Preliminary Report

Effective Size of Age-Structured Populations with Cyclic Change in Size

Tetsuro Nomura

Department of Biotechnology, Faculty of Engineering,
Kyoto Sangyo University, Kyoto 603-8555
e-mail: nomurat@cc.kyoto-su.ac.jp

Assuming a random mating population of monoecious diploid, I derived an expression for the effective size of an age-structured population that varies the size over time in cycles of a given length. From the asymptotic contributions of age groups to the coancestry after many repetitions of cycles, an equation for the effective population size per cycle was derived, which showed a different expression from the previously published equation. Effect of the discrepancy was numerically evaluated with a hypothetical ladybird population with seasonal periodicity in size. The equation derived in this study gave a reasonably precise value, while the published one underestimated the effective size. The effect of estimation error of the census population size on the estimate of the effective size was also evaluated with the obtained formulae.

Key words: Effective population size; Age structure; Overlapping generations; Cyclic change; Ladybird population.

1. Introduction

The effective population size (N_e) is a parameter of central importance in theoretical population genetics and its applied fields such as conservation biology and breeding of domesticated species, because it determines both the increasing rate of inbreeding and the accumulation of genetic drift (Crow and Kimura, 1970; Falconer and Mackay, 1996; Frankham et al., 2002). N_e can be affected by various demographic variables, such as the number of parents, variance of reproductive success among parents, and fluctuation of population size (Caballero, 1994; Crow and Kimura, 1970). Based on a meta-analysis with 192 published estimates of N_e from 102 species, Frankham (1995) concluded that among the demographic variables affecting N_e , the most important one which limits N_e of natural populations to a smaller value is the fluctuation of population size.

For a population with discrete generations, Wright (1938) showed that average N_e over generations during which the population size fluctuates is approximately equal to the harmonic mean of the population size in each generation. This simple result is complicated when the

populations are age-structured and have overlapping generations (Nunney, 2000, 2002; Waples, 2006). To cope with the problem, two simplified models have been proposed. The first model assumes that the fluctuation of size in age-structured population is due to a combination of demographic and environmental stochasticity. Demographic stochasticity occurs because of chance events of reproduction and mortality that are independent among individuals, whereas environmental stochasticity exerts similar impacts on survival and reproduction of all individuals (Lande et al., 2003). Engen et al. (2005) derived an expression of N_e as a function of variance of vital rates due to demographic and environmental stochasticity. In the second model to describe the fluctuation of size in age-structured populations, the change of the population size is assumed to occur in repeated cycles. This model may be a good approximation to situations common in the real world. Many factors such as ecological changes, competition between species, and predator relationships can cause a cyclic change in population size. It could be also approximately applied to species with several breeding seasons within a year. Using this model, the author has derived an expression for the fixation probability of a neutral gene in the previous study (Nomura, 2008). Based on the same model, Wang and Pollak (2002) obtained an expression of N_e from the decreasing rate of heterozygosity. They showed that average N_e within a cycle can be directly related to the result of discrete-generation version by Wright (1938).

In this report, assuming the same model as Wang and Pollak (2002) but with a different approach, I derive an expression for N_e of age-structured populations changing cyclically in size. In the derivation, the approach with population projection matrix used in the previous report (Nomura, 2008) is applied. The obtained result is also simply linked to that of Wright (1938), but shows a different expression from that given by Wang and Pollak (2002). Effect of the discrepancy on calculated N_e is evaluated through numerical analysis. The effect of estimation error of the census population size on the estimate of the effective size is also assessed with the obtained formulae.

2. Background

2.1 Population with discrete generations

In the main part of the present study, we assume a monoecious diploid population. Extension to dioecious diploid species will be briefly discussed later. Mating among parents is assumed to be at random. I first describe the basic concept applied in this study by considering a population with discrete generations.

Let f_t be the coancestry of population in generation t , and N be the population size. Under the assumed conditions, $N_e = N$. By the definition of coancestry (Falconer and Mackay, 1996), f_t is the probability that two randomly sampled genes with replacements from the population are identical by descent. Thus,

$$f_t = \frac{1}{2N} + \left(1 - \frac{1}{2N}\right) f_{t-1},$$

or approximately

$$f_t = \frac{1}{2N} + f_{t-1}. \quad (1)$$

Equation (1) implies that the contribution (denoted by c_t) of the population in generation t to the coancestry in the following generations is

$$c_t = \frac{1}{2N} = \frac{1}{2N_e}. \quad (2)$$

Next consider a population varying in size over k generations as $N_0, N_1, \dots, N_{k-1}$. From (1),

$$f_{t+k-1} = \frac{1}{2N_0} + \frac{1}{2N_1} + \dots + \frac{1}{2N_{k-1}} + f_{t-1}.$$

Thus the average contribution ($\bar{c}$) over k generations is

$$\bar{c} = \frac{1}{k} \sum_{i=0}^{k-1} \frac{1}{2N_i}.$$

The average N_e over k generations is obtained by equating $\bar{c}$ to $1/2N_e$ as

$$\frac{1}{N_e} = \frac{1}{k} \sum_{i=0}^{k-1} \frac{1}{N_i}, \quad (3)$$

which agrees with the result of Wright (1938).

2.2 Age-structured population with a constant size

We extend the above method to an age-structured population with a constant population size, and verify that the published expression of N_e can be obtained from the present method.

Consider a population with n age classes and a constant age distribution such that N_1 individuals enter the population each specified period of time (breeding time). We denote the number of individuals of age i ($1 \leq i \leq n$) by N_i so that the probability of survival to age i is N_i/N_1 . Let p_i be the probability that a gene in a newborn individual came from a parent of age i . We define a stochastic matrix $\mathbf{P}$ by

$$\mathbf{P} = \begin{bmatrix} p_1 & p_2 & p_3 & \cdots & p_{n-1} & p_n \\ 1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \cdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \end{bmatrix}. \quad (4)$$

The matrix $\mathbf{P}$ is referred to as a population projection matrix or Leslie matrix (Caswell, 1989), and was first introduced in population and quantitative genetics by Hill (1972, 1974). The

matrix $\mathbf{P}$ has a single eigenvalue of unity ($\lambda = 1$) and all others are of smaller absolute values. Apparently, the column vector $\mathbf{1}' = [1 \quad 1 \quad \cdots \quad 1]$ is a right eigenvector of $\mathbf{P}$ corresponding to $\lambda = 1$. We set

$$q_i = p_i + p_{i+1} + \cdots + p_n \quad 1 \leq i \leq n$$

then the generation length L , i.e., the average age of parents of newborns, is given by

$$L = \sum_{i=1}^n i p_i = \sum_{i=1}^n q_i. \quad (5)$$

As shown by Hill (1974), the row vector

$$\mathbf{q}' = [q_1 \quad q_2 \quad \cdots \quad q_n]$$

is a left eigenvector of $\mathbf{P}$ corresponding to $\lambda = 1$. Using the theory of population projection matrix (Caswell, 1989), it follows that the matrix

$$\mathbf{A} = \lim_{t \rightarrow \infty} \mathbf{P}^t$$

is given by

$$\mathbf{A} = \mathbf{1} \mathbf{q}' / \mathbf{q}' \mathbf{1} = \mathbf{1} \mathbf{q}' / L.$$

Let $f_{ij}(t)$ be the coancestry between individuals in age class i and age class j at breeding time t , and $\mathbf{F}_t$ be the symmetric matrix of order n with $f_{ij}(t)$ in the (i, j) position. Johnson (1977) found an approximated recurrence relation for $\mathbf{F}_t$ as

$$\mathbf{F}_{t+1} = \mathbf{P} \mathbf{F}_t \mathbf{P}' + \mathbf{D}, \quad (6)$$

where $\mathbf{D}$ is the diagonal matrix defined as

$$\mathbf{D} = \text{diag}[1/2N_1 \quad 1/2N_2 - 1/2N_1 \quad \cdots \quad 1/2N_n - 1/2N_{n-1}].$$

Note that for a population with discrete generations, (6) reduces to the approximated expression (1) (Nomura, 2005). Thus, the argument in the previous section can be applied. The only difference is that the contribution of $\mathbf{D}$ at a given breeding time t asymptotically approaches a steady states, whereas the contribution of the individuals in a given generation in the discrete-generation model immediately attains a steady value after one generation. Let $\mathbf{C}$ be the matrix of the asymptotic contribution of $\mathbf{D}$ in an arbitrary chosen breeding time. From (6),

$$\mathbf{C} = \mathbf{P}^\infty \mathbf{D} \mathbf{P}'^\infty = \mathbf{A} \mathbf{D} \mathbf{A}' = (\mathbf{q}' \mathbf{D} \mathbf{q}) \mathbf{J} / L^2, \quad (7)$$

where $\mathbf{J} = \mathbf{1} \mathbf{1}'$. Equation (7) implies that each element of $\mathbf{C}$ converges to the same scalar $c = \mathbf{q}' \mathbf{D} \mathbf{q} / L^2$.

Letting N_b be the effective population size per breeding time, and applying the same argument as (2), we obtain $c = 1/2N_b$ or

$$N_b = \frac{L^2}{2\mathbf{q}'\mathbf{D}\mathbf{q}} = \frac{L^2}{\frac{1}{N_1} + \sum_{i=2}^n q_i^2 \left(\frac{1}{N_i} - \frac{1}{N_{i-1}} \right)}. \quad (8)$$

Since the effective population size per generation is $N_e = N_b/L$ (Hill, 1972),

$$N_e = \frac{L}{2\mathbf{q}'\mathbf{D}\mathbf{q}} = \frac{L}{\frac{1}{N_1} + \sum_{i=2}^n q_i^2 \left(\frac{1}{N_i} - \frac{1}{N_{i-1}} \right)}, \quad (9)$$

agreeing with the previously published expression (Felsenstein, 1971; Hill, 1972, 1979; Johnson, 1977; Charlesworth, 1994).

3. Age-structured population with a cyclic change in size

3.1 Model

The population model is same as that assumed in the previous study (Nomura, 2008). We consider an age-structured population with overlapping generations that changes the size in a cyclic manner. There are repetitions of cycles with each cycle having a sequence of k phases (numbered by $i = 0, 1, \dots, k-1$) of age structure, each of which is characterized by the numbers of individuals ($N_{1(i)}, N_{2(i)}, \dots, N_{n(i)}$) and the reproductive contributions of individuals ($p_{1(i)}, p_{2(i)}, \dots, p_{n(i)}$) in n age classes. For each phase the projection matrix as (4) is defined by

$$\mathbf{P}_i = \begin{bmatrix} p_{1(i)} & p_{2(i)} & p_{3(i)} & \cdots & p_{n-1(i)} & p_{n(i)} \\ 1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \cdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \end{bmatrix}. \quad (10)$$

With a left eigenvector ($\mathbf{q}_i$: each element is scaled as (5)) of $\mathbf{P}_i$ corresponding to the largest eigenvalue ($\lambda_i = 1$), the generation length (L_i) in phase i is obtained as

$$L_i = \mathbf{q}_i' \mathbf{1}. \quad (11)$$

According to Wang and Pollak (2002), we define the following quantity:

$$\frac{1}{T} = \sum_{i=0}^{k-1} \frac{1}{L_i}. \quad (12)$$

Since $1/L_i$ is the number of generations passing in a time-interval of phase i , the quantity $1/T$ is the number of generations per cycle, or T is the number of cycles per generation. Similarly we

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define the effective generation length (L) as

$$\frac{1}{L} = \frac{1}{k} \sum_{i=0}^{k-1} \frac{1}{L_i}. \quad (13)$$

3.2 Effective population size

Let $x(t) (= 0, 1, \dots, k-1)$ be the phase number of age structure at breeding time t . Without loss of generality, we set the phase of age structure at breeding time t to $x(t) = 0$. Thus, for a given breeding time $t' (\geq t)$,

$$x(t') = \text{mod}(t', k).$$

Using a similar derivation to that applied to a population with a constant age structure (Johnson, 1977; Charlesworth, 1994), we obtain the following exact recurrence relations for coancestry ($f_{ij}(t)$) among age class i and j :

$$\left. \begin{aligned} f_{11}(t+1) &= \frac{2N_{1(x(t+1))} - 1}{2N_{1(x(t+1))}} \sum_{k,l=1}^n p_{k(x(t))} p_{l(x(t))} f_{kl}(t) + \frac{1}{2N_{1(x(t+1))}} \\ f_{ii}(t+1) &= \left(\frac{2N_{i(x(t+1))} - 1}{2N_{i(x(t+1))}} \right) \left(\frac{2N_{i-1(x(t))}}{2N_{i-1(x(t))} - 1} \right) \left(f_{i-1,i-1}(t) - \frac{1}{2N_{i-1(x(t))}} \right) \\ &\quad + \frac{1}{2N_{i(x(t+1))}} \quad \text{for } 1 < i \leq n \\ f_{i1}(t+1) &= \sum_{k=1}^n p_{k(x(t))} f_{i-1,k}(t) \quad \text{for } i > 1 \\ f_{ij}(t+1) &= f_{i-1,j-1}(t) \quad \text{for } i, j > 1 \text{ and } i \neq j \end{aligned} \right\} \quad (14)$$

If the number of individuals in each age class is large,

$$\frac{2N_{i(x(t+1))} - 1}{2N_{i(x(t+1))}} \approx \frac{2N_{i-1(x(t))}}{2N_{i-1(x(t))} - 1} \approx 1.$$

Then equations (14) can be approximately written as

$$\mathbf{F}_{t+1} = \mathbf{P}_{x(t)} \mathbf{F}_t \mathbf{P}'_{x(t)} + \mathbf{D}_{x(t+1)}, \quad (15)$$

where $\mathbf{D}_{x(t+1)}$ is a diagonal matrix defined as

$$\mathbf{D}_{x(t+1)} = \text{diag}[1/2N_{1(x(t+1))} \quad 1/2N_{2(x(t+1))} - 1/2N_{1(x(t))} \quad \cdots \quad 1/2N_{n(x(t+1))} - 1/2N_{n-1(x(t))}].$$

We consider the contribution of $\mathbf{D}_{x(t)} (= \mathbf{D}_0)$ to the coancestry matrix among age classes after v repetitions of cycle (at breeding time $t + vk$). From (15), the contribution to $\mathbf{F}_{t+vk}$ (denoted by $\mathbf{C}_{x(t), t+vk}$) is

$$\mathbf{C}_{x(t), t+vk} = (\mathbf{P}_{k-1} \mathbf{P}_{k-2} \cdots \mathbf{P}_0)^v \mathbf{D}_0 (\mathbf{P}_0 \cdots \mathbf{P}_{k-2} \mathbf{P}_{k-1})'^v = \mathbf{B}_0^v \mathbf{D}_0 \mathbf{B}_0'^v,$$

where $\mathbf{B}_0 = \mathbf{P}_{k-1} \mathbf{P}_{k-2} \cdots \mathbf{P}_0$. Similarly the contribution to $\mathbf{F}_{t+vk+j}$ for $0 < j \leq k-1$ is expressed as

$$\mathbf{C}_{x(t), t+vk+j} = (\mathbf{P}_{j-1} \mathbf{P}_{j-2} \cdots \mathbf{P}_0) \mathbf{B}_0^v \mathbf{D}_0 \mathbf{B}_0'^v (\mathbf{P}_0 \cdots \mathbf{P}_{j-2} \mathbf{P}_{j-1})'.$$

Since the elements of each row of $\mathbf{B}_0$ are non-negative and sum to unity, it is a stochastic matrix and has only one ergodic state (Kemeny and Snell, 1960). Thus, $\mathbf{B}_0$ has a single eigenvalue of unity ($\lambda_0 = 1$) and all others are of smaller absolute values. Using the relevant theory of stochastic matrix (Kemeny and Snell, 1960), the matrix $\mathbf{A}_0 = \lim_{v \rightarrow \infty} \mathbf{B}_0^v$ is given by

$$\mathbf{A}_0 = \lim_{v \rightarrow \infty} \mathbf{B}_0^v = \mathbf{1}\mathbf{r}'_0,$$

where

$$\mathbf{r}'_0 = [r_{1(0)} \quad r_{2(0)} \quad \cdots \quad r_{n(0)}]$$

is a left eigenvector of $\mathbf{B}_0$ corresponding to $\lambda_0 = 1$, scaled as $\mathbf{r}'_0 \mathbf{1} = 1$. Further, noting that the elements of each row of $\mathbf{P}_i$ sum to unity,

$$\lim_{v \rightarrow \infty} (\mathbf{P}_{j-1} \mathbf{P}_{j-2} \cdots \mathbf{P}_0) \mathbf{B}_0^v = (\mathbf{P}_{j-1} \mathbf{P}_{j-2} \cdots \mathbf{P}_0) \mathbf{1} \mathbf{r}'_0 = \mathbf{1} \mathbf{r}'_0.$$

Thus, after many repetitions of cycle, the contribution of $\mathbf{D}_{x(t)} (= \mathbf{D}_0)$ to the coancestry matrix at an arbitrary breeding time (denoted by $\mathbf{C}_0$) asymptotically converges to

$$\mathbf{C}_0 = \mathbf{A}_0 \mathbf{D}_0 \mathbf{A}'_0 = (\mathbf{r}'_0 \mathbf{D}_0 \mathbf{r}_0) \mathbf{J}.$$

In general, defining the matrix $\mathbf{B}_i$ and a left eigenvector of $\mathbf{B}_i$ corresponding to the largest eigenvalue ($\lambda_i = 1$) as

$$\mathbf{B}_i = \mathbf{P}_{i-1} \cdots \mathbf{P}_0 \mathbf{P}_{k-1} \cdots \mathbf{P}_{i+1} \mathbf{P}_i$$

$$\mathbf{r}'_i = [r_{1(i)} \quad r_{2(i)} \quad \cdots \quad r_{n(i)}]$$

$$\mathbf{r}'_i \mathbf{1} = 1,$$

we can express the asymptotic contribution ($\mathbf{C}_i$) of $\mathbf{D}_{x(t+i)} (= \mathbf{D}_i$ for $0 \leq i \leq k-1$) to the coancestry matrix after many repetitions of cycle as

$$\mathbf{C}_i = (\mathbf{r}'_i \mathbf{D}_i \mathbf{r}_i) \mathbf{J}. \quad (16)$$

Equation (16) implies that each element of $\mathbf{C}_i$ converges to the same scalar $c_i = \mathbf{r}'_i \mathbf{D}_i \mathbf{r}_i$. Applying the analogous argument to (8), we equate c_i to $1/2N_{b,i}$, where $N_{b,i}$ is the effective population size per breeding time with phase i . Then,

$$N_{b,i} = \frac{1}{2\mathbf{r}'_i \mathbf{D}_i \mathbf{r}_i} = \frac{1}{r_{1(i)}^2 \left(\frac{1}{N_{1(i)}} \right) + \sum_{j=2}^n r_{j(i)}^2 \left(\frac{1}{N_{j(i)}} - \frac{1}{N_{j-1(i)}} \right)}. \quad (17)$$

Under a constant age structure,

$$[r_{1(i)} \quad r_{2(i)} \quad \cdots \quad r_{n(i)}] = [q_1 \quad q_2 \quad \cdots \quad q_n]/L.$$

Then, equation (17) reduces to (8). Further, the average effective size over k phases is

$$\frac{1}{2N_b} = \frac{1}{k} \sum_{i=0}^{k-1} c_i$$

or

$$\frac{1}{N_b} = \frac{1}{k} \sum_{i=0}^{k-1} \frac{1}{N_{b,i}}, \quad (18)$$

which corresponds to equation (3) in the discrete-generation model. The effective population size (N_c) per cycle is obtained as

$$\frac{1}{2N_c} = \sum_{i=0}^{k-1} c_i$$

or

$$N_c = N_b/k. \quad (19)$$

Finally, following Hill (1972), the effective population (N_e) per generation is obtained as

$$N_e = N_b/L, \quad (20)$$

where L is the effective generation length defined by (13). Equation (20) is alternatively expressed as

$$N_e = N_c/T,$$

where T is the number of cycles per generation defined by (12).

Using the decreasing rate of heterozygosity and applying an approximation by matrix perturbation, Wang and Pollak (2002) obtained expressions for the effective size of age-structured population with cyclic change in size. With the present notations, their expression corresponding to (17) is written as

$$N_{b,i} = \frac{L_i^2}{\frac{1}{N_{1(i)}} + \sum_{j=2}^k q_{j(i)}^2 \left(\frac{1}{N_{j(i)}} - \frac{1}{N_{j-1(i-1)}} \right)}. \quad (21)$$

Under a constant age structure, equation (21) again reduces to (8), but it does not generally agree with (17).

3.3 Extension to dioecious species

Applying the same approach used in the previous study (Nomura, 2008), the derived method can be extended to a population of dioecious species. To cope with the problem, we use the extended projection matrix $\mathbf{P}_i$, defined by Hill (1974) and Johnson (1977). The extended matrix is partitioned into four blocks, which correspond to the alternative pathways of genes between age classes and sexes, that is

$$\begin{bmatrix} \text{males from males} & \text{males from females} \\ \text{females from males} & \text{females from females} \end{bmatrix}.$$

According to this extension, the vector $\mathbf{r}_i$ is written as

$$\mathbf{r}'_i = [r_{m,1(i)} \quad r_{m,2(i)} \quad \cdots \quad r_{m,n_m(i)} \quad r_{f,1(i)} \quad r_{f,2(i)} \quad \cdots \quad r_{f,n_f(i)}],$$

where all variables have the same meanings as those defined in the previous section, but with the subscript s ($= m$ for male, and f for female) standing for sex. With an analogous derivation to (17), we obtain an expression for the effective population size per breeding time with phase i as

$$\begin{aligned} N_{b,i} &= \frac{1}{2\mathbf{r}'_i \mathbf{D}_i \mathbf{r}_i} \\ &= 1 / \left[r_{m,1(i)}^2 \left(\frac{1}{N_{m,1(i)}} \right) + \sum_{j=2}^{n_m} r_{m,j(i)}^2 \left(\frac{1}{N_{m,j(i)}} - \frac{1}{N_{m,j-1(i-1)}} \right) \right. \\ &\quad \left. r_{f,1(i)}^2 \left(\frac{1}{N_{f,1(i)}} \right) + \sum_{j=2}^{n_f} r_{f,j(i)}^2 \left(\frac{1}{N_{f,j(i)}} - \frac{1}{N_{f,j-1(i-1)}} \right) \right] \end{aligned}$$

The effective population sizes (N_c and N_e) per cycle and generation are also computed with (19) and (20).

4. Example and discussion

Harmonia axyridis is a species of ladybird common in Japan. This beetle has a life history of multivoltine with two main reproductive seasons in spring and autumn. I take this beetle as a numerical example. Since April in 2002, I have observed the population dynamics in the campus of Kyoto Sangyo University and the adjacent area. The dynamics is estimated as follows: In early April, hibernated adults resume their reproduction. The reproductive activity peaks at middle spring. The breeding population in this season consists of newborns in the early spring and survivors of hibernated adults. The reproductive activity falls in summer, and most of the adults aestivate. The adults recover their activity in early autumn, and the second peak of reproduction is observed in middle autumn. In late November, the adults begin hibernating. Four or five generations are estimated to pass within a year in the investigated area.

Based on the above observation, I assumed a discrete-time model illustrated in Fig. 1. There are five breeding times ($k = 5$) in a year, each with three age classes ($n = 3$). The number of individuals in each age class and breeding time is given in Fig. 1, which are the hypothetical numbers but the relative sizes were determined on the basis of the census data. By assuming that males and females have the same demographic parameters, the monoecious model could be applied (Charlesworth, 1994). It was also assumed that there are no differences in fecundity among age classes at a given breeding time. The first row of the matrix $\mathbf{P}_i$ and the diagonal elements of $\mathbf{D}_i$ are given in Table 1.

Fig. 2 shows the coancestry $f_{11}(t)$ among individuals in age class 1 at breeding time t from 7th to 9th cycles (years), computed using the exact recurrence relations (14). Although the

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Fig. 1. Dynamics of a ladybird population assumed in numerical analysis. The figure in circle is the number of individuals.

Table 1. First row of matrix $\mathbf{P}_i$ and diagonal elements of matrix $\mathbf{D}_i$.

Phase (i)	First row of $\mathbf{P}_i$			Diagonal elements ($\times 10^{-2}$) of $\mathbf{D}_i$		
	$p_{1(i)}$	$p_{2(i)}$	$p_{3(i)}$	$d_{11(i)}$	$d_{22(i)}$	$d_{33(i)}$
0	0.636	0.273	0.091	0.071	0.067	0.250
1	0.833	0.139	0.028	0.017	0.029	0.333
2	0.250	0.625	0.125	0.063	0.008	0.025
3	0.158	0.316	0.526	0.167	0.021	0.025
4	0.455	0.182	0.364	0.010	0.083	0.042

Fig. 2. Coancestry between 7th and 9th cycles (breeding times 35-49) in a hypothetical ladybird population. The figure on the graph is the phase number of age structure.

Table 2. Left eigenvectors ($\mathbf{r}_i$ and $\mathbf{q}_i$) of matrices $\mathbf{B}_i$ and $\mathbf{P}_i$, and generation length (L_i) of each phase of age structure.

Phase (i)	$\mathbf{r}_i$			$\mathbf{q}_i$			L_i
	$r_{1(i)}$	$r_{2(i)}$	$r_{3(i)}$	$q_{1(i)}$	$q_{2(i)}$	$q_{3(i)}$	
0	0.666	0.254	0.080	1.0	0.364	0.091	1.455
1	0.882	0.104	0.014	1.0	0.167	0.028	1.194
2	0.490	0.474	0.036	1.0	0.750	0.125	1.875
3	0.289	0.418	0.293	1.0	0.824	0.526	2.368
4	0.557	0.201	0.242	1.0	0.546	0.364	1.909

Table 3. Effective sizes per cycle (N_c), per breeding time (N_b), and per generation (N_e) of a hypothetical ladybird population.

Method	N_c	N_b	N_e
Direct ¹⁾	402.2	2011.2	1208.2
N ²⁾	402.1	2010.5	1207.9
WP ³⁾	357.5	1787.3	1073.8

1) direct computation from the increasing rate of coancestry

2) method proposed in this study: equation (17)

3) method of Wang and Pollak (2002): equation (21)

coancestry increases with an oscillation, the essentially same pattern of oscillation is repeated according to the repetitions of cycle. We compare the effective sizes (N_b , N_c and N_e) directly computed from the increasing rate of coancestry with those computed from the equations obtained by the present study (equation (17)) and by Wang and Pollak (2002: equation (21)). The direct computation was made with the increasing rate of coancestry between 8th and 9th cycles (breeding times 40-49). The effective population size (N_c) per cycle was obtained by the harmonic mean of the effective size for the five phases ($i = 0, 1, \dots, 4$) of age structure:

$$\frac{1}{2N_c} = \frac{1}{5} \sum_{i=0}^4 \frac{1}{2N_{c,i}} = \frac{1}{5} \sum_{t=40}^{44} \frac{f_{11}(t+5) - f_{11}(t)}{1 - f_{11}(t)}.$$

Then, the effective sizes (N_b and N_e) per breeding time and generation were computed from equations (19) and (20). The computed effective sizes are listed in Table 3.

The left eigenvectors ($\mathbf{r}_i$ and $\mathbf{q}_i$) of matrices $\mathbf{B}_i$ and $\mathbf{P}_i$, corresponding to the largest eigenvalue, are shown in Table 2. Substituting the elements of $\mathbf{r}_i$ into (17) and using equations (18)-(20), we obtain the three effective sizes from the present method. Similarly, with the elements of $\mathbf{q}_i$ and equations (18)-(21), the three effective sizes from the method of Wang and Pollak (2002) are computed. The results are shown in Table 3. It is seen that the present method gives the effective sizes close to those directly computed, whereas the equation of Wang and Pollak (2002) underestimates the direct values by 10%.

We have derived the expression of the effective population size from the asymptotic contributions of age classes to the coancestry after many repetitions of cycle, whereas Wang and Pollak (2002) underestimates the direct values by 10%.

(2002) based on the decreasing rate of heterozygosity per cycle. The main difference between the obtained results (equations (17) and (21)) is in the expression for the contribution of individuals in each age class in a given phase i . The contribution in (17) is expressed as the asymptotic expectation under the actual repetitions of cycle of k phases. On the other hand, in equation (21) it is obtained from the left eigenvector of $\mathbf{P}_i^\infty$, implying that the contribution of individuals in phase i is approximated by the long-term contribution that would be asymptotically attained if the population was at all generated in the same age structure as phase i . The result of numerical analysis suggests that the difference between the expressions can generate a large difference among the computed effective sizes. The expression obtained in the present study seems to be reasonable, because it is based on the actual repetitions of cycle and has less approximation.

In a practical application, the exact numbers of breeding individuals ($N_{j(i)}$) are unknown, and the estimated numbers should be used. As an application of the obtained formulae, the impact of estimation errors of $N_{j(i)}$ on the estimate of the effective population size was assessed by the following Monte Carlo sensitivity analysis: Assuming the hypothetical lady bird population shown in Fig. 1, I evaluated the response of N_e computed from equations (17) and (20) to perturbations of $N_{1(i)}$, $N_{2(i)}$ and $N_{3(i)}$ in a given phase i in turn while holding the numbers of individuals in other phases the constant values given in Fig. 1. The perturbation was made by adding independent normal random errors with mean 0 and variance $0.01 \times N_{j(i)}^2$ to $N_{j(i)}$ for $j = 1, 2$ and 3 . The variance of error was chosen so that the coefficient of variation of estimated $N_{j(i)}$ was 10%. For each perturbed phase, 1000 replicates were run and the distribution of the estimated effective size was checked. The results are illustrated in Fig. 3. It is seen that the estimate of N_e is more sensitive to the estimation errors of $N_{j(i)}$ in the phases with a smaller population size, i.e., phases 0 and 4 (see also Fig. 1). Although further evaluations with a deterministic sensitivity analysis should be done under a wide range of scenario, the results in Fig. 3 suggest that in a practical survey, the effort to collect an exact data in a breeding period with a smaller population size is critically important for obtaining a reliable estimate of N_e .

Finally we have assumed that a same series of age structure phases is repeated over times. In any natural populations, however, the age structure in a given phase will also be subject to a fluctuation over times, which will reduce the effective population size. In the recent works, Engen et al. (2005, 2007) used the theories of stochastic demography (Lande et al., 2003) to derive formulae for the effective size of age-structured population. In the derivation, they incorporated the fluctuation of age structure in equation (9) by considering a small perturbation of a deterministic (average) age structure defined by the projection matrix (4), and formulated the reduction of the effective size due to the demographic and environmental fluctuations. Their approach could be applied to the present case by considering perturbation of the phase-specific projection matrix (10). This extension should be considered in a future study.

Fig. 3. Distribution of 1000 estimates of the effective size (N_e) of populations generated by a perturbation of the number of individuals in phase i in the hypothetical ladybirds population shown in Fig. 1. The perturbation was made by adding independent normal random errors with mean 0 and variance $0.01 \times N_{j(i)}^2$ to $N_{j(i)}$.

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