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Effective size of populations with unequal sex ratio and variation in mating success

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Summary

To estimate the effective size (N_e) of populations with unequal sex ratio, a well-known formula, $N_e = 4N_mN_f/(N_m + N_f)$, has been frequently used, where N_m and N_f are the numbers of male and female parents, respectively. In this paper, the formula was examined under typical mating systems in animals. It was shown that the formula holds only when there are no variations in the numbers of mates (mating success) of parents of each sex. More appropriate equations were developed by accounting for the variation in mating success. It was found that for animal populations with harem mating system, an equation $N_e = 4N_mN_f/(2N_m + N_f)$ gives a more accurate estimate than the well-known formula. The effective population sizes of several wild, experimental and domestic animals are estimated by applying the derived equations to the published demographic and ecological data.

Zusammenfassung

Effektive Größe von Populationen mit ungleichem Geschlechterverhältnis und Variation im Anpaarungserfolg

Zur Schätzung der effektiven Populationsgröße (N_e) mit ungleichem Geschlechterverhältnis, wurde häufig die allgemein bekannte Formel $N_e = 4N_mN_f/(N_m + N_f)$ verwendet, wobei N_m und N_f die Anzahl männlicher und weiblicher Eltern bezeichnen. In diesem Artikel wurde diese Formel unter verschiedenen Anpaarungssystemen überprüft. Es wurde gezeigt, daß die Formel nur zutrifft, wenn die Anzahl der angepaarten Tiere (Anpaarungserfolg) in jedem Geschlecht nicht variieren. Es wurden genauere Gleichungen entwickelt, die den Anpaarungserfolg mitberücksichtigen. Für Tierpopulationen mit Harempaarung wurde die Gleichung $N_e = 4N_mN_f/(2N_m + N_f)$ als genauerer Schätzer als die allgemein bekannte Formel gefunden. Die effektive Populationsgröße mehrerer Wild-, Versuchs- und Haustierpopulationen wurden mittels der abgeleiteten Gleichung und demographischen und ökologischen Daten geschätzt.

Introduction

The effective size of a population is a parameter central to understanding evolution in small populations, because the magnitude of this parameter determines the genetic effects of both inbreeding and genetic drift (FALCONER 1989; CABALLERO 1994). This parameter is also important for solving some practical issues; it has been used as a key parameter in designing strategies for conservation of endangered animal species (e.g. LANDE and BARROWCLOUGH 1987; NUNNEY and ELAM 1994) and breeding of domestic animals (e.g. BIJMA et al. 2001; NOMURA et al. 2001).

In addition to the number of breeding animals, the effective population size depends on various ecological and demographic variables, such as sex ratio, variation in reproductive success and generation interval (CROW and DENNISON 1988; CABALLERO 1994). Accordingly, a set of formulae to estimate the effective size has been proposed (e.g. NUNNEY 1993; CABALLERO 1994). In most wild animals, however, the available variables are limited to a few simple ones, such as the total number of breeding animals and the sex ratio, due to the lack or insufficiency of information. Thus, as a first approximation, the effective size (N_e)

has been estimated by accounting only for unequal sex ratio (e.g. LACAVA and HUGHES 1984; CHEPKO-SADE et al. 1987; KELLY 2001), using a well-known formula (WRIGHT 1931)

$$N_e = \frac{4N_m N_f}{N_m + N_f}, \quad (1)$$

where N_m and N_f are the numbers of breeding male and female parents, respectively.

In this article, the exact conditions required for the use of Eqn 1 are examined by assuming typical mating systems in animal populations. It is shown that Eqn 1 holds only when there are no variations in the numbers of mates (mating success) of parents within each sex, which is an unrealistic condition in most wild and domestic animal populations. More appropriate equations, but with a simplicity comparable to Eqn 1, are developed. The effective population sizes of several wild, experimental and domestic animals are estimated by applying the derived equations to the published demographic and ecological data.

Theory

A general equation of the effective size of populations with separate sexes regarding autosomal genes is given by HILL (1979), following the methodology of LATTER (1959),

$$\begin{aligned} \frac{1}{N_e} = & \frac{1}{16N_m} \left[2 + \sigma_{mm}^2 + 2 \left(\frac{N_m}{N_f} \right) \sigma_{mm,mf} + \left(\frac{N_m}{N_f} \right)^2 \sigma_{mf}^2 \right] \\ & + \frac{1}{16N_f} \left[2 + \sigma_{ff}^2 + 2 \left(\frac{N_f}{N_m} \right) \sigma_{fm,ff} + \left(\frac{N_f}{N_m} \right)^2 \sigma_{fm}^2 \right], \end{aligned} \quad (2)$$

where σ_{sm}^2 (σ_{sf}^2) is the variance of the number of male (female) offspring (which become parents in the next generation) from parents of sex s ($= m$ or f) and $\sigma_{sm,sf}$ is the covariance of the number of male and female offspring from parents of sex s . In the following, we derive expressions of the effective population size under several mating systems, by considering explicit forms of variance and covariance terms in Eqn 2. Random mating with constant numbers of male and female parents is assumed.

(1) Random union of gametes

In theoretical population genetics, random union of gametes (RUG) has been frequently assumed. In this model, all male and female parents equally contribute their gametes to male and female gametic pools, respectively. Zygotes (offspring) are produced by random union of gametes, each from the male and female gametic pools. The distributions of offspring numbers in the four gametic pathways (male to male, male to female, female to male, and female to female) under RUG model may be approximated by independent Poisson distributions. Thus,

$$\begin{aligned} \sigma_{sm}^2 &= \frac{N_m}{N_s} \\ \sigma_{sf}^2 &= \frac{N_f}{N_s} \\ \sigma_{sm,sf} &= 0 \end{aligned}$$

Substituting these expressions into Eqn 2 leads to Eqn 1.

(2) Individual-based mating system

Some organisms reproduce more or less in a fashion like the RUG model. For example, some aquatic animals release large numbers of gametes into the ocean (FALCONER 1989; NUNNEY 1993). However, this mating system is in reality rather rare. In most animal mating systems, individuals (rather than gametes) come together to mate. In this section, expressions for the effective size of populations with individual-based mating systems are developed.

Let d_{si} be the mating success (the number of mates) of parent $i (= 1, 2, \dots, N_s)$ of sex s , with the mean μ_{d_s} and variance $\sigma_{d_s}^2$. There are $\mu_{d_f} N_f (= \mu_{d_m} N_m)$ matings in the population. Then, $\mu_{d_m} = \mu_{d_f} N_f / N_m$ and $\mu_{d_f} = \mu_{d_m} N_m / N_f$. The litter size (the number of newborns per mating) of mating $j (= 1, 2, \dots, \mu_{d_f} N_f)$ is x_j , with the mean μ_x and variance σ_x^2 . Although the sex ratio in a litter is treated as a variable, the sex ratio in the total newborns ($X = \mu_x \mu_{d_f} N_f$) is fixed to 1 : 1, which will be a reasonable approximation if X is not small. Survivals of newborns are assumed to be random, but the numbers of survived male and female adults are regulated to N_m and N_f , respectively.

As shown in Appendix, the expressions for variance and covariance of offspring numbers are obtained as

$$\left. \begin{aligned} \sigma_{sm}^2 &= \left(\frac{N_m}{N_s} \right) \left[1 + \left(\frac{1}{\mu_{d_s}} \right) \left(\frac{N_m}{N_s} \right) \alpha + \left(\frac{N_m}{N_s} \right) C_{d_s}^2 \right] \\ \sigma_{sf}^2 &= \left(\frac{N_f}{N_s} \right) \left[1 + \left(\frac{1}{\mu_{d_s}} \right) \left(\frac{N_f}{N_s} \right) \alpha + \left(\frac{N_f}{N_s} \right) C_{d_s}^2 \right] \\ \sigma_{sm,sf} &= \left(\frac{N_m}{N_s} \right) \left(\frac{N_f}{N_s} \right) \left[\left(\frac{1}{\mu_{d_s}} \right) \alpha + C_{d_s}^2 \right] \end{aligned} \right\} \quad (3)$$

where $\alpha = C_x^2 - 1/\mu_x$, and $C_x (= \sigma_x/\mu_x)$ and $C_{d_s} (= \sigma_{d_s}/\mu_{d_s})$ are the coefficients of variation of x_j and d_{si} , respectively. Substituting these expressions into Eqn 2 gives

$$N_e = \frac{4N_m N_f}{N_m \left(1 + \frac{\alpha}{\mu_{d_f}} + C_{d_f}^2 \right) + N_f \left(1 + \frac{\alpha}{\mu_{d_m}} + C_{d_m}^2 \right)}. \quad (4)$$

For a Poisson distribution of litter size, i.e. $\alpha = 0$, Eqn 4 reduces to

$$N_e = \frac{4N_m N_f}{N_m (1 + C_{d_f}^2) + N_f (1 + C_{d_m}^2)}. \quad (5)$$

Note that under a Poisson distribution of litter size, Eqn 1 holds only when there are no variations in the mating success, i.e. $C_{d_m}^2 = C_{d_f}^2 = 0$. However, the assumption of fixed mating success will not be realistic in most animal populations, except populations with artificially managed mating. For example, a large variability in the mating success has been reported in various animal populations, such as *Drosophila* (PETIT et al. 1980), red deer (CLUTTON-BROCK et al. 1988), elephant seal (LE BOEUF and REITER 1988) and Japanese monkey (NOZAWA 1972). If we have no information on the variability in the mating success among parents, it is reasonable to assume a Poisson distribution of mating success. Under this assumption, $C_{d_m}^2 = 1/\mu_{d_m}$ and $C_{d_f}^2 = 1/\mu_{d_f}$. Then equation 5 is expressed as

$$N_e = \frac{4N_m N_f}{N_m \left(1 + \frac{1}{\mu_{d_f}} \right) + N_f \left(1 + \frac{1}{\mu_{d_m}} \right)}. \quad (6)$$

Using $\mu_{d_m} = \mu_{d_f} N_f / N_m$ and $\mu_{d_f} = \mu_{d_m} N_m / N_f$, Eqn 6 is rewritten as

$$\begin{aligned} N_e &= \frac{4N_m N_f}{N_m + N_f + \frac{2N_m}{\mu_{d_f}}} \\ &= \frac{4N_m N_f}{N_m + N_f + \frac{2N_f}{\mu_{d_m}}}. \end{aligned}$$

Under harem polygamy, successful males generally mate with most or all of the females in their harem, and the females generally mate with only one male. In this mating system, $C_{d_f}^2 = 0$ and $C_{d_m}^2 = 1/\mu_{d_m} = N_m/N_f$ if the male mating success (harem size) follows a Poisson distribution. Thus, the effective population size is expressed as

$$N_e = \frac{4N_m N_f}{2N_m + N_f}. \quad (7)$$

In animals with polygamous mating systems, variations in mating success would be much larger in male than in female, because of the severe competition among males for mates. To examine the effects of unequal sex ratio and variation in male mating success on the effective population size, the effective population sizes with different variations in male mating success were computed for various sex ratios, using Eqn 5. Female mating success was fixed to 1, i.e. $C_{d_f}^2 = 0$, $\mu_{d_f} = 1$ and so $\mu_{d_m} = N_f/N_m$. Five coefficients of variation in male mating success were considered: $C_{d_m}^2 = n/\mu_{d_m}$, where $n = 0$ (no variation), $1/2$, 1 (Poisson distribution), 2 and 3 . Results are illustrated in Figure 1, in which ratio N_e/N (where $N = N_m + N_f$) is plotted along the proportion of male parents ($r = N_m/N$). When there are no variations in mating success, the effective size is simply computed from Eqn 1. The effective size of populations with no variation in mating success is maximized at the equal sex ratio ($r = 0.5$). As the variation in male mating success increases, the male

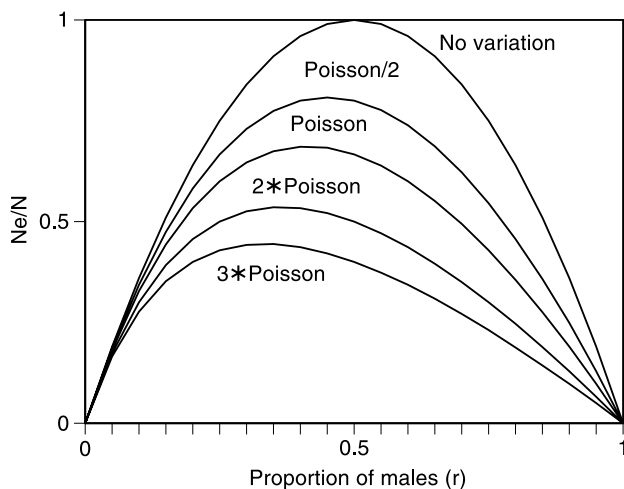


Fig. 1. Effects of sex ratio and variation in male mating success on autosomal effective population size. No variation, no variation in male mating success; Poisson, variance under Poisson distribution; Poisson/2, half variance under Poisson distribution; 2*Poisson, two times variance under Poisson distribution; 3*Poisson, three times variance under Poisson distribution

proportion giving the maximum effective size shifts to a smaller value. The variation in male mating success has a more pronounced effect on the effective size of populations with a smaller bias in sex ratio, i.e. an intermediate value of r .

(3) Extension to X-linked locus or haplo-diploid species

The effective size for X-linked loci or haplo-diploid species is obtained by equating the variance of change in gene frequency or the rate of inbreeding of an autosomal gene in an idealized population to the actual values observed for the X-linked gene in the population under consideration (CABALLERO 1995). Following a variance of drift derivation, POLLAK (1990) obtained an expression of the effective size for X-linked gene,

$$\frac{1}{N_e} = \frac{1}{9N_m} \left[1 + 2 \left(\frac{N_m}{N_f} \right)^2 \sigma_{mf}^2 \right] + \frac{1}{9N_f} \left[1 + \sigma_{ff}^2 + 2 \left(\frac{N_f}{N_m} \right) \sigma_{fm,ff} + \left(\frac{N_f}{N_m} \right)^2 \sigma_{fm}^2 \right], \quad (8)$$

where the male sex is heterogametic. Substituting Eqn 3 into Eqn 8 gives

$$N_e = \frac{9N_m N_f}{4N_m \left(1 + \frac{\alpha}{\mu_{df}} + C_{df}^2 \right) + 2N_f \left(1 + \frac{\alpha}{\mu_{dm}} + C_{dm}^2 \right)}.$$

For a Poisson distribution of litter size ($\alpha = 0$),

$$N_e = \frac{9N_m N_f}{4N_m \left(1 + C_{df}^2 \right) + 2N_f \left(1 + C_{dm}^2 \right)}. \quad (9)$$

If mating success of parents is fixed within each sex, i.e. $C_{dm}^2 = C_{df}^2 = 0$, Eqn (9) reduces to the well-known formula

$$N_e = \frac{9N_m N_f}{4N_m + 2N_f} \quad (10)$$

(WRIGHT 1933). But when mating success follows a Poisson distribution within each sex, i.e. $C_{dm}^2 = 1/\mu_{dm}$ and $C_{df}^2 = 1/\mu_{df}$, Eqn 9 becomes

$$N_e = \frac{9N_m N_f}{4N_m \left(1 + \frac{1}{\mu_{df}} \right) + 2N_f \left(1 + \frac{1}{\mu_{dm}} \right)}. \quad (11)$$

Equation 11 may be rewritten as

$$\begin{aligned} N_e &= \frac{9N_m N_f}{4N_m + 2N_f + \frac{6N_m}{\mu_{df}}} \\ &= \frac{9N_m N_f}{4N_m + 2N_f + \frac{6N_f}{\mu_{dm}}}. \end{aligned}$$

Under harem polygamy, i.e. $C_{dm}^2 = 1/\mu_{dm} = N_m/N_f$ and $C_{df}^2 = 0$, Eqn 9 reduces to

$$N_e = \frac{9N_m N_f}{6N_m + 2N_f}. \quad (12)$$

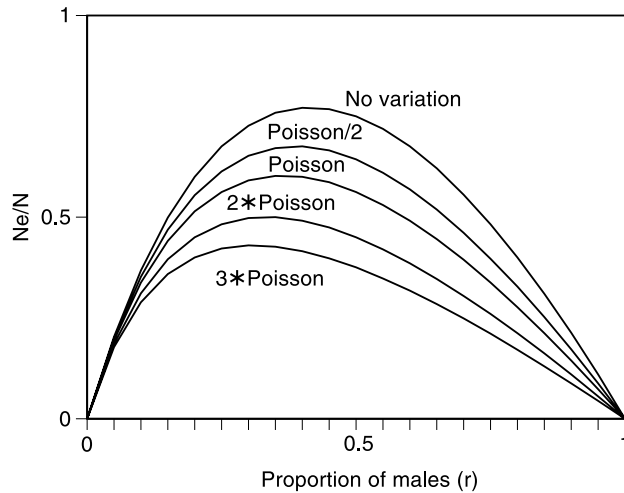


Fig. 2. Effects of sex ratio and variation in male mating success on X-linked effective population size. No variation, no variation in male mating success; Poisson, variance under Poisson distribution; Poisson/2, half variance under Poisson distribution; 2*Poisson, two times variance under Poisson distribution; 3*Poisson, three times variance under Poisson distribution

The effects of sex ratio and variation in male mating success on the X-linked effective size are illustrated in Figure 2, in which same variables as in Figure 1 are assumed. Although the effects are similar to the autosomal effective size, the X-linked effective size is consistently smaller than the corresponding autosomal effective size. However, the difference between the two effective sizes becomes smaller as the variation in male mating success increases.

Applications

(1) Effective size of wild mammalian populations with harem mating system

Wild horses (*Equus caballus*) make harems consisting of one adult male and a number of reproductive-age females. Reproductively matured males that have not acquired harems are usually prevented from breeding to a great degree by this social structure (CHEPKO-SADE et al. 1987). Thus, the sex ratio of breeding animals is biased toward females. BERGER (1987) observed that, of the approximately 54 adult males in the population of wild horses in the Granite Range of Nevada, only 16 were stallions in possession of harems of one or more females ($N_m = 16$). The total number of adult females was $N_f = 58$. Thus, the average harem size is $\bar{d}_m = 58/16 = 3.6$. From Eqn 1, CHEPKO-SADE et al. (1987) estimated $N_e = 50.2$. If Poisson distribution of harem size is assumed, Eqn 7 gives an estimate $N_e = 41.2$, which is 82.1% of the estimate from Eqn 1.

Elk (*Cervus elaphus*) also have a harem mating system, in which breeding males have an average harem size of 14.3 (Lacava and Hughes 1984). For a population of $N_m = 7$ and $N_f = 100$, the effective size is computed as $N_e = 26.2$ from Eqn 1, while the estimate from Eqn 7 is $N_e = 24.6$. Note that the difference among the two estimates is rather small because of the extremely biased sex ratio (cf. Figure 1).

Northern elephant seal (*Mirounga angustirostris*) is a more extreme example of harem mating system, in which one successful male mates with 44 females on average (Nunney

1993). Supposing a population with $N_m = 10$ and $N_f = 440$, the effective sizes from Eqn 1 and Eqn 7 are 39.1 and 38.3, respectively.

(2) Effective troop size of Japanese monkeys

A monkey troop is integrated socially by the rank system among the individual members. Using data from 22 monkey troops, NOZAWA (1972) obtained high rank correlations (0.26–1.0, avg. = 0.82) between social and sexual ranks. Following NOZAWA (1972), we assumed that the numbers of mates of males (d_{mi}) arranged in a decreasing order of the social rank follows a geometrical series with a common ratio a ($0 < a < 1$);

$$\{d_{m1}, d_{m2}, d_{m3}, \dots, d_{mN_m}\} = \{d_{m1}, d_{m1}a, d_{m1}a^2, \dots, d_{m1}a^{N_m-1}\}.$$

NOZAWA (1972) found that

$$a = 1 - \frac{5}{N_f}$$

is best fitted to the data of 22 troops. Under this assumption, the squared coefficient of variation in male mating success is expressed as

$$C_{d_m}^2 = N_m \left(\frac{1-a}{1+a} \right) \left(\frac{1+a^{N_m}}{1-a^{N_m}} \right) - 1.$$

Substituting this expression into (5) leads to

$$N_e = \frac{4N_f}{1 + C_{d_f}^2 + N_f \left(\frac{1-a}{1+a} \right) \left(\frac{1+a^{N_m}}{1-a^{N_m}} \right)}. \quad (13)$$

The observed adult numbers in the Takasakiyama troop of Japanese monkey (*Macaca fuscata*) in May 1953 were $N_m = 36$ and $N_f = 60$ (NOZAWA 1972). The effective troop sizes estimated from Eqn 1 and Eqn 7 are $N_e = 90$ and 65.5, respectively. If a fixed female mating success is assumed ($C_{d_f}^2 = 0$), the estimate from Eqn 13 is $N_e = 62.4$. NOZAWA (1972) provided a formula similar to Eqn 13, from which $N_e = 67.0$ is obtained.

It is known that the Japanese monkey has a long reproductive span. According to SUGIYAMA (1985), the age of reproductive onset in female monkeys is 4–6 years old and the reproductive performance is maintained over 20 years. Thus, the multiple matings in female monkeys and the consequent variation in female mating success cannot be neglected. On the assumption of a Poisson distribution of female mating success, i.e. $C_{d_f}^2 = 1/\bar{d}_f$, the effective troop size was computed from Eqn 13 for various values of \bar{d}_f . The result is presented in Figure 3, from which it is seen that although the effective troop size is enlarged by an increase in average mating success in female, it rapidly converges to the value (62.4) expected under $C_{d_f}^2 = 0$.

(3) Effective size of *Drosophila* experimental populations

Males in *Drosophila melanogaster* can mate with more than one female. In the experimental populations with equal sex ratio, PETIT et al. (1980) observed that 25% of the males did not mate, that 50% of matings were performed by 50% of the males who mated only once, and that the other 50% of the matings were performed by 25% of the males who mated two (or rarely three) times. Thus, the coefficient of variation of male mating success is estimated as $C_{d_m}^2 = 0.5$. Since females in *Drosophila melanogaster* will not mate in less than 2-day

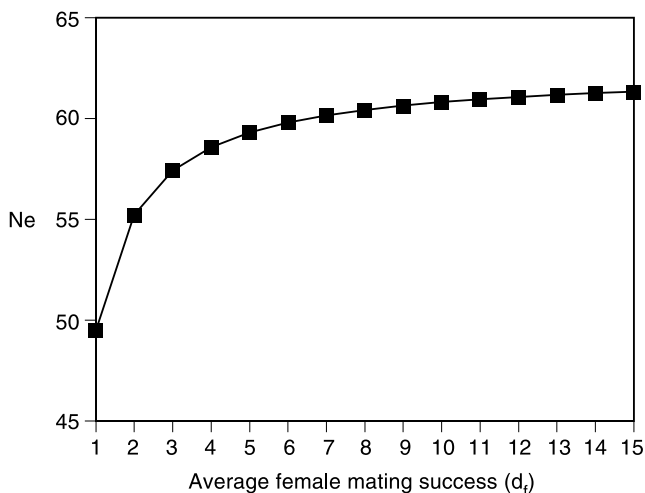


Fig. 3. Effects of average female mating success on effective size of Japanese monkey troop. Poisson distribution of female mating success is assumed

intervals (Manning 1962), it is likely that most females mate only once under a usual experimental condition. Thus, approximately $C_{df}^2 = 0$. Suppose a population with equal sex ratio ($N_m = N_f = N/2$). From Eqn 5 the ratio N_e/N is obtained as

$$\frac{N_e}{N} = \frac{1}{1 + C_{dm}^2/2} = 0.80.$$

Based on the amount of random genetic drift accumulated in an autosomal marker allele, KERR and WRIGHT (1954) estimated the effective size of *Drosophila* experimental populations. The estimated value of N_e/N was 0.67, suggesting that although strong selection against homozygotes of the marker allele (aristapedia gene) is an important cause of the reduction in the effective size (KERR and WRIGHT 1954), most of the reduction is explained by the variation in male mating success.

For an X-linked locus, the ratio N_e/N is obtained from Eqn 9 as

$$\frac{N_e}{N} = \frac{9}{12 + 4C_{dm}^2} = 0.64.$$

From random genetic drift observed in a sex-linked marker allele, WRIGHT and KERR (1954) estimated $N_e/N = 0.61$ in their experimental populations.

(4) Effective size of honeybee colonies

Honeybee (*Apis mellifera*) is a typical haplo-diploid species. The mating system is characterized by the fact that each queen (diploid) is polyandrous but each drone (haploid) is monogamous. Each queen receives sperm from 10 or so drones but readily limits the number of matings by simply closing her sting chamber (SEELEY 1985).

Suppose 10 interbred colonies. If each queen mates on average with 10 drones, then $N_m = 100$ and $N_f = 10$. Assuming that the number of matings in queen follows a Poisson distribution and each drone mates only once, we get $C_{d_f}^2 = 0.1$ and $C_{d_m}^2 = 0$. The effective size of interbred colonies estimated from Eqn 10 is 21.4, while the estimate from Eqn 9 is 19.6.

(5) Effective population size of Japanese Black cattle

The Japanese Black cattle is the most common beef breed in Japan, with a population of 0.61 million reproductive cows. This breed is characterized by prominent intramuscular fat deposition (marbling). Since liberalization of beef import restriction in 1991, domestic production of high-quality beef has received more emphasis in Japan, and the genetic evaluation of meat characteristics, with the best linear unbiased prediction (BLUP) methodology, was initiated in 1991. However, due to the intensive use of a few sires with high marbling estimated breeding values, the decline of genetic diversity is an increasing problem. From the analysis of inbreeding, NOMURA et al. (2001) reported a drastic decrease of the effective size after 1991.

Assuming that $N_m/N_f \rightarrow 0$ in Eqn 5, an approximated formula for estimating the effective size is obtained as

$$N_e = \frac{4N_m}{1 + C_{d_m}^2}.$$

Applying this formula to the demographic data of Japanese Black cattle population (NOMURA et al. 2001), the effective size per year was estimated. In the estimation, the mating success of a sire was approximated by the number of registered progeny from the sire in a given year. The estimates from 1986 to 1996 are shown in Table 1, together with the corresponding estimates from the rate of inbreeding per year. In a strict sense, the annual effective size should be calculated with the lifetime progeny numbers of sires and the average generation interval (HILL 1979). However, the simple estimates with the annual progeny numbers of sires roughly agree with those from the annual rate of inbreeding. The drastic reduction of the effective size after 1991 could well be documented by the simple estimates.

Table 1. Annual effective population sizes of Japanese Black cattle, estimated from the demographic parameters (N_e) and from the annual rate of inbreeding ($N_{e(\Delta F)}$). The number of sires (N_m), and the average, variance and coefficient of variation (C_{d_m}) of the progeny numbers of sires are also listed

Year	N_m	No. of progeny/sire			N_e	$N_{e(\Delta F)}$
		Average	Variance	C_{d_m}		
1986	1009	61.4	54168.1	3.79	262.6	279.9
1987	1018	63.2	50597.2	3.56	297.9	452.2
1988	1067	70.2	73514.5	3.86	268.1	291.5
1989	1045	75.3	84012.6	3.85	264.3	292.5
1990	1063	72.4	73646.5	3.75	282.5	301.3
1991	981	75.7	89053.4	3.94	237.2	204.2
1992	965	68.0	84272.8	4.27	200.8	210.6
1993	884	65.8	81186.5	4.33	179.0	135.9
1994	859	65.9	91057.4	4.58	156.4	150.4
1995	834	69.4	126962.7	5.13	121.9	192.5
1996	779	69.7	131043.2	5.19	111.4	134.3

It is notable that the major cause of the reduction is not the decrease in the number of sires (N_m) but the increase in the coefficient of variation of progeny number (C_{d_m}).

Discussion

Unequal sex ratio of breeding animals is one of the most important reasons for the effective population size to be less than the number of breeding animals (FRANKHAM 1995). Unequal sex ratios are generally associated with polygamous mating systems. Polygamy occurs in a majority of mammals, a minority of birds and some reptiles, fish, amphibians and insects (BRITON et al. 1994). Under polygamous mating systems, parents of the minor sex (usually male) compete for mates, and the variation in mating success will be enhanced. In the present study, to estimate the effective size of populations with a variability in mating success, more appropriate Eqns 7 and 12 than the well-known formulae (Eqns 1 and 10) have been developed.

Throughout our derivation, random mating has been assumed. In several wild animals, however, behavioral avoidance of extreme inbreeding (incest avoidance) has been reported (e.g. MOORE 1993; SMITH 1993). WRIGHT (1969 p.212) has explored the effects of avoidance of consanguineous mating on the effective population size. He concluded that eliminating matings among close relatives has a trivial effect on the effective population size unless the population size is extremely small. Perhaps non-random mating associated with the population subdivision into semi-isolated demes (e.g. colonies or troops) will have a more pronounced effect on the effective population size of wild animals, as suggested by several theoretical studies (for a review, see WANG and CABALLERO 1999) and field researches (CHEPKO-SADE et al. 1987). In planning *in-situ* conservation, seeking information on the pattern and rate of migration would be of special importance.

Although our modelling does not explicitly specify the age structure of breeding animals, the effect of age structure could be roughly inferred from our results. In a population of animals with a longer reproductive span, breeding animals could have a larger number of mates in their lifetime, leading to an increase of μ_{d_i} in Eqns 6 and 11. Thus, as the generation interval increases, the effect of overlapping generations decreases and the effective population size converges to a limiting value (see Figure 3). A more detailed formulation of the effect of overlapping generations is given by NUNNEY (1993) and NUNNEY and ELAM (1994). They showed that although highly polygamous mating systems can give very small values of N_e/N when the generation interval is short, the ratios N_e/N approach a limiting value as the generation interval is lengthened. This conclusion supports our view.

In our derivation, we have assumed that the variation in offspring number (family size) is fully due to non-inherited causes. When the variation in family size is partially determined by inherited causes, the effective population size is not a simple function of the variance and covariance of family size such as Eqns 2 and 8. The formulation is complicated by the correlation between family sizes of parents and their descendants; the offspring and later descendants of a parent with a large (or small) family size inherit the property. The problem of heritable variation of family size in the formulation of the effective population size has been addressed by several authors (ROBERTSON 1961; SANTIAGO and CABALLERO 1995; NOMURA 1996, 1997, 1999; BIJMA et al. 2000, 2001), mainly in the context of artificial selection. The argument could be applied to natural selection (NEI and MURATA 1966).

In wild animal populations, environmental correlation may be a more important cause for the resemblance of family size between parents and offspring (CROW and DENNISON 1988). The correlation could be positive if parents and offspring both occupy an especially favourable niche. For example, from mother-daughter regression, KELLY (2001) estimated the heritability of female family size in Serengeti cheetahs as 0.89. This high heritability estimate strongly suggests the presence of an environmental correlation. The effect of the

environmental correlation on the effective population size is kept completely as long as the offspring remain in the same niche and is partially reduced if part of them migrates to other niches. Thus, the effect could be incorporated in the formulation of the effective population size in a way analogous to the consideration of heritable variation in family size. This problem will be considered in future studies.

FRANKHAM (1995) comprehensively reviewed the published estimates of the ratio N_e/N (192 from 102 species), showing that most of the estimates for mammals with low fecundity are surprisingly constant (around 0.4–0.7), irrespective of the wide variation in methods used for the estimation. Although the development of precise equation accounting for various factors will be of theoretical interest, rough estimates from simple equations could be tentatively used for practical purposes, especially for the conservation of endangered species.

In planning the management of genetic resources, the simple estimate of effective size from demographic parameters would be important especially for the populations of feral livestock. In intensively managed livestock breeds, where pedigree information is available, an accurate estimate could be obtained from the rate of inbreeding. However, the demographic estimates would also be useful for roughly monitoring the effect of alternating the breeding scheme, such as the initiation of BLUP evaluation in Japanese Black cattle, on the genetic diversity. The equations provided in the present study will serve for these purposes.

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Appendix

Derivation of expressions for variance and covariance of offspring numbers

In the derivation of expressions for variance and covariance of offspring numbers, the theory of conditional variance (MOOD et al. 1987 p.159) is used:

$$V[v] = V[E[v|u]] = E[V[v|u]], \quad (\text{A1})$$

where $E[v|u]$ and $V[v|u]$ are the expectation and variance of v conditional on a given u , respectively.

Suppose a population with N_m breeding males and N_f breeding females. The number of mates (mating success) of parent $i (= 1, 2, \dots, N_s)$ of sex s is d_{si} , with the mean μ_{d_s} and variance $\sigma_{d_s}^2$. Thus there are $\mu_{d_j} N_f (= \mu_{d_m} N_m)$ matings in the population. Let x_j be the litter size (the newborn number) of mating $j (= 1, 2, \dots, \mu_{d_j} N_f)$ in the population, and n_{mj} and l_{mj} be the numbers of the male newborns and the male survivors of reproducing age in the litter, respectively. From Eqn A1, the variance of l_{mj} can be written as

$$V[l_{mj}] = V[E[l_{mj}|n_{mj}]] + E[V[l_{mj}|n_{mj}]]. \quad (\text{A2})$$

On the assumption of random survival of newborns with the survival rate v_m , the distribution of l_{mj} conditional on a given n_{mj} may be approximated by a binomial distribution

$$l_{mj} \sim B(n_{mj}, v_m).$$

Then

$$E[l_{mj}|n_{mj}] = n_{mj} v_m$$

and

$$V[l_{mj}|n_{mj}] = n_{mj} v_m (1 - v_m).$$

Substituting these expressions into Eqn A2 gives

$$V[l_{mj}] = v_m^2 V[n_{mj}] + v_m (1 - v_m) E[n_{mj}]. \quad (\text{A3})$$

The distribution of n_{mj} conditional on a given litter size x_j is also approximated by a binomial distribution

$$n_{mj} \sim B(x_j, 1/2),$$

where $1/2$ is the expected sex ratio in a litter. Then

$$E[n_{mj}|x_j] = 0.5 x_j$$

and

$$V[n_{mj}|x_j] = 0.25 x_j.$$

With these expressions, the expectation and variance of n_{mj} in Eqn A3 are obtained as

$$E[n_{mj}] = E[E[n_{mj}|x_j]] = \frac{1}{2} \mu_x$$

and

$$V[n_{mj}] = V[E[n_{mj}|x_j]] + E[V[n_{mj}|x_j]] = \frac{1}{4} (\mu_x + \sigma_x^2),$$

where μ_x and σ_x^2 are the mean and variance of x_j , respectively. Then Eqn A3 is written as

$$V[l_{mj}] = \frac{1}{2}v_m \left(1 - \frac{1}{2}v_m\right)\mu_x + \frac{1}{4}v_m^2\sigma_x^2. \quad (\text{A4})$$

Since the total number of newborns is $X = \mu_{d_s}N_s\mu_x$, the survival rate of male is expressed as

$$v_m = \frac{N_m}{X/2} = \frac{2}{\mu_{d_s}\mu_x} \left(\frac{N_m}{N_s}\right).$$

Substituting this expression into Eqn A4 leads to

$$V[l_{mj}] = \frac{1}{\mu_{d_s}} \left(\frac{N_m}{N_s}\right) \left[1 + \frac{1}{\mu_{d_s}} \left(\frac{N_m}{N_s}\right) \alpha\right] \quad (\text{A5})$$

where $\alpha = C_x^2 - 1/\mu_x$, and $C_x (= \sigma_x/\mu_x)$ is the coefficient of variation of x_j .

Let k_{smi} be the number of male offspring (of reproducing age) from parent i of sex s . Using Eqn A1 the variance of k_{smi} can be written as

$$\begin{aligned} \sigma_{sm}^2 &= V[E[k_{smi}|d_{si}]] + E[V[k_{smi}|d_{si}]] \\ &= (E[l_{mj}])^2 \sigma_{d_s}^2 + V[l_{mj}]\mu_{d_s}. \end{aligned}$$

Substituting $E[l_{mj}] = N_m/(\mu_{d_s}N_s)$ and Eqn A5 into the above equation, we get an expression of σ_{sm}^2 as

$$\sigma_{sm}^2 = \left(\frac{N_m}{N_s}\right) \left[1 + \left(\frac{1}{\mu_{d_s}}\right) \left(\frac{N_m}{N_s}\right) \alpha + \left(\frac{N_m}{N_s}\right) C_{d_s}^2\right],$$

where $C_{d_s} (= \sigma_{d_s}/\mu_{d_s})$ is the coefficient of variation of d_{si} . Analogously we get

$$\sigma_{sf}^2 = \left(\frac{N_f}{N_s}\right) \left[1 + \left(\frac{1}{\mu_{d_s}}\right) \left(\frac{N_f}{N_s}\right) \alpha + \left(\frac{N_f}{N_s}\right) C_{d_s}^2\right]$$

and

$$\sigma_{sm,sf} = \left(\frac{N_m}{N_s}\right) \left(\frac{N_f}{N_s}\right) \left[\left(\frac{1}{\mu_{d_s}}\right) \alpha + C_{d_s}^2\right].$$

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