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# Relationship between Population Size and Fitness

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**Abstract:** Long-term effective population size, which determines rates of inbreeding, is correlated with population fitness. Fitness, in turn, influences population persistence. I synthesized data from the literature concerning the effects of population size on population fitness in natural populations of plants to determine how large populations must be to maintain levels of fitness that will provide adequate protection against environmental perturbations that can cause extinction. Integral to this comment on what has been done and what needs to be done, the evidence suggests that there is a linear relationship between log population size and population fitness over the range of population sizes examined. More importantly, populations will have to be maintained at sizes of >2000 individuals to maintain population fitness at levels compatible with the conservation goal of long-term persistence. This approach to estimating minimum viable population size provides estimates that are in general agreement with those from numerous other studies and strengthens the argument that conservation efforts should ultimately aim at maintaining populations of several thousand individuals to ensure long-term persistence.

**Key Words:** extinction, inbreeding depression, plants, population viability

Relación entre Tamaño Poblacional y Adaptabilidad

**Resumen:** El tamaño poblacional a largo plazo, que determina tasas de endogamia, está correlacionado con la adaptabilidad de la población. A su vez, la adaptabilidad influye en la persistencia de la población. Sinteticé datos de la literatura relacionados con los efectos del tamaño poblacional sobre la adaptabilidad en poblaciones naturales de plantas para determinar como deben mantener niveles de adaptabilidad que proporcionen protección adecuada a poblaciones grandes contra perturbaciones ambientales que pueden causar su extinción. La evidencia sugiere que hay una relación lineal entre el logaritmo del tamaño poblacional y la adaptabilidad de la población en el rango de tamaños poblacionales examinados. Más relevantemente, las poblaciones se deberán mantener en tamaños de >2000 individuos para mantener niveles de adaptabilidad compatibles con la meta de conservación de persistencia a largo plazo. Este método para la estimación del tamaño poblacional mínimo viable proporciona estimaciones que concuerdan en lo general con numerosos estudios y refuerza el argumento de que, a fin de cuentas, los esfuerzos de conservación deben tener como meta el mantenimiento de poblaciones de varios miles de individuos para asegurar la persistencia a largo plazo.

**Palabras Clave:** depresión endogámica, extinción, viabilidad poblacional

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## Introduction

The long-term effective size of a population is expected to have far-reaching effects on the fitness of that population. The most immediate effect on fitness of a reduction in population size is an increase in the inbreeding

coefficient and the concomitant inbreeding depression that has been found in virtually all species studied thus far (e.g., Crnokrak & Roff 1999; Keller & Waller 2002; Reed & Frankham 2003). The effects of inbreeding on fitness in natural populations can be extremely strong (e.g., Jiménez et al. 1994; Keller 1998; Crnokrak & Roff 1999;

Kruuk et al. 2002). Because an organism's environment undergoes almost constant stochastic fluctuations, any factor that reduces fitness, and therefore recovery time after a perturbation, will make the population more susceptible to extinction when further perturbations occur. When considering the probability of extinction, and its relationship with fitness, it is important to consider not only direct genetic effects, but the interaction between genetic factors and other deterministic and stochastic factors that affect population persistence.

A second, and not mutually exclusive, factor influencing the fitness of a population is the degree to which the fate of alleles is determined by random genetic drift. Genetic drift results when the product of effective population size ( $N_e$ ) and the coefficient of selection ( $s$ ) against an allele is  $\leq 1.0$  (Crow & Kimura 1970). Thus, selection is weaker in small populations than in large populations, leading to an increase in the proportion of deleterious recessive alleles and their possible fixation. This can lead to an extinction vortex, where the loss in fitness resulting from the fixation of deleterious alleles suppresses population size, which in turn increases the amount of drift and eventually ends in extinction. Extinction through the accumulation of deleterious alleles has been coined mutational meltdown (Lande 1994, 1995; Lynch et al. 1995).

Smaller populations are also less likely to give rise to rare beneficial alleles that can have significant effects on the progress of evolution (Elena et al. 1996; Burch & Chao 1999; Estes & Lynch 2003). Further, the beneficial mutations that do occur are more likely to be lost through drift in smaller populations (Kimura 1983). In fact, smaller populations generally seem to be less capable of adapting to novel environmental challenges, as the result of the loss of adaptive or potentially adaptive genetic variation through genetic drift (e.g., Brakefield & Saccheri 1994; Frankham et al. 1999; Whitlock & Fowler 1999; Reed et al. 2003a)

Two studies have reported impacts of genetic effects on extinction risk in wild populations (Newman & Pilon 1997; Saccheri et al. 1998). In addition, small natural populations of a bird, a reptile, and a mammal have been found to decline in numbers—in part because of inbreeding depression—and have recovered following immigration from another population (Westemeier et al. 1998; Madsen et al. 1999; Comiskey et al. 2002). Using computer simulations, Brook et al. (2002) showed that median extinction times were reduced 24–31% when even conservative levels of inbreeding depression were included in the models. Thus, there can be little doubt that there are genetic impacts on population persistence.

A meta-analysis by Reed and Frankham (2003) demonstrated a significant and positive relationship between current population size and population fitness, despite the great amount of inherent noise in any such study. Since the data for Reed and Frankham (2003) were gathered, a number of other investigators have reported a positive re-

lationship between population size and fitness (Dudash & Fenster 2000; Eisto et al. 2000; Young et al. 2000; Cassel et al. 2001; Jacquemyn et al. 2001; Mavraganis & Eckert 2001; Lienert et al. 2002; Paschke et al. 2002; Severns 2003). Yet two questions remain unresolved. How large do populations have to be to maintain levels of fitness that result in long-term population viability? Is the relationship between population size and fitness linear or does it reach an asymptote? To address these questions, I analyzed data sets on the relationship between population size and population fitness.

## Methods and Results

I identified 11 data sets (from 10 studies) relevant to the research questions. All the data sets involved plants and assayed population size and some measure of fitness. I chose these 11 data sets because data were presented in tables or figures that allowed the calculation of an intercept and a slope from a best-fit regression line. Additionally, the studies chosen presented counts or estimates of population size, not just areas. In some cases, the authors examined more than one fitness component. In such cases, I used the component that I believe correlated most strongly with total fitness (Crawley 1997; Reed & Bryant 2004).

The major obstacle to analyzing the data was the fact that a variety of fitness traits were assayed (Table 1): percent germination, seedlings produced per plant, total number of seeds produced per plant, or total seed mass produced per plant. Direct comparisons of the linear regressions of the raw data, therefore, would be meaningless. To counter this problem I converted the fitness in each population to a relative fitness, for which the highest value (within a data set) was given a value of one and all other values were expressed as a proportion of this maximum fitness. This transformation puts the different studies on the same scale and makes them comparable.

A y-intercept and slope was calculated for the best-fit linear regression line of each data set individually (Table 2). The y-intercepts were highly variable (mean = 0.0400, SE = 0.0651), but the slopes were fairly homogeneous (mean = 0.2461, SE = 0.0168). The mean linear regression formula for all 11 data sets was relative fitness =  $0.0400 + 0.2461 (\log_{10} N)$ , where  $N$  is the population size. Thus, a population of 10 individuals has 28.6% of standard fitness, one of 100 individuals has 53.2% of standard fitness, one of 1000 individuals has 77.8% of standard fitness, and one of 10,000 individuals has 102.4% of standard fitness.

I used the linear regression formula estimated from the individual data set to determine the population size required to maintain 95% of standard fitness (Table 1). One shortcoming of measuring relative fitness becomes apparent in reading Table 1: standard fitness depends on the size

**Table 1.** Details of the individual studies used in the analysis of the relationship between population size and fitness.

Species	95% W <sup>a</sup>	Fitness trait <sup>b</sup>	N <sup>c</sup>	Reference
<i>Aquilegia canadensis</i>	1,994	seedlings/plant	5–825	Mavraganis & Eckert 2001
<i>Arnica montana</i>	893	seed set	3–750	Luijten et al. 2000
<i>Cochlearia bavarica</i>	6,438	seeds/plant	10–2560	Paschke et al. 2002
<i>Gentiana lutea</i>	>100,000	seeds/plant	1–5,000	Kéry et al. 2000
<i>Gentianella germanica</i>	9,013	seeds/plant	40–5000	Fischer & Matthies 1998
<i>Ipomopsis aggregata</i>	2,375	% germination	15–3328	Heschel & Paige 1995
<i>Limnanthes floccosa</i>	86,250	seed set	350–45,689	Dole & Sun 1992
<i>Primula elatior</i>	510	total seed mass	4–275	Jacquemyn et al. 2001
<i>Primula veris</i>	66,621	seeds/plant	1–13,750	Kéry et al. 2000
<i>Senecio integrifolius</i>	2,518	seed set	10–4107	Widén 1993
<i>Silene regia</i>	1,227	% germination	15–1190	Menges 1991

<sup>a</sup>Minimum estimated population size needed to maintain 95% of the standard fitness.

<sup>b</sup>Fitness component measured.

<sup>c</sup>Range of population sizes assayed for fitness.

of largest population assayed in each study. The relationship between maximum population size and estimated population size needed to maintain 95% of standard fitness was positive—the larger the population sampled, the larger the estimated size needed to maintain fitness (Fig. 1). Thus, estimates of the population size required to maintain fitness may be biased downward.

I used forward model selection to test whether a quadratic regression model fit significantly better than a linear regression model (Table 3; Zar 1999) for each data set. The addition of a quadratic term did not significantly improve the fit of the model for any of the data sets. Thus, there was no evidence that the relationship between fitness and log population size is nonlinear, and fitness did not appear to be approaching an asymptote over the population sizes assayed for any of the 11 data sets.

## Discussion

My results demonstrate two major findings. First, to maintain population fitness at levels adequate to buffer pop-

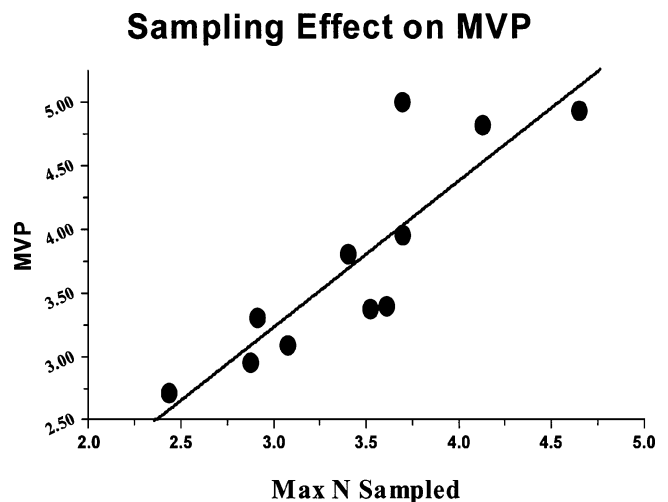
ulations against extinction resulting from environmental stochasticity (e.g., disease epidemic, drought, and severe winters), populations must be maintained at sizes of at least 2000 individuals. Second, the evidence suggests that population fitness has a linear relationship with log<sub>10</sub> population size. The evidence does not support the idea that fitness reaches asymptote at some finite population size, despite the fact that two of the data sets included populations of >10,000 individuals.

Population size should have a direct link to fitness via inbreeding depression and random genetic drift. But these types of data are always noisy. Environmental differences among field sites and sampling variance obscure patterns in fitness caused by differences in population size. Many of the estimates of population size in this data set

**Table 2.** The y-intercept and slope of the best-fit linear regression line estimated from the plant data assayed.

Species	n	y-intercept	Slope
<i>Aquilegia canadensis</i>	44	0.3201	0.1909
<i>Arnica montana</i>	14	0.0827	0.2939
<i>Cochlearia bavarica</i>	22	-0.0116	0.2525
<i>Gentiana lutea</i>	27	0.2144	0.1375
<i>Gentianella germanica</i>	11	-0.3863	0.3379
<i>Ipomopsis aggregata</i>	10	0.1462	0.2381
<i>Limnanthes floccosa</i>	8	-0.1711	0.2271
<i>Primula elatior</i>	14	0.0967	0.3151
<i>Primula veris</i>	19	-0.2157	0.2417
<i>Senecio integrifolius</i>	6	0.1302	0.2410
<i>Silene regia</i>	23	0.2348	0.2315
Mean*	18.0	0.0400	0.2461

\*Among study means.



**Figure 1.** The relationship between maximum population size assayed for fitness (independent variable, log<sub>10</sub> transformed) within a data set and the estimated population size (log<sub>10</sub> transformed) required to maintain 95% of standard fitness (dependent variable) ( $r^2 = 0.753$ ,  $p < 0.001$ ).

**Table 3.** The proportion of the variance in plant fitness explained by a linear regression model ( $r^2$  linear) and by a quadratic regression model ( $r^2$  quadratic).

Species	$r^2$ linear	$r^2$ quadratic	Test <sup>a</sup>	Shape of quadratic curve <sup>b</sup>
<i>Aquilegia canadensis</i>	0.198	0.200	$F = 0.00$ , $p > 0.50$	DCD
<i>Arnica montana</i>	0.574	0.600	$F = 0.71$ , $p > 0.50$	DCD
<i>Cochlearia bavarica</i>	0.695	0.718	$F = 1.53$ , $p > 0.20$	ICU
<i>Gentiana lutea</i>	0.235	0.240	$F = 0.76$ , $p > 0.50$	DCD
<i>Gentianella germanica</i>	0.678	0.825	$F = 6.69$ , $p < 0.10$	ICU
<i>Ipomopsis aggregata</i>	0.702	0.784	$F = 2.65$ , $p > 0.20$	DCD
<i>Limnanthes floccosa</i>	0.482	0.514	$F = 0.32$ , $p > 0.50$	ICU
<i>Primula elatior</i>	0.447	0.514	$F = 3.19$ , $p > 0.20$	DCD
<i>Primula veris</i>	0.656	0.689	$F = 0.11$ , $p > 0.50$	ICU
<i>Senecio integrifolius</i>	0.730	0.815	$F = 1.36$ , $p > 0.50$	DCD
<i>Silene regia</i>	0.240	0.244	$F = 0.11$ , $p > 0.50$	DCD

<sup>a</sup>Forward selection procedure testing whether the addition of the quadratic term significantly improves the accuracy of the prediction of fitness using population size as the independent variable (Zar 1999).

<sup>b</sup>Abbreviations: DCD, a decreasing concave-down function, where fitness increases at a decreasing rate with increases in population size; ICU, an increasing concave-up function, where fitness increases at an increasing rate with increasing population size.

encompassed only 1 year, and none encompassed more than 3 years. Contemporary population size is often a poor surrogate for long-term effective population size. Thus, the effects of fluctuating population size may not be apparent. Despite these caveats, these data strongly support the theoretical conclusion that smaller populations have lower fitness on average than larger populations.

It might be expected that fitness would increase with increasing population size at a decreasing rate or reach an asymptote at some finite population size. The data sets analyzed reveal no such pattern. A second-degree polynomial did not provide a statistically better fit to the data than did a linear function in any of the 11 data sets. The power to detect such nonlinearities in the individual studies was very low in most studies and only moderate in the largest ones. A closer look at the data, however, reveals that the best-fit quadratic in 4 of the 11 data sets did not meet the expectation of being a decreasing concave-down function, but rather was an increasing concave-up function (i.e., fitness increases at an increasing rate with increases in population size). In fact, the only data set

that comes close to being significantly nonlinear is an increasing concave-up function. Thus, the most parsimonious answer is that the relationship is typically linear. More studies, especially with larger populations, will be needed to confirm or refute this preliminary finding. If true, this would suggest that the greater number of beneficial mutations available to larger populations and selection against deleterious alleles of very small effect remain important factors in determining population fitness, even at population sizes of several thousand.

Although population size clearly has major implications for population fitness, one may wonder how much fitness wild populations can lose and still be viable. The answer to this will undoubtedly depend on the initial fitness of the population, and the relationship between fitness and the probability of extinction will be nonlinear over much of the parameter space. Populations with intrinsic growth rates ( $r$ ) that are approaching zero will be particularly vulnerable to further decreases in fitness. Although the exact mean fitness needed to prevent extinction for a given conservation time frame, for a particular population, may never be known, some guidelines are available. Preston and Snell (2001) modeled populations of rotifers for which they had extensive demographic and life-history data. They found that reducing the extrinsic rate of increase,  $r$ , by 5%, 10%, and 20% increased the probability of extinction over 100 years by 10%, 30%, and 70%, respectively. Using demographic data from 102 natural populations of vertebrates, Reed et al. (2003b) found that decreasing the replacement rate ( $R_0$ ) by 50% increases the probability of extinction by approximately 250% on average over the course of 40 generations.

The relationship between population size and population fitness reported here, in combination with the population sizes at which endangered species usually exist, suggests that many populations have reduced fitness as a result of the expression of deleterious recessive alleles from inbreeding or genetic drift. These results strengthen concerns about the loss and fragmentation of habitat for endangered populations of plants and animals. I suggest that populations be managed to maintain 95% of their original fitness, much the same as management programs aim at maintaining certain levels of the original genetic diversity. This will require populations of approximately 5000 individuals. This number is very similar to minimum viable population sizes suggested for various other reasons: 4500 individuals to maintain an equilibrium between the loss of genetic diversity via drift and its replacement by mutation (Franklin 1980); 2000 individuals based on the effects of mutation, drift, and selection (Schultz & Lynch 1997; Reed & Bryant 2000; Whitlock 2000); 1500–5500 individuals based on temporal variation in population size for wild populations (Thomas 1990; Reed & Hobbs 2004); and 7000 individuals based on 102 population viability models (Reed et al. 2003b). A consensus on what constitutes a minimum viable population size is needed, so

that biodiversity persistence can be considered explicitly in reserve-network design (Margules & Pressey 2000; Cabeza & Moilanen 2001).

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