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# Number of Censuses Required for Demographic Estimation of Effective Population Size

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**Abstract:** Adequate population viability assessment may require estimation of effective population size ( $N_e$ ). But failure to take into account the effect of temporal fluctuation in population size (FPS) on  $N_e$  may routinely lead to unrealistically optimistic viability assessments. We thus evaluate a technique that accounts for the effect of FPS on  $N_e$ . Using time series of annual counts of 48 free-ranging animal populations, we show that  $N_e$  is dependent on timescale: as more census records are incorporated, estimates of FPS tend to increase, and thus estimates of  $N_e$  tend to decrease. Estimates based on, say, 10 annual counts tend to grossly underestimate the influence of FPS on estimates of long-term  $N_e$ , often by more than 100%. Moreover, a newly derived expression for the confidence intervals of  $N_e/N$  (in which  $N$  is population size) reveals that estimates of  $N_e$  based on only a few annual counts are quite unreliable. Our work thus emphasizes the need for long-term population monitoring and provides a framework for interpreting  $N_e$  estimates calculated from limited census data.

Número de Censos Requeridos para una Estimación Demográfica Efectiva de Tamaño Poblacional

**Resumen:** Evaluaciones adecuadas de viabilidad poblacional pueden requerir estimaciones de tamaño poblacional efectivo ( $N_e$ ). Sin embargo, omisiones en la consideración del efecto de la fluctuación temporal del tamaño poblacional (FPS) en  $N_e$  pueden conducir rutinariamente a estimaciones de viabilidad irrealmente optimistas. Es por ello que evaluamos una técnica que toma en consideración el efecto de FPS en  $N_e$ . Utilizamos series de tiempo de conteos anuales de 48 poblaciones de animales de rango libre, mostramos que  $N_e$  es dependiente de la escala temporal: mientras más registros de censos son incorporados, las estimaciones de FPS tienden a incrementar y por lo tanto las estimaciones de  $N_e$  tienden a disminuir. Estimaciones basadas, en por ejemplo, 10 conteos anuales tienden a subestimar la influencia de FPS en las estimaciones de largo plazo de  $N_e$  (frecuentemente por más de un 100%). Mas aún, una nueva expresión derivada para intervalos de confianza de  $N_e/N$  (en la cual  $N$  es el tamaño poblacional) revela que las estimaciones de  $N_e$  basadas en solo unos cuantos conteos anuales son poco confiables. Nuestro trabajo hace énfasis en la necesidad de monitoreos poblacionales a largo plazo y provee un marco de trabajo para interpretar estimaciones de  $N_e$  calculadas a partir de datos de censos limitados.

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## Introduction

A principal goal of conservation biology is to maintain biodiversity. Requisite for meeting this goal is the conservation of genetic diversity, a key determinant of population viability (Jiménez et al. 1994; Keller et al. 1994;

Frankham 1995a; Newman & Pilson 1997; but see Britten 1996). Adequate assessment of viability requires, in part, determining whether the population is large enough to avoid inbreeding or to maintain adaptive genetic variation. The most appropriate metric for this determination is effective population size ( $N_e$ ; Barton & Whitlock 1997), which calibrates the influence of genetic drift in a real population to that in an ideal population (i.e., one with random mating, even sex ratio, discrete generations, and constant size; Wright 1931). An

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ideal population would lose neutral genetic diversity at a rate of  $1/2N$  per generation, where  $N$  is population size. Violations of the ideal assumptions, however, cause real populations, if isolated (Mills & Allendorf 1996), to lose genetic diversity at a (typically faster) rate of  $1/2N_e$  per generation. Beyond retarding the loss of heterozygosity and allelic diversity (Crow & Kimura 1970), maintaining large  $N_e$  increases the likelihood that favorable mutations will become widespread (Falconer & Mackay 1996) and deleterious mutations will be eliminated (Lynch et al. 1995), and it improves the population's ability to cope with environmental change (Bürger & Lynch 1995). Maintaining  $N_e$  above some threshold thus is arguably essential for population viability (e.g., Soulé 1980; Lynch 1996).

An important application of  $N_e$  in conservation biology is the estimation of the minimum viable effective population size. Early work suggested that  $N_e$  must be at least 50 to avoid inbreeding depression and thereby ensure short-term viability, and at least 500 to maintain adaptive genetic variation and thereby ensure long-term viability (Franklin 1980; Soulé 1980). Recent experimental work, however, suggests that  $N_e \approx 50$  is inadequate to ensure short-term viability (Latter et al. 1995; Newman & Pilon 1997). In addition, recent theoretical work suggests that  $N_e \approx 500$  is inadequate to ensure long-term viability; effective sizes on the order of 1000–5000 may be necessary to maintain adaptive variation and avoid the accumulation and fixation of mildly deleterious mutations (reviewed by Lande 1995a; Lynch 1996).

Effective population size is also useful for defining the goals of conservation efforts. For example, the maintenance of 90% of neutral genetic variation over 200 years has been suggested as a general goal (Franklin 1980; Soulé 1980; Soulé et al. 1986; Lande 1995b). Goals of this form may be described as  $N_e = -t/2 \ln[H_t]T$  (Wright 1931), where  $t$  is the time horizon of the goal,  $H_t$  is the fraction of neutral heterozygosity to be maintained, and  $T$  is generation time. Within this framework,  $N_e$  has been applied to species recovery plans (e.g., U.S. Fish & Wildlife Service 1987, 1993, 1994).  $N_e$  has also been used to specify proposed risk categories of the World Conservation Union (i.e., critical, endangered, vulnerable; Mace & Lande 1991) and to prioritize salmon stocks for conservation (Allendorf et al. 1997).  $N_e$  thus is an important tool in conservation biology.

The application of  $N_e$ , however, has been limited by difficulty in obtaining accurate estimates, whether by genetic methods (reviewed by Neigel 1996) or demographic methods (reviewed by Caballero 1994; Husband & Barrett 1995; Nunney 1995). The usual approach for obtaining demographic estimates of  $N_e$  is to model the influence of variance in lifetime reproduction, uneven sex ratio, and overlapping generations, while assuming that the population size is constant (Crow & Denniston 1988; Caballero 1994; Nunney & Elam 1994). Another

factor, temporal fluctuation in population size (FPS), has perhaps the most important influence on  $N_e$  (Wright 1938; Frankham 1995b; Vucetich et al. 1997a). Estimates based on data collected during a single season (Nunney & Elam 1994) ignore the influence of FPS and thus may represent gross overestimates of  $N_e$ . We show here that a greater number of periodic counts of a given population typically yields a lower estimate of  $N_e/N$ . This property arises because longer time series of census data tend to yield higher estimates of FPS (Ariño & Pimm 1995). Using a newly derived expression, we evaluate the confidence intervals for  $N_e/N$  estimates as influenced by the number of annual population counts. We also discuss how time series data may be used to adjust estimates of  $N_e$  for the influence of FPS.

### Fluctuating Population Size and the Estimation of $N_e$

The influence of FPS on long-term  $N_e$  is quantified by Wright (1938), Crow and Kimura (1970), Lande and Barrowclough (1987), Grant and Grant (1992), and Vucetich et al. (1997a):

$$N_e = q \left( \sum_{t=1}^q N_{e,t}^{-1} \right)^{-1} \quad (1)$$

where  $N_{e,t}$  is traditionally the effective size for generation  $t$  (but see Grant & Grant 1992) and  $q$  is the total number of  $N_{e,t}$  estimates. Equation 1 was originally shown to approximate both the variance and inbreeding effective size for cyclical populations with discrete (nonoverlapping) generations (Wright 1938; Crow & Kimura 1970). This harmonic-mean estimator has since been shown to approximate the effective size of populations undergoing more general fluctuations (e.g., Motro & Thomson 1982) and to yield estimates for populations with overlapping generations falling within the range of independently derived values (Vucetich et al. 1997a). Moreover, we have recently shown that equation 1 is inversely related to a standard measure of FPS, the standard deviation of log-transformed population size (Vucetich et al. 1997a). Because equation 1 quantifies FPS, and FPS estimates are independent of sampling frequency (Gaston & McArdle 1994), whether  $N_{e,t}$  is used to represent the effective size for generation  $t$  or for year  $t$  is inconsequential. Moreover,  $N_{e,t}$  quantifies the rate of drift on a per-generation basis, whether estimated from data collected during a single year (Nunney & Elam 1994) or across multiple years (see below).

Because  $N_e$  is strongly dependent on population size, which varies both within and between populations, theoretical evaluation of factors influencing  $N_e$  is facilitated by standardizing equation 1. The most straightforward standardization is the ratio of effective size to census

size (e.g., Nunney 1991, 1995; Briscoe et al. 1992; Frankham 1995b; Husband & Barrett 1995; Vucetich et al. 1997a). Here, we use the ratio of the quantity in equation 1 divided by the average census size (e.g., Frankham 1995b; Vucetich et al. 1997a):

$$(N_e/N)_q = \frac{\left( q / \sum_{t=1}^q N_{e,t}^{-1} \right)}{\left( \sum_{t=1}^q N_t / q \right)} = q^2 \left( \sum_{t=1}^q N_t \sum_{t=1}^q N_{e,t}^{-1} \right)^{-1}, \quad (2)$$

where  $N_{e,t}$  is the (per-generation) effective size calculated in year  $t$ ,  $N_t$  is the census size in year  $t$ , and  $q$  is the number of annual estimates. This approach is appropriate if the population trajectory is stable or if the approach is used to estimate past genetic deterioration (Table 1). But if  $N$  is increasing or decreasing over time and the estimate will be used to forecast genetic deterioration, then the denominator should represent the expected population size during the period of interest. In such cases, the denominator could be replaced with the average of recent values of  $N$ , for example, or an extrapolation of the already-observed trend.

The subscript  $q$  on the left side of equation 2 emphasizes our main focus:  $N_e$  depends on the number of annual estimates incorporated. Because FPS tends to increase the

longer a population is observed (Lawton 1988), estimates of  $N_e$  should decrease as  $q$  increases. We now evaluate the number of annual estimates ( $q$ ) required to account adequately for the influence of FPS on  $N_e$ .

### Increased Fluctuation over Time and the Estimation of $N_e$

Various mechanisms have been proposed to explain the well-documented observation of increasing FPS with increasing numbers of periodic population counts (reviewed by Ariño & Pimm 1995). For example, the temporal dynamics of many environmental factors are likely to be characterized by small, short-term trends superimposed on larger, longer-term trends (i.e., a reddened spectrum; Williamson 1984; Steele 1985). The variance in such systems appears to increase over time. This pattern is unlikely to be simply an artifact of measurement error because such error is typically assumed to be a white-noise phenomenon (e.g., Halperin & Gurian 1970), and the observed variance should thus asymptote over short time scales (Ariño & Pimm 1995). Perhaps because population dynamics are partly driven by fluctuations in the abiotic environment, population size also tends to exhibit increasing fluctuation over time (Lawton 1988; Pimm & Redfearn 1988; Ariño & Pimm 1995; Curnutt et al. 1996), suggesting that incorporating more population counts will tend to yield lower estimates of  $N_e$ .

To explore the effect of increasing FPS on  $N_e$  estimates, we analyze the effect of the number of population counts (i.e.,  $q$ ) incorporated on estimates of  $N_e$ . Our analysis is based on a collection of 48 time series of population counts. These time series, each at least 18 years long, represent a variety of animal taxa, including 24 mammalian, six avian, and 18 invertebrate species (Packer et al. 1991; Turchin & Taylor 1992; Foley 1994; Vucetich et al. 1997b; C. Bocetti, unpublished data). To explore the influence of  $q$  on the ratio  $N_e/N$ , we assume that the populations are ideal except for FPS. Thus, we assume that  $N_{e,t} = N_t$ . This unrealistic assumption is necessary to isolate the influence of FPS. In practice, the influence of other factors known to depress  $N_e$  should also be incorporated. Ignoring these factors here, we calculate  $(N_e/N)_q$  over a range of  $q$  for each time series using equation 2. Consistent with the behavior of FPS, the sample median of  $(N_e/N)_q$  decays asymptotically as  $q$  increases (Fig. 1). Overall, our analysis suggests that estimates based on only a few counts tend to underestimate the influence of FPS on the  $N_e/N$ , thereby tending to overestimate  $N_e$ .

Because only a few annual counts are often available for populations of conservation concern, we examine the possibility that  $N_e$  estimates based on short time series adequately account for the influence of FPS. Specifically, we calculate the percent error between  $(N_e/N)_q$

**Table 1.** An illustration of the accuracy of equation 2 for estimating genetic deterioration.\*

t	$N_t$	$N_{e,t}/N_t$	$N_{e,t}$	$H_t$	$H_t^*$	Fractional error
1	26	0.5	13	1.000	1.000	0.000
2	22	0.5	11	0.955	0.963	-0.009
3	22	0.5	11	0.911	0.927	-0.018
4	17	0.5	8.5	0.858	0.893	-0.041
5	18	0.5	9	0.810	0.860	-0.062
6	20	0.5	10	0.769	0.828	-0.076
7	23	0.5	11.5	0.736	0.797	-0.083
8	24	0.5	12	0.705	0.768	-0.088
9	31	0.5	15.5	0.683	0.739	-0.083
10	41	0.5	20.5	0.666	0.712	-0.069
11	44	0.5	22	0.651	0.685	-0.053
12	34	0.5	17	0.632	0.660	-0.045
13	40	0.5	20	0.616	0.636	-0.032
14	43	0.5	21.5	0.602	0.612	-0.017
15	50	0.5	25	0.589	0.589	0.000

\*We illustrate the dynamics ( $N_t$ ) of a hypothetical population with an increasing trend. Time (t) is measured in years.  $N_{e,t}/N_t$  is assigned arbitrarily. (In practice,  $N_{e,t}/N_t$  would be estimated from equation 4.)  $N_{e,t}$  is obtained by multiplying columns 2 and 3. The proportion of heterozygosity remaining ( $H_t$ ) is calculated in the traditional way ( $H_{t-1}(1-1/2N_{e,t})$ ).  $H_t^*$  is calculated as  $(H_{t-1}^*)(1-1/2N_e)$ , where  $N_e$  is calculated as  $(N_e/N)N = (0.445)(13.491)$  (following equation 2). The hypothetical population is assumed to have a generation time of 1 year. The fractional error tends to be negative (positive) for increasing (decreasing) trends but tends to zero toward the end of the time series. The magnitude of the error depends on the size of  $N_e$  (Crow & Kimura 1970).

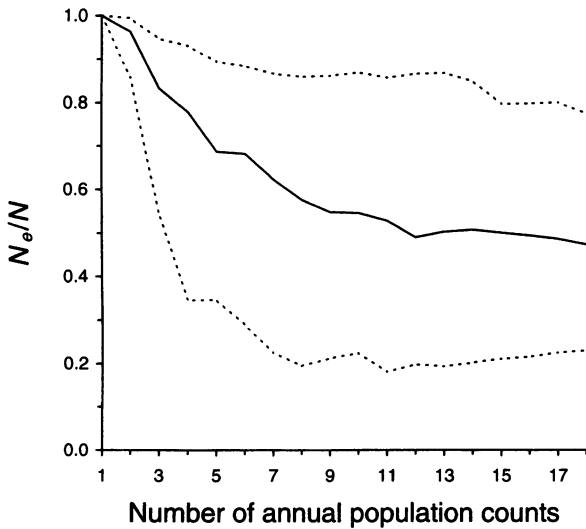


Figure 1. The estimated relationship (equation 2) between  $N_e/N$  and the number of annual population counts ( $q$ ) included in the  $N_e/N$  estimate (based on 48 empirical time series). The solid line represents the median, and the dotted lines represent the first and third quartiles. The upper limit of the x-axis is 18 because the shortest time series consisted of 18 annual counts.  $(N_e/N)_1 = 1$  because FPS cannot be observed when  $q = 1$ . The median appears to converge on 0.5, consistent with a previous analysis showing that the median  $N_e/N$  was approximately 0.5 when populations were assumed ideal except for the influence of FPS (see Fig. 1 of Vucetich et al. 1997a).

and  $(N_e/N)_{q_{max}}$  for each of the 48 time series, where  $q$  represents some specified number of annual estimates (e.g., 4, 6, or 10) and  $q_{max}$  is the total number of counts in the time series. The frequency distribution of these errors (Fig. 2) suggests that estimates based on short time series should be viewed skeptically. In fact, these errors probably represent underestimates because longer time series would tend to increase FPS even further (i.e., long-term  $N_e/N$  will be lower than  $(N_e/N)_{q_{max}}$ ). Overall,  $N_e/N$  estimates based on less than 10 counts are apparently subject to very large errors. The magnitude of these errors depends on the value of  $N_{e,t}/N_t$  (unrealistically assumed to equal unity). In practice, these estimated errors should be adjusted by multiplying by the average  $N_{e,t}/N_t$ , whenever such an estimate is available. In many cases, it would be appropriate to use  $N_{e,t}/N_t \approx 1/2$  as a benchmark (Nunney 1991, 1993, 1995; Nunney & Elam 1994).

Extending the analysis, we assess the number of counts required to account for the influence of FPS within a specified level of error. To do so, we calculate the percent error between  $(N_e/N)_q$  and  $(N_e/N)_{q_{max}}$  for each of the time series, where  $q = 1, 2, \dots, q_{max}$ . (The

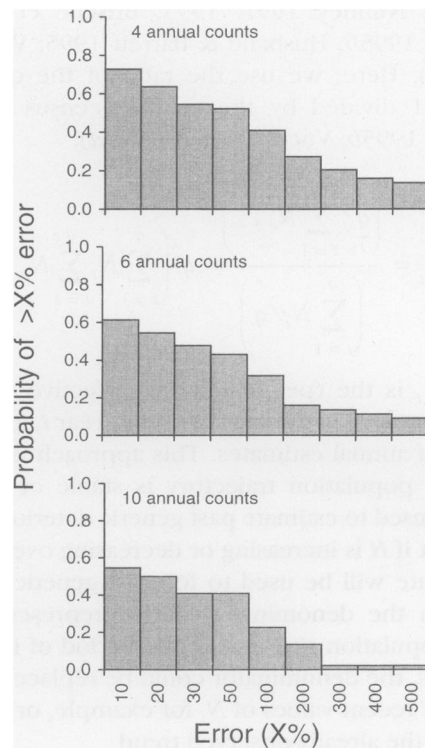


Figure 2. The probability of obtaining  $>X\%$  error for various numbers of annual censuses included in the estimate. The error is defined as the percent difference between the long-term  $N_e/N$  estimates and those based on 4, 6, or 10 annual population counts.

percent error tends to decrease, as with increases in  $q$ , falling perforce to zero at  $q = q_{max}$ .) Then, for each of the time series, we observe the number of counts (i.e., the value of  $q$ ) for which  $(N_e/N)_q$  first falls below the specified level of error. Based on these observed values of  $q$ , we estimate cumulative distributions of the minimum number of counts required to account for the influence of FPS on  $N_e$  estimates. Figure 3 clearly shows that more than just a few counts will typically be required to adjust  $N_e$  adequately for the effect of FPS.

We conclude these analyses by considering two details. First, populations characterized by small FPS may require relatively few annual counts for accurate estimation of  $N_e$ . Though plausible, this supposition appears to be incorrect. For example, the minimum number of counts required to achieve less than 10% error is not significantly correlated with  $(N_e/N)_{q_{max}}$  (Spearman's rank correlation:  $r_s = -0.22, p = 0.17$ ). Thus, accurately estimating long-term  $N_e$  may often require as much data for a population with high  $N_e/N$  (low FPS) as for one with low  $N_e/N$  (high FPS). Second, recall our assumption that  $N_e/N$  would not decrease further even if more than  $q_{max}$  counts were available. This assumption may be routinely violated because FPS is unlikely to approach an asymp-

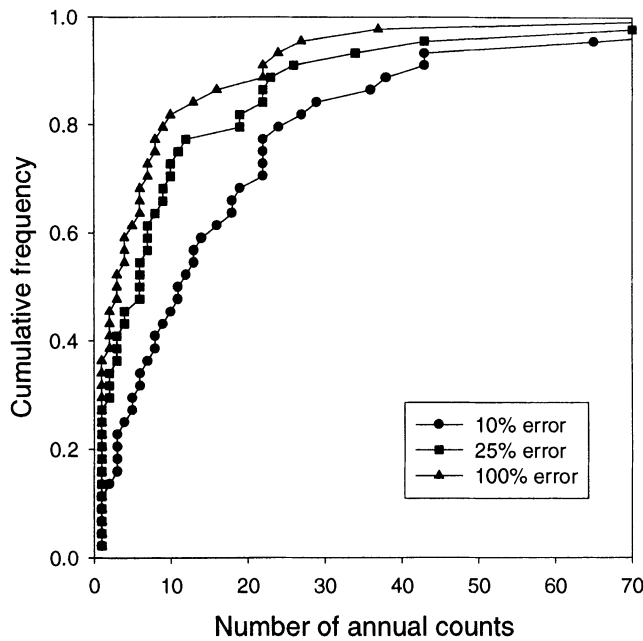


Figure 3. The estimated cumulative distribution frequency for the minimum number of annual population counts to achieve <10%, <25%, or <100% error in the estimation of  $N_e/N$  relative to the long-term  $N_e/N$  (based on 48 time series). The long-term  $N_e/N$  is estimated from the complete time series. Any point on a trajectory is interpretable as the minimum number of annual population counts required (x axis) to be 100 (1 - CF)% certain that an  $N_e/N$  estimate will be within 10%, 25%, or 100% of the estimated long-term  $N_e/N$ . (CF is the y-axis.) Three data points exceed 70 years. This figure suggests, for example, that the median number of counts required to estimate  $N_e/N$  with <10% error is ~12 years.

tote within the short time frames over which populations are usually studied (Murdoch 1994; Ariño & Pimm 1995). A positive correlation between the minimum requisite number of counts and the length of the time series ( $r_s = 0.60, p < 0.0001$ ; Fig. 4) suggests that this assumption was probably violated for some, if not all, time series. Therefore, we have probably underestimated the number of counts required to account adequately for the influence of FPS (Figs. 2 & 3).

**Confidence Intervals for  $N_e/N$**

Besides underestimating the effect of FPS,  $N_e$  estimates based on only a few counts may also be quite unreliable. To evaluate this assertion, we computed confidence intervals around  $N_e/N$  for populations that are ideal except for FPS (Fig. 5; an Appendix for its derivation is available from the authors upon request):

$$\left[ \frac{(N_e/N)(\chi^2_{(1-\alpha_1, q)})^2}{(q\sqrt{N_e/N} - q - \sqrt{N_e/N}\chi^2_{(1-\alpha_1, q)})^2}, \frac{(N_e/N)(\chi^2_{(\alpha_2, q)})^2}{(q\sqrt{N_e/N} - q - \sqrt{N_e/N}\chi^2_{(\alpha_2, q)})^2} \right], \quad (3)$$

where  $\chi^2_{(p, q-1)}$  denotes the  $p$ th percentile of the Chi-square distribution with  $q - 1$  degrees of freedom. These computations show that estimates based on small  $q$  may contain little information about  $N_e/N$ , as reflected by the wide confidence intervals. In addition, geometric increases in  $q$  only result in linear decreases in confidence interval width. Thus, when  $q$  is small, minor increases in  $q$  lead to substantial decreases in confidence-interval width. When  $q$  is large, however, substantial increases in  $q$  are required to reduce confidence-interval width appreciably. We emphasize that because these confidence intervals are based on the assumption that populations are ideal except for FPS (i.e.,  $N_{e,t} = N_t$ ), they are presented simply to illustrate the large number of annual counts required to account adequately for the influence of FPS.

**Comprehensive Estimates of  $N_e$**

Until now we have assumed that populations are ideal except for FPS (i.e.,  $N_{e,t} = N_e$ ). To account hypothetically for the remaining influential factors (i.e., variance in fecundity, uneven sex ratio, and overlapping generations), as one would do in practice,  $N_{e,t}$  in equation 1

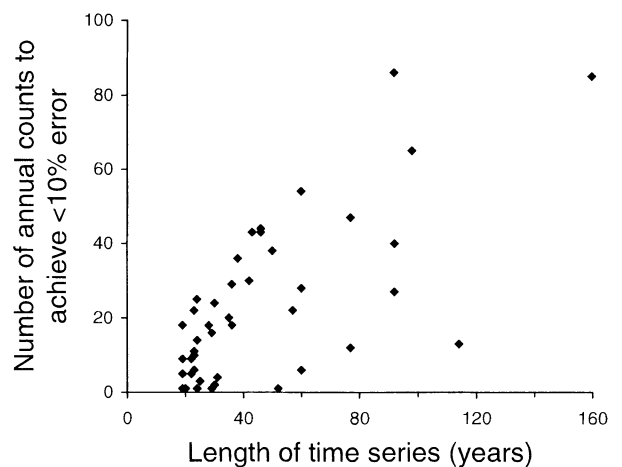


Figure 4. The relationship between the total length of time series ( $q$ ) for 48 populations and the estimated minimum number of annual censuses required to achieve <10% error (relative to the  $N_e/N$  estimate based on the complete time series).

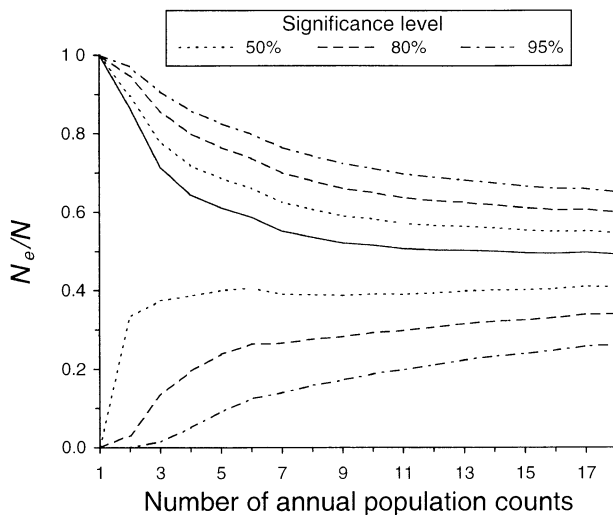


Figure 5. Average  $N_e/N$  values (based on 48 empirical time series) for  $q$  annual population estimates (solid line) and corresponding confidence intervals for the estimated values of  $N_e/N$  (equation 3).

can be replaced by an estimate of the (variance) effective size (Nunney 1991):

$$N_{e,t} = N_t \left\{ 4r(1-r)T / [rA_f(1 + I_{A_f}) + (1-r)A_m(1 + I_{A_m}) + (1-r)I_{bf} + rI_{bm}] \right\}, \quad (4)$$

where  $r$  is the sex ratio,  $T$  is the average generation time,  $A_f$  and  $A_m$  are the average adult life spans for both sexes,  $I_{A_f}$  and  $I_{A_m}$  are the standardized variances in adult life span, and  $I_{bf}$  and  $I_{bm}$  are the standardized variances in reproductive success. Practical considerations for estimating these parameters are described elsewhere (Nunney & Elam 1994). In many cases, the available number of  $N_t$  estimates may exceed the available number of  $N_{e,t}$  estimates. In such cases, the long-term effective size should be estimated by substituting  $N_{e,t}$  in equation 1 with the quantity  $zN_t$ , where  $z$  represents the average  $N_{e,t}/N_t$  computed from the limited estimates available. Such estimates should also be interpreted cautiously because  $N_{e,t}/N_t$  estimates may vary substantially over time (e.g., Peterson et al. 1998), and because the assumption of independence between  $N_{e,t}/N_t$  and FPS has not yet been thoroughly evaluated.

## Discussion

Our results show that  $N_e$  is strongly dependent on time scale (Fig. 1). As longer time scales are considered, estimates of  $N_e$  tend to decrease, and thus estimates of the rate of genetic drift tend to increase. The  $N_e$  values derived from few annual estimates will likely underestimate long-term rates of genetic deterioration because they typically will fail to reflect the influence of infrequent population bottlenecks. Forecasts of genetic deterioration

thus should be limited accordingly. Moreover, conservation goals aimed at preserving some fraction of neutral genetic diversity over long time scales (e.g., 100–200 years) often may be unrealistic because proper evaluation of such goals may be infeasible. These conclusions are based on the recognition that fluctuation in population size is dependent on time scale (Ariño & Pimm 1995) and that FPS is an important predictor of  $N_e$  (Frankham 1995b; Vucetich et al. 1997a). Because FPS is also an important predictor of the demographic component of extinction risk (Lande 1993; Foley 1994), forecasts of demographic extinction risk should similarly be limited to realistically short time scales.

We do not intend to imply, however, that demographic estimators of  $N_e$  are completely uninformative or that only genetic estimators should be used. Judicious use of genetic estimators (reviewed by Neigel 1996) requires similar considerations (Nunney & Elam 1994). For example, it would be dubious to use  $N_e$  estimates based on the temporal method (Waples 1989) to calculate rates of drift for time scales exceeding the sampling interval. Recent advances in molecular techniques (e.g., polymerase chain reaction [PCR] amplification of microsatellite markers), however, permit the comparison of DNA samples from museum specimens (“ancient” DNA; Herrmann & Hummel 1993) with those from extant populations, so it is now feasible in some cases to estimate long-term  $N_e$  (Waples 1989). Demographic estimators should remain useful, though, partly because they can reveal the relative importance of underlying ecological processes influencing  $N_e$ . Thus, rather than discouraging the use of demographic estimators outright, we emphasize the need for long-term population monitoring and cautious application when their use relies on few periodic estimates.

Although the difficulty of obtaining accurate estimates of long-term  $N_e$  for any individual population is discouraging, the successful recovery of a threatened or endangered population may depend little on accurate estimation of its effective size. Recent theoretical work suggests that long-term minimal viable  $N_e$  is roughly 1000–5000 (Lande 1995a; Lynch 1996), and recent work suggests that values of  $N_e/N$  may average about 0.1 (Frankham 1995b; Vucetich et al. 1997a). Taken together, these considerations suggest that a typical minimum viable population size may be roughly 5000–50,000. Because most populations do not receive serious conservation attention until their numbers have dwindled below well below 5000, it would seem misguided to be overly concerned with the precision and accuracy of  $N_e$  estimates;  $N_e$  may be several orders of magnitude smaller than the predicted minimal viable  $N_e$ . Nevertheless, additional studies aimed at the accurate estimation of long-term  $N_e/N$  may prove to be valuable. For example, large numbers of accurate estimates would permit the clarification of any taxonomic patterns in long-term  $N_e/N$  (Frankham 1995b; Waite & Parker 1996;

Vucetich et al. 1997a). Then, for any taxon characterized by a narrow range of  $N_e/N$ , converting to an approximate minimal viable population size would be straightforward.

In summary, because fluctuations in population size (FPS) typically have a strong influence on  $N_e$  (Frankham 1995b; Vucetich et al. 1997a), accurate estimation of long-term  $N_e$  typically requires many annual population counts. We thus urge cautious application and interpretation of estimates of  $N_e$  based on limited numbers of counts. Unfortunately, no universal prescription can be offered as to the number of counts that should be conducted. Our findings, however, do provide a suite of conditional prescriptions (Fig. 3). For instance, about 20 annual counts may often be required to obtain (over)estimates of long-term  $N_e$  with less than 10% error (and 95% confidence limits differing by less than a factor of two). Although a discouragingly large number of counts is required to obtain unbiased and reliable estimates, our findings provide a basis for meaningful interpretation of  $N_e$  estimates calculated from limited census data.

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