 can be used to calculate overall $V_{k\cdot}$.

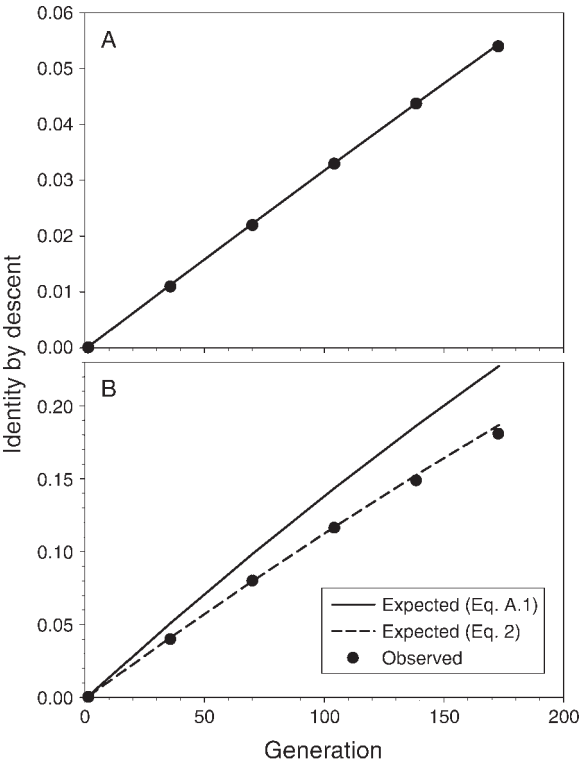

FIG. 1. Comparison of observed rate of increase in identity by descent (IBD) in simulated data with theoretical expectation. For both panels, maximum age is 4 years, and vital rates are the same in both sexes: $s_x = 0.7$ for $x = 1$–3 years, relative birth rates $b_x = 1, 2, 3, 4$ for $x = 1$–4 years, and generation length $L = 2.613$ years. (A) Fixed cohort size $N_1 = 1000$, sex ratio is 1:1, and variance in reproductive success is Poisson among same-age individuals ($\alpha = 1$), leading to $N_e = 1719$ from both Eq. 2 and Appendix Eq. A.1, so the expected rate of change in IBD is described by a single line. (B) $N_1 = 500$, sex ratio of newborns is 70% male, and variance in reproductive success in both sexes is overdispersed (Poisson scaling factor $\alpha = 3$). Under these conditions, $N_e = 465$ using Eq. 2 and $N_e = 373$ from the Appendix: Eq. A.1.

Because we consider only a single year of reproduction, we can use a discrete generation formula to calculate N_b. In general, it will be the case that annual $\bar{k}_{\cdot} \neq 2$, which means that inbreeding and variance N_b will differ. For populations that are changing in size, variance N_e is sensitive to the number of offspring and generally must be scaled to $\bar{k} = 2$ to produce a meaningful result (Crow and Morton 1955). Therefore, we calculate inbreeding N_b because this can be interpreted directly in terms of the number of parents (Kimura and Crow 1963) and because scaling to $\bar{k} = 2$ is not necessary for inbreeding N_e (Waples 2002*a*). For a species with separate sexes, the inbreeding effective size can be calculated as follows (after Crow and Denniston [1988] and Caballero [1994], using current notation):

$$N_b = \frac{\bar{k}_\cdot N_T - 2}{\bar{k}_\cdot - 1 + \frac{V_{k\cdot}}{\bar{k}_\cdot}}. \quad (4)$$

The identical result can be obtained by calculating inbreeding N_b separately for each sex using sex-specific $\bar{k}_s$ and V_{ks} and combining them using a variation of Wright's sex ratio adjustment (Crow and Denniston 1988):

$$N_e = \frac{4N_{b(m)}N_{b(f)}}{N_{b(m)} + N_{b(f)}}.$$

One can also calculate N_b using only mature adults as potential parents. Although excluding immature individuals changes both the mean and variance of k, it is easy to show that these changes exactly cancel out so that inbreeding effective size is the same regardless whether immature (or senescent) individuals are included or not (Waples and Waples 2011). Finally, our model enumerates family size at birth and assumes random survival at each age. If this assumption is true, the same results should be obtained if one were to compute the k_i values in terms of offspring that survive to reproduce. However, if family correlated mortality occurs before newborns reach maturity, counting family size at the two life stages could produce different V_k and hence different N_e values. In that case, enumerating family size in terms of production of mature adults would provide a more accurate picture of the effective number of breeders per year.

We should emphasize that N_b is not the same quantity that Hill defined as the "annual effective size" (denoted by N_y in Hill 1972 and N_a in Hill 1979), which is the size of a discrete generation population that experiences the same amount of drift as occurs over a single year in a population with overlapping generations. Because a single year represents only part of a generation for an age-structured population, N_y is larger than N_e by a factor equal to the generation length: $N_y = LN_e$ (Hill 1972, 1979). In contrast, because N_b represents parental contributions in only one year, it is generally less than N_e, although exceptions can occur for certain life histories.

Validation

We evaluated accuracy of the new method by comparing observed rates of increase in identity by descent (IBD) in simulated data with rates predicted from standard population genetics theory, assuming that true N_e is as predicted from the model. We used SPIP (Anderson and Dunham 2005) to generate genetic data for age-structured populations and used the options that specify a fixed cohort size (N_1 in current notation) and allow one to track founder alleles in subsequent generations. In the latter option, after a warm-up period to ensure that stable age distribution is reached, each individual at year 0 (the founders) is assigned two unique alleles at each locus. In subsequent generations, it is easy to calculate the mean fraction of loci at which the two alleles that an individual carries are IBD (traced to the same founder). These simulations used separate sexes, in which case IBD is still 0 after one generation because founder alleles cannot unite in offspring until the second generation. Therefore, we calculated the elapsed number of generations as $\Delta L = t/L - 1$, where L is the generation length and t is the year at which IBD is measured. The expected value of IBD after ΔL generations was then calculated as

$$E(\mathrm{IBD}_{\Delta L}) = 1 - [1 - 1/(2N_e)]^{\Delta L}.$$

We calculated observed IDB by averaging results for 20 gene loci across all of the N_1 newborns at time t. This process was repeated 10 times to generate 10 replicate values of IBD for each time period, and these were averaged to represent the "observed" IBD values.

We considered two different scenarios, both of which used the same vital rates for each sex (see Fig. 1 for details). In the first scenario, sex ratio was equal and reproductive variance was Poisson, so N_e is the same for Eq. 2 and Appendix Eq. A.1. The observed rate of increase in IBD across 500 years (almost 200 generations) tracked the expected rate of increase almost perfectly (Fig. 1A). Notably, this occurred in spite of the fact that, even with cohort size fixed at N_1 newborns, survival and newborn sex ratio are random variables in SPIP. This means that random variations in sex ratio, population size, and the number in each age class did not materially affect results. In the second scenario, newborn sex ratio was skewed (70% male) and reproductive variance was overdispersed ($\alpha = 3$ in both sexes), in which case Eq. A.1 predicted a lower N_e than Eq. 2. The observed rate of increase in IBD closely paralleled the rate predicted using Eq. 2 but was lower than the rate predicted by Eq. A.1 (Fig. 1B).

Software

We have developed a software program, AgeNe that implements all of the analyses just described (see Supplement). Input data for AgeNe are vital rates (s_x and b_x, as illustrated in Tables 1 and 3) and Poisson scaling factors for each sex for an arbitrary number of ages, as well as the number of newborns in each cohort and their initial sex ratio. Only relative fecundities are required as inputs; b_x values for both sexes are automatically scaled to produce a stable population. Outputs include L, $\bar{k}$, and V_k for each sex and overall, N_A and N_T, N_e from Eqs. 2 and 3, N_b from Eq. 4, and the ratios N_e/N_A and N_e/N_T. To calculate N_e under sex change, AgeNe also requires the user to input the initial sex and the fraction of the population at each age that is the terminal sex.

Discussion

The hybrid method described here facilitates practical application of Hill's method by retaining the link that Felsenstein's method has to demographic data contained in a standard life table. Although such data can be

challenging to collect in nature, recent dramatic increases in the power of genetic-based parentage analysis (reviewed by Jones et al. 2010) have made it possible to gather information about reproductive success that previously was all but unattainable.

Even in the absence of detailed demographic information, AgeNe provides a simple way of conducting sensitivity analyses to assess the effects of various factors on N_e and N_e/N. For example, Nunney (1991, 1996) noted that an unbalanced sex ratio can result from two different factors (a skewed primary sex ratio, or different survival rates in males and females) and showed that the former reduces N_e more strongly. These two factors can be evaluated separately in AgeNe by (1) making age-specific survival rates equal in males and females but allowing the newborn sex ratio to depart from unity, and (2) by using an even primary sex ratio but allowing different survival rates in the two sexes. Similarly, Nunney (1996) identified three components that contribute to variance in lifetime reproductive success of females: (1) random variation across years, (2) changes in fecundity with age, and (3) different mean fecundities for same-aged individuals. In AgeNe, the first component can be studied by using a single b_x value for all ages and a Poisson scaling factor of $\alpha = 1$ (in which case seasonal variations in reproductive success within an individual are random), and the second component can be evaluated by setting $\alpha = 1$ but allowing b_x to vary with age. The third component can be mimicked by choosing $\alpha > 1$, to reflect the fact that, in any given year, V_k will be larger than $\bar{k}$ because not all individuals have the same expected fecundity.

An advantage of the hybrid model is its flexibility and the ease with which it can simultaneously evaluate the joint effect of numerous demographic factors that can affect N_e. In this respect, it serves to complement the analytical models developed by Nunney, which used several simplifying assumptions that were sequentially relaxed to evaluate specific factors. The new method could also be useful in studies that combine demographic, genetic, and/or simulation approaches to estimating N_e in age-structured species (e.g., Ryman et al. 1981, Harris and Allendorf 1989, Jorde and Ryman 1995, Hard et al. 2006).

An important new feature of AgeNe is that it can facilitate comparison of N_e and N_b in age-structured populations. The difficulty in integrating data on variance in individual reproductive success across multiple breeding periods has proven to be the most challenging problem in computing N_e in iteroparous species, but this problem is greatly reduced for N_b, which only requires data for a single time period. As noted, improvements in parentage analysis make these demographic data increasingly feasible to collect in the wild. Furthermore, the last few years have seen a rapid expansion of interest in single-sample genetic methods to estimate effective size (Nomura 2008, Tallmon et al. 2008, Waples and Do 2008, Zhdanova and Pudovkin 2008, Wang 2009, Waples and Waples 2011). When applied to data for a single cohort, these methods yield an estimate of N_b, and AgeNe provides a simple way of calculating N_b from demographic data to allow a direct comparison with genetic estimates. A systematic evaluation of the relationship between N_b and N_e in iteroparous species would perhaps uncover simple patterns that can be generalized to species with similar life histories. To date, most quantitative comparisons of N_b and N_e have been conducted for semelparous species with variable age at maturity (Nunney 2002, Waples 2002*b*, 2006, Vitalis et al. 2004); Palstra et al. (2009) is an exception, as it considers a species with a certain degree of iteroparity.

AgeNe requires data in an age-based (Leslie matrix) format. Cochran and Ellner (1992) describe the transformations necessary to convert stage-based (Lefkovitch matrix) data into age-structured format. For example, the probability of moving from one stage to another can be used to generate a distribution of realized ages on entering the second stage. It should be recognized, however, that the transformations used by Cochran and Ellner assume no demographic stochasticity: that is, that deviations from model predictions due to finite population size can be ignored. This common assumption is also explicit in the Felsenstein and Hill models, as well as the current model. The finding (Fig. 1) that simulated data using a model that incorporates demographic stochasticity in population size agreed closely with our theoretical predictions is encouraging, as it suggests that ignoring demographic stochasticity might not be a serious problem, at least for moderate to large populations. However, most populations also experience environmental stochasticity, and the joint effects of these factors on N_e in age-structured populations can be complex (Engen et al. 2005, 2007, 2010).

Our hybrid model makes certain other assumptions that limit its applicability in some cases. For example, it adopts the common assumption that individual variations in fertility are not heritable. Nei and Murata (1966) provided an approximate formula for reductions in N_e due to heritability of fertility in a monoecious diploid with discrete generations and constant N:

$$N_e \approx \frac{4N}{(1 + 3h^2)V_k + 2} \tag{5}$$

where h^2 is heritability. With $h^2 = 0$, this reduces to the familiar equation for N_e in species with discrete generations (e.g., Crow and Kimura 1970). This equation shows that if h^2 is even a modest 0.2, N_e of an otherwise ideal population is reduced by nearly one-quarter. Based on the close similarity of Eqs. 2 and 5, we expect that the consequences should be roughly the same for overlapping generations (as suggested by Ryman et al. 1981).

Our model also assumes a fixed population size and includes a simple way to assure this by rescaling fecundities to produce a constant N. In general, this is

not unreasonable, given that populations that persist for any period of time must eventually reach a dynamic equilibrium for population growth rate, with central tendency of $\lambda = 1$. Rescaling survival rates can also affect population growth rate, but this approach is less desirable here for two reasons: (1) it is less straightforward because survival is multiplicative across years; (2) it is less general because it is possible to stipulate a vector of b_x values for which no manipulation of survival rates will produce a stable population size. In contrast, any nonzero vector of b_x values can be scaled to produce a constant N, given any nonzero vector of s_x values.

Strictly speaking, scaling of vital rates is not necessary, as Felsenstein (1971) showed analytically (and Waples and Yokota 2007 verified numerically) that his model also works for populations with a constant growth rate (either positive or negative). Under those conditions, effective size would change for each generation with the change in N, with changes in inbreeding N_e (which depends on the number in the parental generation) lagging behind those for variance N_e (which depends on the number in the progeny generation).

Our hybrid model, like the models of Hill and Felsenstein, assumes that age-specific survivals and fecundities are independent. At least two types of departures from this assumption are commonly found in nature. First, in some species (especially mammals with long gestation times and/or extended parental care), females skip one or more years between reproductive events, and as a consequence only part of the female population reproduces in a given year. Within any year, it is easy to adjust female $\bar{k}$ and V_k to account for this. However, a key feature of this type of life history is that, to a large extent, *different* females reproduce in successive years. This negative correlation between female reproduction in successive years is not accommodated in the hybrid model (nor in those of Hill or Felsenstein). Because this negative correlation will reduce lifetime V_k for females, the estimate of N_e based on the hybrid model would be biased upward. Second, some individual differences in mean fecundity might be fixed over time (e.g., because of persistent individual differences in size, behavior, physiology, or expression of traits under sexual selection). Our model can accommodate overdispersed variance in reproductive success within a year but has no way to track persistent individual differences across time. Lee et al. (2011) showed that this type of scenario can reduce N_e considerably.

Other interesting life history features are directly amenable to study with AgeNe. For example, the genetically important aspect of fecundity is not the number of offspring produced but the number that survives to pass on genes to subsequent generations. The hybrid model assumes random, genotype-independent survival, in which case production of newborns is a good predictor of production of offspring that survive to maturity. However, in some (perhaps many) populations, not all individuals produce offspring with equal fitness. In the common lizard (*Lacerta vivipara*), both males and females exhibit senescence, whereby older individuals produced less viable offspring (Richard et al. 2005). In black rockfish (*Sebastes melanops*), as well as other species of marine fish, older individuals produce eggs and larvae with higher survival rates, presumably because of better provisioning of the egg with energy resources (Berkeley et al. 2004). Notably, this "big old fat fecund female fish" (BOFFFF) effect depends on age much more than size and is not accounted for by simply tracking fecundity. Because AgeNe quantifies b_x in terms of the number of offspring that survive to age 1, it is easy to adjust the effective fecundities of older fish to account for higher offspring survival. The hybrid model also provides an easy way to evaluate the consequences for N_e and N of size-selective or sex-selective harvest that can truncate age and size structure in harvested populations (Hard et al. 2006, Jørgensen et al. 2007).

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APPENDIX

Four different gametic pathways (*Ecological Archives* E092-126-A1).

SUPPLEMENT

AgeNe, a program to calculate N_e and N_b in age-structured populations (*Ecological Archives* E092-126-S1).