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Reviewed work(s):

Source: *Conservation Biology*, Vol. 13, No. 4 (Aug., 1999), pp. 860-868

Published by: [Blackwell Publishing for Society for Conservation Biology](#)

Stable URL: <http://www.jstor.org/stable/2641700>

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Erosion of Heterozygosity in Fluctuating Populations

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Abstract: *Demographic, environmental, and genetic stochasticity threaten the persistence of isolated populations. The relative importance of these intertwining factors remains unresolved, but a common view is that random demographic and environmental events will usually drive small populations to the brink of extinction before genetic deterioration poses a serious threat. To evaluate the potential importance of genetic factors, we analyzed a model linking demographic and environmental conditions to the loss of genetic diversity in isolated populations undergoing natural levels of fluctuation. Nongenetic processes—environmental stochasticity and population demography—were modeled according to a bounded diffusion process. Genetic processes were modeled by quantifying the rate of drift according to the effective population size, which was predicted from the same parameters used to describe the nongenetic processes. We combined these models to predict the heterozygosity remaining at the time of extinction, as predicted by the nongenetic portion of the model. Our model predicts that many populations will lose most or all of their neutral genetic diversity before nongenetic random events lead to extinction. Given the abundant evidence for inbreeding depression and recent evidence for elevated extinction rates of inbred populations, our findings suggest that inbreeding may be a greater general threat to population persistence than is generally recognized. Therefore, conservation biologists should not ignore the genetic component of extinction risk when assessing species endangerment and developing recovery plans.*

Erosión de la Heterocigosidad en Poblacione Fluctuantes

Resumen: *La estocasticidad demográfica, ambiental y genética amenaza la persistencia de poblaciones aisladas. La importancia relativa de estos factores interconectados permanece sin resolverse, pero una visión común es que los eventos demográficos y ambientales al azar usualmente conducen a poblaciones pequeñas al borde de la extinción cuando el deterioro genético representa una amenaza seria. Para evaluar la importancia potencial de los factores genéticos, analizamos un modelo conectando condiciones demográficas y ambientales a la pérdida de diversidad genética en poblaciones aisladas bajo niveles de fluctuación natural. Los procesos no genéticos—estocasticidad ambiental y demografía poblacional—fueron modelados de acuerdo a procesos de difusión añadidos. Los procesos genéticos fueron modelados cuantificando la tasa de deriva de acuerdo al tamaño poblacional efectivo, el cual se predijo de los parámetros utilizados para describir los procesos no genéticos. Combinamos estos modelos para predecir la heterocigosidad remanente al tiempo de extinción, predecido por la porción no genética del modelo. Nuestro modelo predice que muchas de las poblaciones perderían la mayoría de su diversidad genética neutral antes de que los eventos no genéticos las conduzcan a la extinción. Dada la abundante evidencia de la depresión por intracruza y la evidencia reciente de la elevada tasa de intracruza poblacional, nuestros resultados sugieren que la intracruza podría ser una amenaza general para la persistencia de poblaciones aún mayor de lo que se ha reconocido. Por lo tanto, los conservacionistas no deberían ignorar el componente genético del riesgo de extinción cuando se evalúan planes de amenaza de especies y de recuperación.*

Paper submitted May 26, 1998; revised manuscript accepted December 9, 1998.

Introduction

How important is genetic deterioration as a contributor to the extinction risk of conserved populations? This fundamental question remains unresolved and contentious. Many empirical findings have indirectly suggested that genetic factors could contribute to extinction risk (e.g., reviews by Allendorf & Leary 1986; O'Brien & Evermann 1988; Frankham 1995a; Lacy 1997), yet genetic deterioration has been commonly viewed as a minor component of extinction risk. This perspective is reflected in the low ranking of genetic factors (15 out of 18) among cited causes of species endangerment in the continental United States (Czech & Krausman 1997). Until recently, no evidence directly supported the hypothesis that genetic deterioration contributes to the extinction of wild populations (Frankham & Ralls 1998; Saccheri et al. 1998). A compelling view in the absence of such evidence is that stochastic demographic and environmental events are likely to drive small populations to the brink of extinction before genetic deterioration poses a serious threat (Lande 1988; Pimm et al. 1988, 1989; Caro & Laurenson 1994).

Here, we reevaluate this perspective using a model that links demographic and environmental conditions with rates of inbreeding and genetic deterioration in isolated populations. If demographic and environmental stochasticity usually lead to extinction before genetic diversity is substantially reduced, then inbreeding is unlikely to be an important component of extinction risk even for species thought to be vulnerable to inbreeding depression. However, if inbreeding is predicted to eliminate most or all of the genetic diversity before demographic and environmental factors cause extinction, then the contribution of inbreeding to extinction risk should be reconsidered. Although extinction is typically caused by multiple, only partially separable factors (Gilpin & Soulé 1986), an improved understanding of these factors and the time scales on which they operate would allow us to devise better conservation strategies.

Environmental stochasticity by itself represents an important category of extinction risk even for large populations (Lande 1993; Caughley 1994; Foley 1994). In addition, environmental stochasticity causes fluctuation in population size, which accelerates genetic deterioration (Vucetich et al. 1997a) and potentially increases extinction risk due to inbreeding depression. To evaluate this process, we modeled the loss of neutral genetic diversity through inbreeding in isolated populations. Using the term *inbreeding* strictly to refer to a metric for the rate of loss of heterozygosity (Templeton & Read 1994), we calculated the proportion of initial heterozygosity remaining at the expected persistence time (calculated from analytical expressions) and the proportion of initial heterozygosity expected to remain at the time of extinction (estimated from simulations). Recognizing that de-

mographic and environmental conditions cause all populations to fluctuate, we ask whether realistic levels of fluctuation could substantially erode heterozygosity before demographic and environmental conditions cause extinction.

Methods

Because heterozygosity is lost through genetic drift at the rate of $1/2N_e$ per generation, the proportion of expected heterozygosity (hereafter, simply heterozygosity) remaining in a population after t generations, H_t , is $(1 - 1/2N_e)^t$, where N_e is the average effective population size, assuming neutrality and no mutation (Wright 1931). We calculated the proportion of initial heterozygosity remaining at the expected (mean) time to extinction, $H_{E[TE]}$ (i.e., H_t when $t = E[TE]$, where TE is the time to extinction and $E[\]$ indicates the expected value). Using diffusion theory applied to population dynamics, the approximation for the expected time to extinction (in generations) of an isolated population is (Foley 1994)

$$E[TE] = \frac{1}{2sE[r]G} (e^{2s \ln(K)} (1 - e^{-2s \ln(N_0)}) - 2s \ln(N_0)), \tag{1}$$

where K is carrying capacity; $E[r]$ is the expected value of r , the annual growth rate; s is expected growth rate divided by variance in growth rate ($Var[r]$); G is generation time in years; and N_0 is initial population size. Considerations for estimating these parameters for natural populations and assumptions underlying diffusion models (e.g., stationarity of demographic processes) are discussed elsewhere (Dennis et al. 1991; Foley 1994, 1997).

Calculating $H_{E[TE]}$ also requires an estimate of the average effective size of a population over its life span, which can be expressed as a function of $SD[\log(N)]$, a measure of temporal fluctuation in population size (Vucetich et al. 1997a; also see Vucetich & Waite 1998):

$$N_e = \left[\frac{E[N]}{2} \right] \left[1 + \frac{\ln(10)^2 SD[\log(N)]^2}{2} \right]^{-2}, \tag{2}$$

where $E[N]$ is the expected size of N , the population, over its life span, and $SD[\log(N)]$ is the standard deviation of log-transformed population size. Based on the properties of the diffusion model, $E[N]$ may be expressed as

$$E[N] = \frac{[K^{2s+1} - 1] [-2s(e^{2sn_0} - 1)]}{(2s + 1) [2sn_0 e^{2sn_0} - e^{2s(k+n_0)} + e^{2sk}]}, \tag{3}$$

where $n_0 = \ln(N_0)$ and $k = \ln(K)$. The derivation for this expression follows that given in Appendix A of Hanski et al. (1996; a detailed outline is available from the authors upon request).

Equation 1 depends on $\text{Var}[r]$, and equation 2 depends on $\text{SD}[\log(N)]$, both of which are measures of population fluctuation. Deriving an expression for $\text{Var}[r]$ in terms of $\text{SD}[\log(N)]$, we show that $\text{Var}[r]$ in equation 1 can be replaced by $\ln(10)^2 \text{SD}[\log(N)]^2$ (Appendix). This replacement allows us to evaluate the influence of $\text{SD}[\log(N)]$ on the rate of genetic deterioration relative to the expected time of extinction due to nongenetic processes only. Replacing t and N_e in the expression $H_t = (1 - 1/2N_e)^t$ with the expressions for $E[\text{TE}]$ (equation 1) and N_e (equation 2), we investigate the influence of various demographic parameters, including $\text{SD}[\log(N)]$, on the proportion of initial heterozygosity that would remain if an isolated population persisted until $E[\text{TE}]$ (i.e., $H_{E[\text{TE}]}$).

In addition to this analytical approach, we also performed simulations to quantify genetic deterioration prior to extinction. Specifically, we estimated the heterozygosity expected to remain at the time to extinction, $E[H_{\text{TE}}]$. These simulations were performed by modeling: $n_{t+1} = n_t + r_t$, where n_t is the log-transformed population size and r_t is the annual log-transformed growth rate (drawn randomly from a normal distribution with mean $E[r]$ and variance $\text{Var}[r]$; Foley 1994). Each population was monitored until the year preceding extinction (i.e., $n_t \leq 0$), and the average effective size was calculated directly from the population trajectory with equation 2, where $E[N]$ was replaced by the arithmetic mean of the trajectory. Based on this value of N_e and the recorded time to extinction (in generations), we calculated the proportion of heterozygosity remaining.

The $E[H_{\text{TE}}]$ was estimated for each set of parameter values as the arithmetic mean of the heterozygosity remaining at the time to extinction for 10,000 simulated populations.

Results

Heterozygosity at the Expected Time to Extinction

Calculations of $H_{E[\text{TE}]}$ reveal a suite of conditions leading to significant loss of heterozygosity through inbreeding (Fig. 1). The curves in Fig. 1, however, suggest that the contribution of inbreeding to extinction risk is greatest at low (≤ 0.25) and high values of $\text{SD}[\log(N)]$ (≥ 1.25). More specifically, large populations undergoing minor fluctuation ($\text{SD}[\log(N)] \leq 0.25$) and small populations undergoing either minor or pronounced fluctuation (≥ 1.25) are predicted to lose most or all of their heterozygosity at neutral loci if they persist as long as the (mean) expected time to extinction (Fig. 1). These findings are meaningful because many populations across a variety of taxa are characterized by $\text{SD}[\log(N)] \leq 0.25$ (Fig. 2), suggesting that substantial loss of heterozygosity may commonly occur before $E[\text{TE}]$ (predicted by equation 1). $H_{E[\text{TE}]}$ is also sensitive to changes in generation time (G), where shorter G leads to smaller values of $H_{E[\text{TE}]}$ (Fig. 1). In contrast, $H_{E[\text{TE}]}$ is relatively insensitive to changes in growth rate (r) when $\text{SD}[\log(N)] \geq 0.25$ or when r is positive (Fig. 1). Provided that the initial popu-

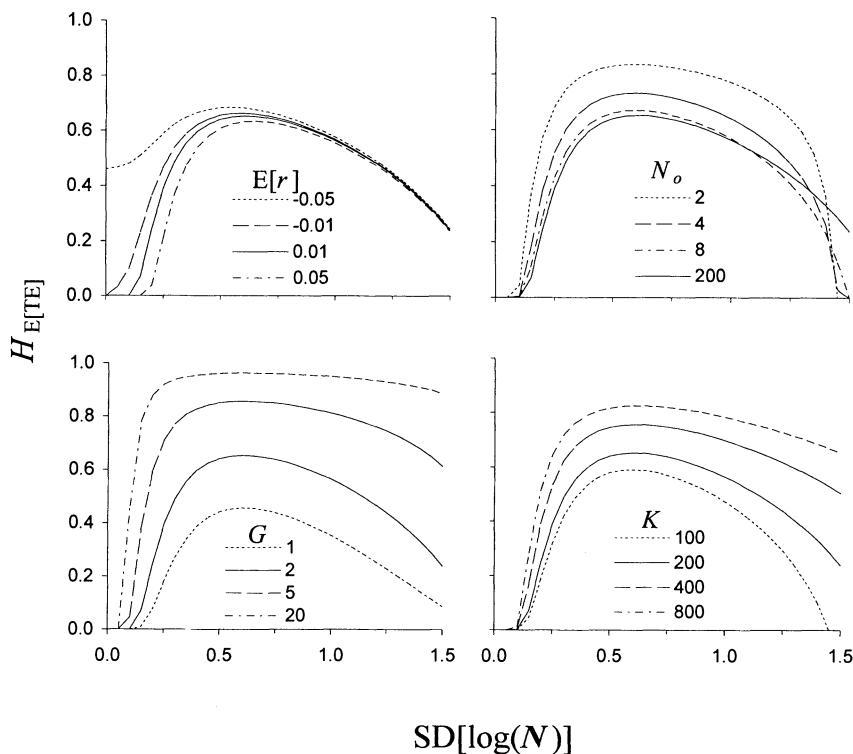


Figure 1. Analytical solutions for the effect of temporal fluctuation in population size ($\text{SD}[\log(N)]$) on the proportion of heterozygosity remaining at the expected time to extinction ($H_{E[\text{TE}]}$) for various values of expected growth rate (r), initial population size (N_0), generation time (measured in years; G), and carrying capacity (K). Except where otherwise indicated, K and N_0 equal 200, $E[r] = 0.01$, and $G = 2$ years. To facilitate comparison, the solid curve is identical in all panels. Because larger $\text{SD}[\log(N)]$ leads to shorter expected time to extinction ($E[\text{TE}]$; equation 1) and smaller effective population size (N_e ; equation 2; see methods), the overall extinction risk increases with $\text{SD}[\log(N)]$ and decreases with N_0 , K , and r .

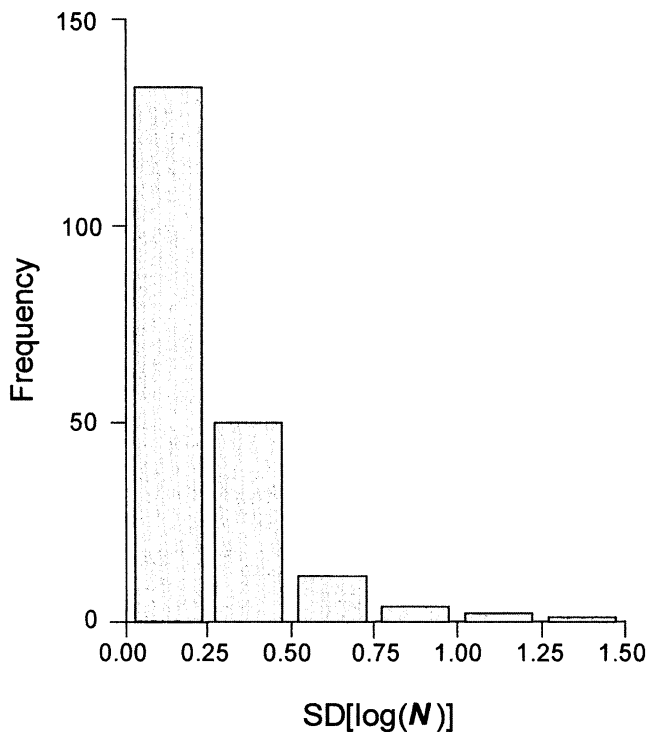


Figure 2. Frequency distribution of the standard deviation of log transformed population size ($SD[\log(N)]$), a measure of temporal fluctuation. The data, taken from Fig. 3.1 of Pimm 1991, represent 202 populations and a variety of taxa. For two-thirds of the populations, $SD[\log(N)]$ was < 0.25 , a region in which $H_{E[TE]}$ and $E[H_{TE}]$ are highly sensitive to variation in $SD[\log(N)]$ (see Fig. 1).

lation size (N_0) exceeds a few individuals, $H_{E[TE]}$ is also relatively insensitive to increases in N_0 (Fig. 1).

Proper interpretation of these results depends on the recognition that because larger $SD[\log(N)]$ leads to shorter expected time to extinction (equation 1) and smaller effective population size (equation 2; see methods), the overall extinction risk increases with $SD[\log(N)]$. When $SD[\log(N)]$ is small, N_e tends to be large, but $E[TE]$ tends to be long enough that isolated populations are expected to lose most or all of their heterozygosity due to the long time over which genetic drift occurs. By contrast, when $SD[\log(N)]$ is large, $E[TE]$ tends to be short and N_e tends to be small. Small populations with large $SD[\log(N)]$ are expected to go extinct relatively quickly (Fig. 1). Although drift would occur for just a short time, such populations are predicted to lose much of their heterozygosity before $E[TE]$ because N_e is small (equation 2).

Additional calculations show that some real populations undergoing typical levels of fluctuation would be expected to lose nearly all of their heterozygosity if they were to persist as long as $E[TE]$ (Table 1). Even large pop-

ulations, if they remain isolated, may eventually suffer massive losses in heterozygosity (e.g., moose, Table 1; Fig. 1). Conversely, large populations undergoing substantial fluctuation are predicted to retain much of their heterozygosity if they persist as long as $E[TE]$ (e.g., checkerspot butterfly, Table 1). Such populations should be least prone to inbreeding depression (but see Lynch 1996). Although much additional data are needed, Table 1 prompts the speculation that isolated vertebrate populations may be more likely than isolated invertebrate populations to suffer severe genetic erosion during their life span.

We emphasize that $H_{E[TE]}$ (or $E[H_{TE}]$; see below) refers to the remaining proportion of H relative to that of the founding population at time $t = 0$. In some cases it may be useful to consider the proportion of H remaining relative to the source population. In such cases, our predictions should be scaled downward according to the size of the founding population. For example, if the founding population comprises two individuals, then $H_{E[TE]}$ (or $E[H_{TE}]$) would be multiplied by 0.75.

Expected Heterozygosity at Time to Extinction

Simulations of $E[H_{TE}]$ corroborate the general patterns exhibited by $H_{E[TE]}$ (Fig. 2). Most isolated populations (i.e., where $SD[\log(N)] \leq 0.25$ and $K < 800$) are expected to lose most of their heterozygosity prior to the time of extinction. Similar to the behavior of $H_{E[TE]}$, $E[H_{TE}]$ is sensitive to changes in generation time (G) and relatively insensitive to changes in $E[r]$, N_0 , and K (for $100 < K < 800$; Fig. 3). In contrast to the behavior of $H_{E[TE]}$, $E[H_{TE}]$ is a strictly increasing function of $SD[\log(N)]$: Consequently, populations exhibiting greater than typical levels of fluctuation (i.e., $SD[\log(N)] \geq 0.25$; Fig. 2) are not expected to lose nearly all of their heterozygosity prior to extinction. That populations exhibiting pronounced fluctuation (say, $SD[\log(N)] \geq 0.5$) may retain a significant proportion of their heterozygosity is deceptive for two reasons. First, few populations exhibit fluctuations where $SD[\log(N)]$ exceeds 0.5. Second, when $SD[\log(N)]$ exceeds 0.5, the population is likely to go extinct rapidly due to environmental stochasticity (for the parameter space considered here, all populations with $SD[\log(N)] \geq 0.50$ had $E[TE] < 20$ years).

Mutation and Migration

To account for processes capable of contributing to genetic diversity over time, we consider the following expression for heterozygosity (Hartl & Clark 1989):

$$H_t = 1 - \left\{ \left[\frac{1}{2N_e} + \left(1 - \frac{1}{2N_e} \right) (1 - H_{t-1}) \right] (1 - m)^2 \right\}, \quad (4)$$

where m is the rate of either mutation or immigration. To calculate $H_{E[TE]}$ under various rates of mutation, we iter-

Table 1. Proportion of heterozygosity remaining at the expected time to extinction ($H_{E[TE]}$) for a variety of taxa.^a

Taxon	$E[r]$	$Var[r]$	$SD[\log(N)]$	K	G^b	$E[TE]^c$	N_e	$H_{E[TE]}$	Source
Insects and spiders									
checkerspot butterfly (<i>Euphydryas editha</i>)	0.307	1.460	0.525	7259	1	122	368	0.85	Foley 1997
checkerspot butterfly (<i>E. editha</i>)	0.126	0.840	0.398	1998	1	121	127	0.62	Foley 1997
orb spider (<i>Metapeira</i> sp.)	0.545	0.971	0.428	235	1	94	28	0.19	Foley 1997
Birds									
Great Tit (<i>Parus major</i>)	0.025	0.265	0.224	146	2	62	15	0.137	Foley 1997
Tawny Owl (<i>Strix aluco</i>)	0.007	0.004	0.027	32	6	2524	12	<0.001	Foley 1997
Whooping Crane (<i>Grus americana</i>)	0.052	0.015	0.053	150	2	1.0×10^4	65	<0.001	Dennis et al. 1991
Mammals									
gray wolf (<i>Canis lupus</i>)	0.005	0.054	0.101	50	6	59	7	0.02	Vucetich et al. 1997b
moose (<i>Alces alces</i>)	0.018	0.005	0.031	2400	5	4.7×10^4	1048	<0.001	Vucetich et al. 1997b
brown bear (<i>Ursus arctos</i>)	0.018	0.011	0.046	58	10	814	22	<0.001	Foley 1997
lion (<i>Panthera leo</i>)	0.040	0.079	0.122	125	4	194	29	0.04	Packer et al. 1991

^aAverage growth rate ($E[r]$), variance in growth rate ($Var[r]$), and carrying capacity (K) were estimated from time series data (Foley 1997). Standard deviation of the log-transformed population size ($SD[\log(N)]$) was calculated from $Var[r]$ (see methods). Expected time to extinction ($E[TE]$) and effective population size (N_e) were calculated according to equations 1 and 2. Initial population size (N_0) was arbitrarily assumed to equal 2.

^bGeneration time in years.

^cExpected time to extinction in generations.

ated equation 4 for $E[TE]$ generations (see equation 1). The $E[H_{TE}]$ was estimated as the arithmetic mean for 10,000 values of H_{TE} , where each H_{TE} was obtained by observing a simulated population until the year prior to its extinction and then iterating equation 4 for that number of generations. Mutation rates $\leq 10^{-5}$ appear to have vir-

tually no effect on either $H_{E[TE]}$ or $E[H_{TE}]$ (Fig. 4). When $SD[\log(N)] \leq 0.25$, populations persist long enough for mutation rates of 10^{-3} to increase $H_{E[TE]}$ and $E[H_{TE}]$, but the increase is minor (i.e., no more than about 25% of H is retained for either $H_{E[TE]}$ and $E[H_{TE}]$ where $SD[\log(N)] \leq 0.25$).

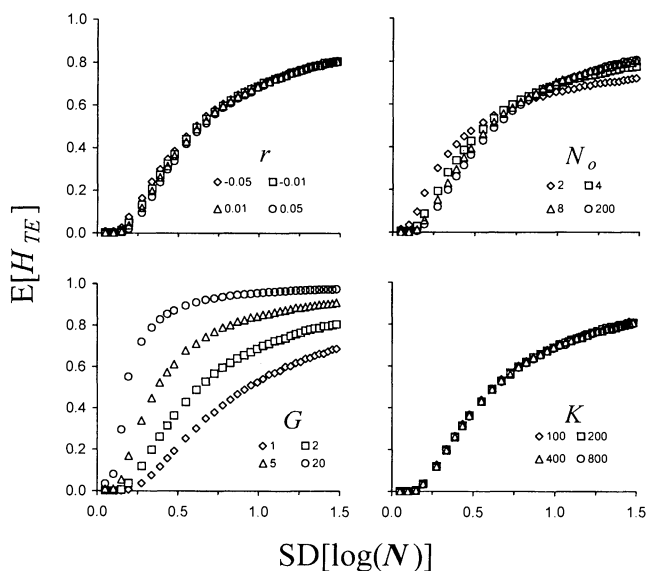


Figure 3. Simulation results for the effect of temporal fluctuation in population size ($SD[\log(N)]$) on the expected heterozygosity remaining at the time to extinction ($E[H_{TE}]$) for various values of expected growth rate (r), initial population size (N_0), generation time (measured in years; G), and carrying capacity (K). Except where otherwise indicated, K and N_0 equal 200, $E[r] = 0.01$, and $G = 2$ years.

Discussion

Genetic deterioration is often thought to be a relatively unimportant component of extinction risk because stochastic demographic and environmental events may lead to extinction before enough genetic diversity is lost to pose any serious threat (e.g., Lande 1988). Our calculations (of heterozygosity at the expected time to extinction, $E[H_{TE}]$) and simulations (of heterozygosity expected at the time to extinction, $H_{E[TE]}$) suggest that many small, isolated populations may lose most or all of their neutral genetic diversity before demographic and environmental events lead to extinction. These results are corroborated by the congruence in demographic conditions leading to massive genetic erosion and long persistence times ($>2N_e$ generations; unpublished results), which arises because the distribution of allele frequencies at neutral loci is nearly uniform and about half of such loci become fixed within $2N_e$ generations (Fig. 1 in Kimura 1955; Hartl & Clark 1989).

Studies of laboratory and free-ranging populations suggest that losses in heterozygosity of the magnitude predicted by our model may lead to significant loss of fitness (Jimenez et al. 1994; Keller et al. 1994; but see Hedrick & Miller 1992; Holsinger 1996) and even increased extinction risk (Frankham 1995b; Newman &

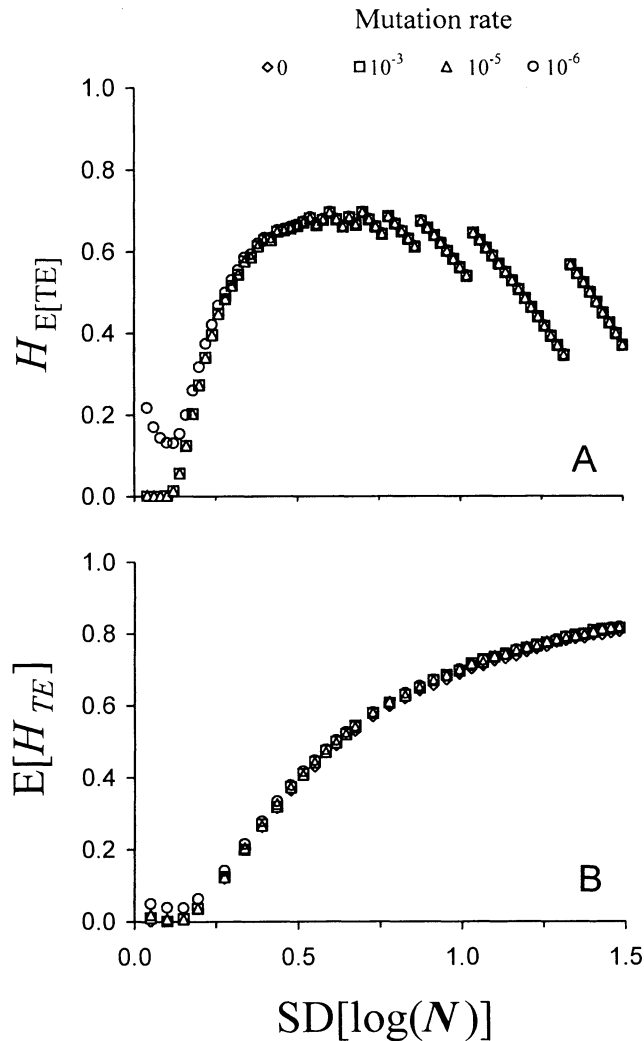


Figure 4. (A) Effect of mutation on the relationship between temporal fluctuation in population size ($SD[\log(N)]$) and heterozygosity remaining at the expected time to extinction ($H_{E[TE]}$). (B) Effect of mutation on the relationship between temporal fluctuation in population size ($SD[\log(N)]$) and expected heterozygosity remaining at the time to extinction ($E[H_{TE}]$). For all points, carrying capacity (K) and initial population size (N_0) equal 200, average annual growth rate (r) equals 0.01, and generation time (G) equals 2 years. Note that the curves in A are discontinuous because equation 4 requires that $E[TE]$ be rounded to the nearest integer.

Pilson 1997; Frankham & Ralls 1998; Saccheri et al. 1998). These empirical findings are consistent with theoretical work by Mills and Smouse (1994), who used a Leslie matrix model to explore the potential fitness consequences of inbreeding under a variety of plausible conditions. Our model extends their findings by isolating the influence of population variability and genera-

tion time on heterozygosity (Figs. 1 & 3). Although we made no assumption about the fitness consequences of inbreeding, given that losses in neutral genetic diversity may be associated with increased extinction risk, our findings have obvious implications for the genetic management of conserved populations. Given that loci under moderate selection will behave almost as if neutral, provided that N_e is less than a few hundred (Lynch 1996), our results suggest that isolated populations may suffer massive losses in genetic variation associated with polygenic traits. Finally, the loss of neutral genetic diversity may compromise a population's capacity to adapt to changing environmental conditions (Lande & Shannon 1996; Myers 1996).

Nonetheless, by restricting our analysis to loss of heterozygosity at neutral loci, we have ignored evolutionary processes that may substantially affect extinction risk. Our model incorporates neither the accumulation of mildly deleterious alleles (i.e., mutational meltdown; Lande 1994, 1995; Lynch et al. 1995) nor the removal of deleterious alleles by selection (i.e., purging; Templeton 1987; Hedrick 1994; Fu et al. 1998; see also Willis & Wiese 1997). Future work should investigate the potential influence of these processes on extinction risk in light of our findings.

Predicting the effect of inbreeding depression in real populations has proven difficult due to inherent variability in the underlying genetic processes even within taxa (Lacy et al. 1996; see also Lacy & Ballou 1998). The potential contribution of genetic deterioration to extinction risk for any particular population depends strongly on the timing of extinction. According to equation 1, small populations that go extinct before $E[TE]$ are unlikely to exhibit symptoms of inbreeding depression because they will have lost little genetic diversity during that short period. In contrast, small populations that persist well beyond the $E[TE]$ are likely to suffer inbreeding depression. Our model focused on calculating genetic diversity at $E[TE]$. An important limitation of most measures of extinction risk, including $E[TE]$, is their failure to convey the uncertainty in predicted times to extinction (Vucetich & Waite 1998b). This uncertainty translates into uncertainty in predicted genetic deterioration during the life span of a population. For example, the 70% confidence interval for time to extinction (i.e., [0.16 MTE, 1.9 MTE] for an exponential distribution) corresponds to an approximately 20–100% loss in genetic diversity (Fig. 6). Thus, inherent statistical variation will typically preclude precise prediction of genetic deterioration for any particular population.

Quantifying fluctuation in population size, and hence the rate of loss of heterozygosity, is likewise subject to substantial uncertainty. The proportion of initial heterozygosity remaining at $E[TE]$ is very sensitive to variation in $SD[\log(N)]$, especially for $SD[\log(N)] \leq 0.25$ (Fig. 1). Increasing $SD[\log(N)]$ from 0.1 to 0.2 could increase

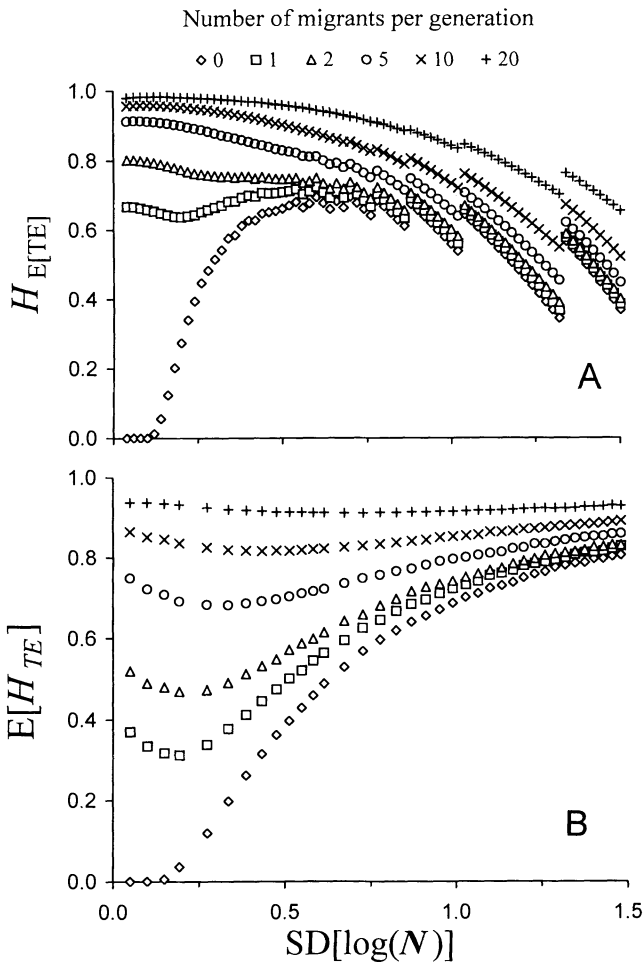


Figure 5. (A) Effect of immigration on the relationship between temporal fluctuation in population size ($SD[\log(N)]$) and heterozygosity remaining at the expected time to extinction ($H_{E[TE]}$). (B) Effect of immigration on the relationship between temporal fluctuation in population size ($SD[\log(N)]$) and expected heterozygosity remaining at the time to extinction ($E[H_{TE}]$). For all points, carrying capacity (K) and initial population size (N_0) equal 200, average annual growth rate (r) equals 0.01, and generation time (G) equals 2 years. Note that the curves in A are discontinuous because equation 4 requires that $E[TE]$ be rounded to the nearest integer.

$H_{E[TE]}$ from 0.0 to >0.5 . Unfortunately, estimates of $SD[\log(N)]$ for real populations will rarely be adequate for predicting whether the population is likely to retain virtually none or perhaps most of its genetic diversity. Suppose $SD[\log(N)]$ for a particular population were estimated as 0.15 after 15 annual censuses. The 90% confidence interval for this estimate would extend from 0.04 to 0.40. (Even this level of uncertainty assumes that the census counts are accurate.) Again, this uncertainty would typically correspond to values of $H_{E[TE]}$ ranging

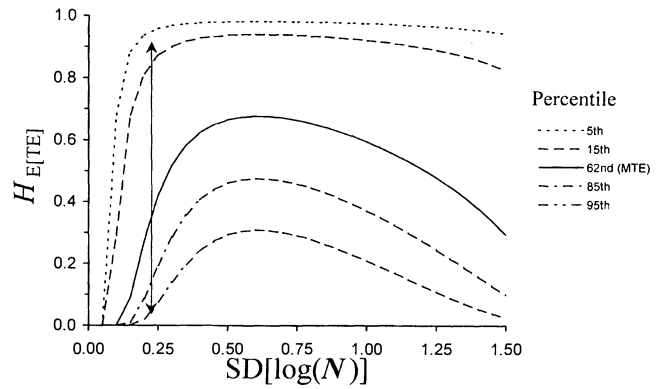


Figure 6. Effect of temporal fluctuation in population size ($SD[\log(N)]$) on the proportion of heterozygosity remaining at the expected time to extinction ($E[TE]$), and at the 5th, 15th, 85th, and 95th percentiles of the distribution of times to extinction. The curves were calculated by converting the $E[TE]$ to various percentiles for an exponential distribution of times to extinction (Vucetich & Waite 1998b). The vertical line illustrates that the 90% confidence interval for the time to extinction (due to nongenetic factors) corresponds to a loss of heterozygosity ranging from 4 to 95% (for a [typical] value of $SD[\log(N)] = 0.15$; see Fig. 2). Given this inherent uncertainty, the potential importance of genetic factors for extinction risk in any particular population cannot be adequately assessed. For all curves, carrying capacity (K) and initial population size (N_0) equal 200, average population growth rate (r) equals 0.01, and generation time (G) equals 2 years.

from 0 to >0.5 . Because most animal populations are characterized by values of $SD[\log(N)] < 0.25$ (Pimm 1991; Fig. 2), making accurate predictions of genetic deterioration will be nearly impossible even under ideal conditions. More generally, given the inherent uncertainties associated with genetic drift (Lacy et al. 1996), persistence time (Vucetich & Waite 1998b; Fig. 3), and population fluctuation (Gaston & McArdle 1994), accurate assessments of the potential importance of genetic diversity typically will be unobtainable for any particular population. This limitation in no way implies that genetic deterioration should be ignored. In the absence of information suggesting otherwise, our findings suggest that pronounced loss of heterozygosity is likely to occur in many conserved populations.

Our results (Figs. 1, 3, & 4) suggest that small populations, if isolated, are prone to massive losses in genetic diversity. Such losses, however, may be counterbalanced by immigration. To quantify this effect, we calculated $H_{E[TE]}$ for populations receiving various numbers of migrants per generation by iterating equation 4 for $E[TE]$ generations (equation 1), where the migration rate (m)

was the number of migrants per generation divided by average population size ($E[N]$; equation 3). We also estimated $E[H_{TE}]$ as the arithmetic mean for 10,000 observations of H_{TE} . Each H_{TE} was obtained by observing a simulated population until the year prior to extinction and then iterating equation 4 for that number of generations, where m was the number of migrants per generation divided by average population size as estimated directly from the simulated trajectory. In many cases, more than two migrants per generation would be required to prevent either $H_{E[TE]}$ or $E[H_{TE}]$ from dropping below 0.80 (Fig. 5). Although one migrant per generation has long been thought to be sufficient to maintain an equilibrium inbreeding coefficient of ~ 0.2 (Wright 1931), recent analyses have shown that the requisite number of migrants increases as the recipient population's N_e/N ratio decreases (Vucetich 1999) and N increases (Vucetich 1999; Mills & Allendorf 1996). Consequently, for many conserved populations, one migrant per generation may be inadequate.

Recognizing that temporal fluctuation in population size is a strong predictor of demographic and environmental components of extinction risk (Lande 1993) as well as the rate of genetic deterioration (Vucetich et al. 1997a), our model implicates inbreeding as a potentially general threat (see also Saccheri et al. 1998). If our model had typically predicted only minor losses in genetic diversity, then inbreeding could not have been reasonably implicated as an important general contributor to extinction risk. But because the model predicts substantial losses in genetic diversity under many plausible conditions (for populations with $N \leq 800$ and $N_e \leq 500$), genetic deterioration should not be dismissed as a trivial component of extinction risk and should not be ignored when endangerment is assessed and recovery plans are devised.

Acknowledgments

We thank K. Field, R. Frankham, R. Lande, P. Parker, R. Peterson, S. Pimm, L. Vucetich, and two anonymous reviewers for helpful comments on the manuscript; S. Sheldon for thought provoking dialogue; and L. Vucetich for assistance with the derivation in the Appendix. This work was supported in part by a McIntire-Stennis grant to T.A.W.

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Appendix

To derive an expression for $\text{Var}[r]$ in terms of $\text{SD}[\log(N)]$, we begin by writing the diffusion model for population dynamics as $n_{t+1} = n_t + r_t$, where n_t is the log-transformed population size at time t and r_t is the log transformed growth rate. Expressing r_t as $n_{t+1} - n_t$ allows the variance in growth rate to be expressed as $\text{Var}[n_{t+1} + (-n_t)] = \text{Var}[n_{t+1}] + \text{Var}[n_t] - 2\text{Cov}[n_{t+1}, n_t]$. The covariance term should be adjusted because animal population dynamics are more accurately characterized by $n_{t+1} = \phi n_t + r_t$, where ϕ measures the autocorrelation between n_{t+1} and n_t ; $\text{Var}[r_t] = \text{Var}[n_{t+1}] + \text{Var}[n_t] - 2\phi\text{Cov}[n_{t+1}, n_t]$. The subscript t can be omitted because the variance properties of n_t and n_{t-1} are virtually identical. This omission yields $\text{Var}[r] = \text{Var}[n] + \text{Var}[n] - 2\phi\text{Cov}[n] = [2 - 2\phi][\ln(10)\text{SD}[\log(N)]]^2$. Based on an analysis of 115 populations, animal population dynamics appear to be typically intermediate between Brownian motion and white noise (Ariño & Pimm 1995). Assuming the midpoint along this continuum ($\phi = 1/2$), the variance reduces to $[\ln(10)\text{SD}[\log(N)]]^2$. This derivation is well supported by multiple linear regression of $\text{SD}[\log(N)]$ and ϕ (the dependent variables) on $\text{Var}[r]$ (the independent variable) from times series of census data for 48 real animal populations ($r^2 = 0.98$, $F = 492.0$, $P = 2.6 \times 10^{-31}$, $\text{df} = 46$; data described in Vucetich et al. 1997a). Sensitivity analyses show that $H_{\text{E[TE]}}$ and $E[H_{\text{TE}}]$ increase asymptotically with linear increases in ϕ (range in ϕ for the 48 time series: -0.55 - 1.18).

