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Review

Population Variability and Extinction Risk

JOHN A. VUCETICH,*‡ THOMAS A. WAITE,† LINDA QVARNEMARK,†
AND SIRI IBARGÜEN†

*School of Forestry, Michigan Technological University, Houghton, MI 49931, U.S.A.
†Department of Evolution, Ecology, and Organismal Biology, and Department of Anthropology,
Ohio State University, Columbus, OH 43210, U.S.A.

Abstract: *Population models generally predict increased extinction risk (ER) with increased population variability (PV), yet some empirical tests have provided contradictory findings. We resolve this conflict by attributing negative measured relationships to a statistical artifact that arises because PV tends to be underestimated for populations with short persistence. Such populations do not go extinct quickly as a consequence of low intrinsic variability; instead, the measured variability is low because they go extinct so quickly. Consequently, any underlying positive relationship between PV and ER tends to be obscured. We conducted a series of analyses to evaluate this claim. Simulations showed that negative measured relationships are to be expected, despite an underlying positive relationship. Simulations also identified properties of data, minimizing this bias and thereby permitting meaningful analysis. Experimental data on laboratory populations of a bruchid beetle (Callosobruchus maculatus) supported the simulation results. Likewise, with an appropriate statistical approach (Cox regression on untransformed data), reanalysis of a controversial data set on British island bird populations revealed a significant positive association between PV and ER (p = 0.03). Finally, a similar analysis of time series for naturally regulated animal populations revealed a positive association between PV and quasiextinction risk (p < 0.01). Without exception, our simulation results, experimental findings, reanalysis of published data, and analysis of quasiextinction risk all contradict previous reports of negative or equivocal relationships. Valid analysis of meaningful data provides strong evidence that increased population variability leads to increased extinction risk.*

Variabilidad Poblacional y Riesgo de Extinción

Resumen: *Los modelos poblacionales generalmente predicen un mayor riesgo de extinción (ER) al aumentar la variabilidad poblacional (PV), a pesar de ello, algunas pruebas empíricas han proporcionado resultados contradictorios. Nosotros hemos resuelto este conflicto mediante la atribución de mediciones de relaciones negativas a un producto estadístico que surge debido a que la PV tiende a ser subestimada para poblaciones de persistencia corta. Estas poblaciones no se extinguen rápidamente como resultado de una variabilidad intrínseca baja; por lo contrario, la variabilidad medida es baja debido a que las poblaciones se extinguen tan rápidamente. Consecuentemente, cualquier relación positiva subyacente entre la PV y el ER tienden a ser opacadas. Llevamos a cabo una serie de análisis para evaluar este argumento. Las simulaciones mostraron que las relaciones negativas medidas son de esperarse, a pesar de una relación positiva subyacente. Las simulaciones también identificaron propiedades de los datos que minimizan este sesgo y por lo tanto permiten un análisis significativo. Los datos experimentales en poblaciones de laboratorio de un coleóptero bruchidae (Callosobruchus maculatus) respaldan los resultados de las simulaciones. De la misma manera, el uso de una técnica estadística adecuada (por ejemplo, la regresión Cox en datos sin transformar), usada en la repetición del análisis de un juego de datos controvertidos de poblaciones de aves de la Isla Británica reveló una asociación positiva significativa entre la PV y el ER (p = 0.03). Finalmente, un análisis similar de series de tiempo para poblaciones de animales reguladas de manera natural revelaron una asociación positiva entre la PV y el riesgo de cuasi-extinción (p < 0.01). Sin excepciones, nuestros resultados de simulaciones, los resultados experimentales, la repetición del análisis de datos publicados, y el análisis de riesgo de cuasi-extinción contradicen informes*

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previos de relaciones negativas o equívocas. Los análisis válidos de datos significativos proveen una evidencia sólida de que los incrementos en la variabilidad poblacional conducen a un incremento en el riego de extinción.

Introduction

Population variability models routinely predict increased extinction risk (ER) with decreases in (initial) population size, carrying capacity, and average potential growth rate, and with increases in variability in growth rate (Lande & Orzack 1988; Dennis et al. 1991; Boyce 1992; Foley 1994). Although direct empirical tests of the predicted effect of growth rate apparently have not been conducted, empirical studies have provided consistent support for the predicted effects of population size (Jones & Diamond 1976; Pimm et al. 1988, 1993; Berger 1990; Schoener & Spiller 1992) and carrying capacity (Diamond 1969; Brown 1971; Newmark 1987; Richman et al. 1988). By contrast, tests of the predicted effect of population variability (PV) have yielded variable, controversial results. Several studies provide apparent support for the predicted positive relationship (Karr 1982; Pimm et al. 1988; Forney & Gilpin 1989; Bengtsson & Milbrink 1995). Other studies reveal no significant relationship (Bengtsson 1989; Pollard & Yates 1992) or provide evidence for a negative relationship (Schoener 1991; Schoener & Spiller 1992; Lima et al. 1996; for discussions of the statistical validity of several of these studies see Diamond & Pimm 1993; Pimm 1993; Tracy & George 1993; Gaston & McArdle 1994).

We conducted simulations, experimentation, and analysis of field data to resolve the mismatch between predicted and measured relationships between PV and ER. Using simulations, we (1) quantified conditions producing a negative observed relationship even when the underlying relationship is positive and (2) reconciled the disagreement between the theoretical positive relationship and evidence of a negative relationship. Using experimental data on laboratory populations of a bruchid beetle (*Callosobruchus maculatus*), we tested the predicted positive relationship between PV and ER and evaluated the potential for observing spuriously negative relationships. We also reanalyzed a controversial data set on British island bird populations (Pimm et al. 1988; Tracy & George 1992). Finally, we analyzed the relationship between PV and quasiextinction risk in time series of natural animal populations. We begin by reviewing the theoretical basis for the predicted positive relationship between PV and ER.

Theoretical Relationships between Population Variability and Extinction Risk

Theoretical relationships between variance in log-transformed growth rate, σ_r^2 (a metric for PV) and ER (ex-

pressed as the inverse of the mean or median time to extinction) are routinely positive. Two examples are the bounded diffusion model (equation 8 in Foley 1994) and unbounded diffusion model (equation 17 in Dennis et al. 1991; our Fig. 1). The relationship between diffusion and age-structured matrix models (Lande & Orzack 1988) implies that matrix models also predict a positive relationship. Simulations also indicate a positive relationship for a wide range of density dependence in the θ logistic model (equation 8 in Middleton & Nisbet 1997; our Fig. 1). Although nonpositive relationships are plausible (Pimm 1991; Schoener & Spiller 1992), numerous theoretical treatments besides those described above (MacArthur & Wilson 1967; MacArthur 1972; Richter-Dyn & Goel 1972; Leigh 1975, 1981; Belovsky 1987; Goodman 1987) yield the same prediction: increased population variability leads to increased extinction risk.

Empirical Relationships between Population Variability and Extinction Risk

Several investigations have been designed to test this predicted relationship between PV and ER. A positive relationship was inferred from the comparison of PV (measured as the observed coefficient of variation in population size [CV] from weekly counts) for experimental populations of *Daphnia magna* and *D. longispina* that went extinct during the experiment versus those that persisted (Bengtsson & Milbrink 1995). An earlier experiment with a similar design failed to find any significant differences in CV between populations of *D. magna*, *D. longispina*, and *D. pulex* that went extinct versus those that persisted (Bengtsson 1989).

A positive relationship between PV and ER was inferred from the comparison of PV between extinct and extant bird species on Barro Colorado Island (BCI; Karr 1982), where PV for each species was estimated as the CV in rate of capture at a nearby site on the mainland. The data set represents 716 captures of 38 species, including only species represented in at least three of the eight samples collected over a 13-year span. The CV of species that had gone extinct (123.7) on BCI was significantly higher than that of species that remained (86.3; $p < 0.005$). Unlike other analyses (e.g., Bengtsson 1989; Bengtsson & Milbrink 1995), this is a reasonable test because CV estimates were based on data from nearby mainland populations that never went extinct. Therefore, PV of BCI populations should not have been underestimated to any greater degree for those populations with shorter persistence (see Statistical Considerations).
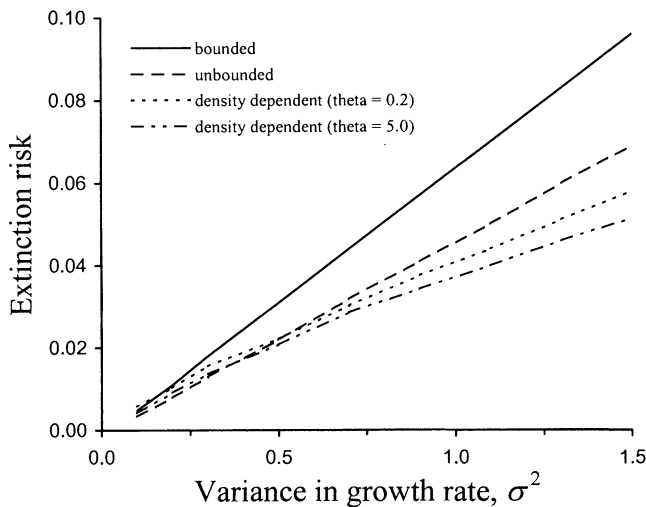
Figure 1. *The theoretical relationship between population variability, measured as variance in growth rate, and extinction risk for several population models. Extinction risk is measured as the inverse of the mean time to extinction or, for the unbounded model, as the inverse of the median time to extinction. In all cases, initial population size is 100 and average growth rate is 0.01. For the bounded diffusion model, carrying capacity is 100.*

A positive relationship between PV and ER was also inferred from the original analysis of data on 355 small populations of 100 bird species on 16 British islands (Pimm et al. 1988). Regression analysis revealed a significantly positive slope for the relationship between the CV of abundance of pairs of birds (dependent variable) and residuals (independent variable), where the residuals were obtained from a regression of abundance (dependent variable) on the corrected risk of extinction (independent variable). The risk of extinction was calculated as the inverse of the average time to extinction for all populations within a species, and the corrected risk of extinction was estimated as this quantity raised to the $1/N$ power, where N is the average abundance. These transformations were required to overcome the heteroscedasticity of the untransformed data (Pimm et al. 1988). The analysis and interpretation were challenged by a subsequent analysis, however, which suggested a weak relationship between PV and ER ($r^2 = 0.045, p = 0.095$; Tracy & George 1992). This dispute involved differing judgements about which variables to include, how to transform them, and how to assign statistical significance (Tracy & George 1992, 1993; Diamond & Pimm 1993; see also Haila & Hanski 1993; Rosenzweig & Clark 1994).

The analysis of data for several species of spiders (*Metepeira datona, Argiope argentata, Gasteracantha cancriformis,* and *Eustala cazieri*) on islets in the Bahamas superficially suggests a negative relationship between
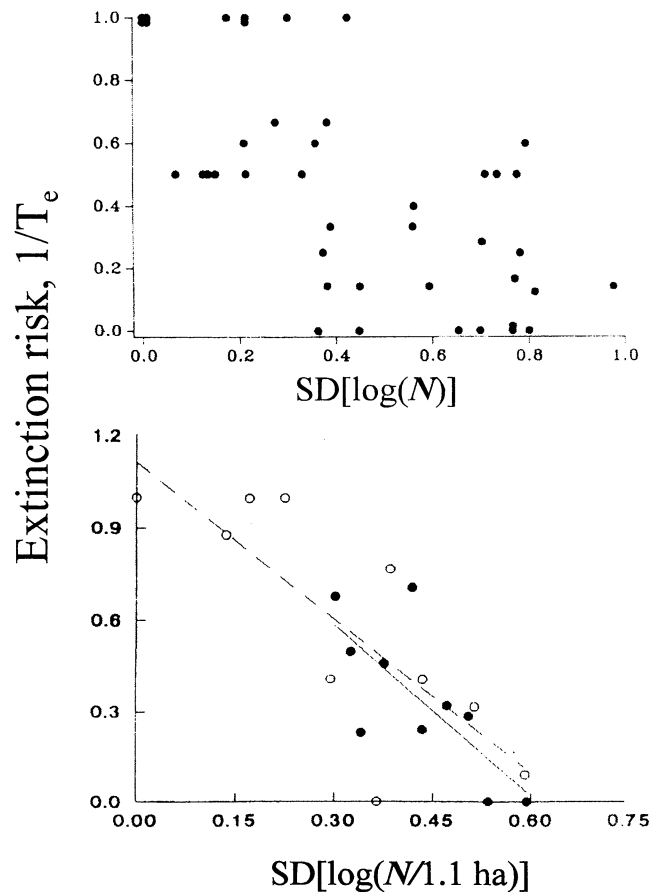

Figure 2. *Relationship between population variability (PV) and extinction rate (ER) for islet populations of orb spiders (upper panel; adapted from Schoener & Spiller 1992) and subpopulations (within a metapopulation) of several small mammalian species (lower panel; adapted from Lima et al. 1996). Points where PV = 0 and ER = 1 represent a statistical artifact because when ER = 1.0, estimates of PV are based on a single count and PV is necessarily zero. This underestimation of underlying variability, which is especially strong for populations with short persistence, is the basis for spuriously negative measured relationships between PV and ER.*

PV and ER (measured as $1/T_e$; Schoener 1991; Schoener & Spiller 1992; Fig. 2). Population variability was estimated according to two basic measures: standard deviation of log-transformed population size (σ_n) and coefficient of variation in population size (CV) (see Table 1 in Schoener and Spiller [1992]). These measures were calculated for data, both untransformed and transformed (e.g., counts of zero excluded, one added to each count). The relationship between PV and ER was either negative or nonsignificant for six of the seven PV metrics. The exception was the CV with counts of zero included. A positive relationship would be hard to interpret, however,

Table 1.   Correlation coefficients for the relationship between standard deviation in log-transformed population size (σ_n) and extinction risk (ER) as a function of the maximum ER (i.e., inverse of minimum observed time to extinction [T_e]) permitted in the correlation.[a]

Max. ER	Min. T_e	Full data set[b]		Truncated data set[c]	
		correlation coefficient	power[d]	correlation coefficient	power[d]
1.000	1	−0.07 (5000)	0.20	−0.30 (4268)	0.03
0.500	2	0.27 (4783)	0.53	0.02 (4118)	0.10
0.333	3	0.41 (4410)	0.81	0.25 (3841)	0.39
0.250	4	0.46 (4009)	0.86	0.34 (3565)	0.65
0.200	5	0.47 (3608)	0.87	0.40 (3293)	0.66
0.167	6	0.52 (3248)	0.88	0.47 (3011)	0.76
0.143	7	0.53 (2936)	0.89	0.50 (2771)	0.80
0.125	8	0.54 (2638)	0.90	0.52 (2509)	0.84
0.111	9	0.55 (2367)	0.92	0.54 (2282)	0.89
0.100	10	0.56 (2150)	0.96	0.55 (2085)	0.92

[a]*Parenthetical numerals are sample sizes (i.e., number of simulations).*

[b]*Complete set of 5000 bivariate data points.*

[c]*A subset in which data with realized values of population variability (σ_n) of >1 are excluded.*

[d]*Proportion of 10,000 bootstrap samples that resulted in a significantly positive correlation coefficient (i.e., probability of rejecting the null hypothesis when false), each bootstrap sample representing a correlation coefficient calculated from 40 data points drawn at random from either the full or the truncated data set.*

because this metric estimates the variability of population processes even when the population is extinct (Gaston & McArdle 1994). Similarly, a negative relationship was observed between PV (σ_d, where d is a time series of log-transformed density estimates) and ER for subpopulations of five Neotropical small-mammal species (Lima et al. 1996; our Fig. 2).

Of six published data sets used to test the predicted positive relationship between PV and ER—*Daphnia* spp., Panamanian birds, British birds, *Drosophila* spp., orb spiders, and small mammals—only one appears to provide unequivocal support (i.e., Karr 1982). Experimental populations of *Daphnia* spp. have yielded mixed results, suggesting that the effect of PV on ER may be inconsequential under some conditions. Given the controversy over data analysis, the British bird data provide equivocal evidence. By contrast, the data sets for spiders and small mammals provide superficially compelling evidence for a negative relationship between PV and ER (but see Pimm [1993] for a critique of Schoener & Spiller [1992]). Studies of wild butterfly populations (Pollard & Yates 1992) and laboratory populations of *Drosophila* spp. (Forney & Gilpin 1989) have also considered the role of PV and ER. Neither study was designed to isolate the effect of PV, however, so any inferences about its effect on EV would be dubious. Thus, the weight of the evidence as currently interpreted fails to support the prediction that increased PV leads to increased ER.
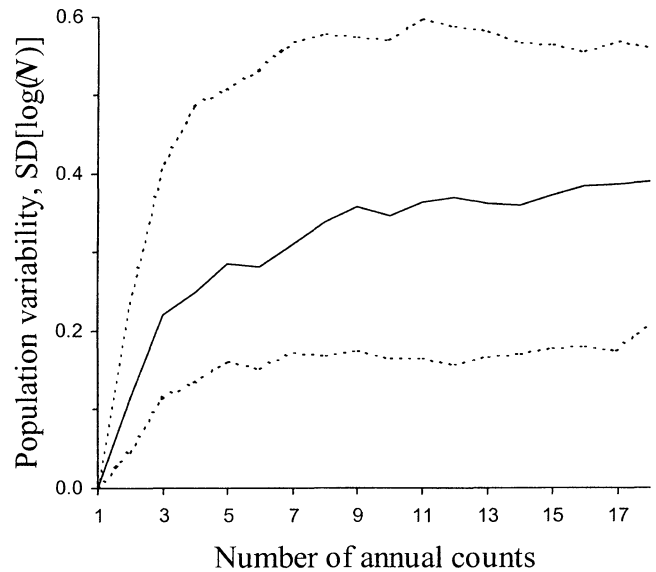
Figure 3. Relationship between length of time series and observed population variability for 48 empirical time series from naturally regulated populations representing a variety of taxa (for further description of data set, see Vucetich & Waite 1998). The solid curve represents the median, and the dotted curves represent the first and third quartiles. The upper limit of the x-axis is 18 because the shortest time series comprised 18 annual counts.

Statistical Considerations

Estimates of PV tend to increase the longer a population is observed (Lawton 1988; Pimm & Redfearn 1988; Ariño & Pimm 1995; Fig. 3). Consequently, PV estimates based on few observations (or many observations during a short time span) tend to be underestimates (see also Ludwig 1999). If highly variable populations are in fact especially vulnerable to extinction, then they may go extinct so quickly that PV would be underestimated. In the extreme, consider populations where observed ER = 1. Such populations go extinct after a single count and thus PV = 0. More generally, because PV tends to be underestimated for short time series, this bias is to be expected whenever ER is relatively high. This bias is evident in the data sets for spiders and small mammals (Fig. 2). For example, the small cluster of points in the upper left corner of the upper panel represents populations for which PV ≈ 0 and ER ≈ 1 (for additional examples see Schoener & Spiller 1992). Likewise, populations for which ER = 0.5 caused underestimation of PV because extinction occurred after just two counts. Owing to this bias, the observed relationship between PV and ER may be statistically nonsignificant or even negative, despite an underlying positive relationship. Recognizing that the rate of increase in PV decelerates with increasing length of a time series (Fig. 3), we promote the restriction of

analyses to data for which PV has been estimated adequately (i.e., low ER).

This bias was first recognized by Pimm (1993:46), who stated that a "high extinction rate restricts variability and progressively so at lower [population] densities." Pimm indicated that the bias can be overcome by restricting analysis to populations whose average size exceeds some threshold. Specifically, he observed that the standard deviation of log-transformed population size (σ_n) for any population that goes extinct after just two counts must be $\leq x\sqrt{2}$, where x is the average σ_n. Based on this criterion and the observation that nearly all populations exhibit $\sigma_n < 1.3$ (Pimm 1991), he suggested that an average population size of eight $(= 10^{an/\sqrt{2}} = 10^{1.3/\sqrt{2}})$ would be an appropriate threshold. In support of this recommendation, the correlation between PV and ER is slightly positive for the spider data when analysis is restricted accordingly (Schoener & Spiller 1992; Pimm 1993). We show, however, that this threshold is inadequate. We also show that although average population size and the time to extinction are tightly correlated, time to extinction is a more appropriate criterion than average population size. Our contribution is meant to refine Pimm's (1993) insight.

This refinement is needed for several reasons. First, because the maximum value of σ_n is typically <0.5 for most vertebrate species (e.g., Fig. 3.1 in Pimm 1991), the minimum threshold for such populations is 2.3 $(= 10^{0.5/\sqrt{2}})$ individuals. Nevertheless, populations with an average size below this threshold would rarely be observed, so, according to Pimm's criterion, biased results would rarely be a concern. To the contrary, most of the small-mammal populations represented in Fig. 2 experienced high ER, which probably caused underestimation of PV. These data illustrate a second reason for refining Pimm's (1993) insight: restrictions based on minimal population size do not apply to data expressed in terms of population density. A third reason for refining the insight is to draw attention to it. According to the *Index of Scientific Information*, Pimm's (1993) paper has been cited just five times to date, whereas Schoener and Spiller's (1992) paper has been cited 41 times and generally uncritically. Thus, it seems clear that many workers in the field are unfamiliar with the statistical concerns initially voiced by Pimm (1993).

Methods and Results

Simulations

We observed the relationship between PV and ER based on 5000 simulated trajectories. In doing so, we explored the potential for the bias described above to obscure a positive relationship, and we developed criteria for the suitability of data for testing the relationship. Trajectories were governed by a random walk (Foley 1994): $n_t =$

$n_{t-1} + r_t$, where n_t is the log-transformed population size at time t, r_t is the log-transformed growth rate (selected randomly from a normal distribution with mean 0.01 and variance, σ_r^2), and n_t is limited by a reflecting boundary set at 10, which corresponds roughly to the typical size of populations of orb spiders (Schoener & Spiller 1992) and British island birds (Pimm et al. 1988). In our simulations, σ_r^2 took values of 0.04, 0.06,..., 3.0. This range represents values commonly observed in nature (Pimm 1991; Schoener & Spiller 1992; Vucetich & Waite 1998, 1999, 2000). For each value of σ_r^2, we simulated "replicate" populations. For all simulations, $n_o =$ 10. For each simulated population, we observed the extinction risk (measured as $1/T_e$) and population variability (measured as σ_n) directly from the trajectory. Because empirical studies traditionally express PV as variability in population size (e.g., Fig. 2), we used σ_n to facilitate direct comparison. By contrast, population models traditionally express PV as σ_r^2 and thus predict a positive relationship specifically between σ_r^2 and ER. Nevertheless, our use of σ_n is justified because $\log(\sigma_n)$
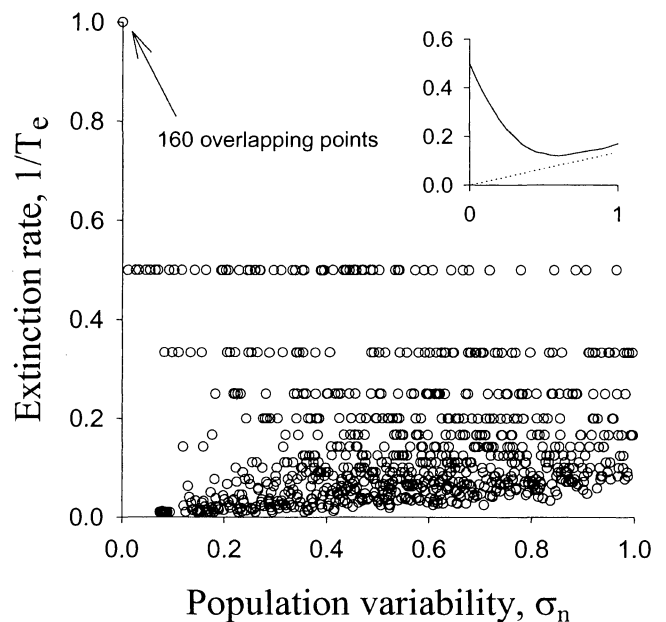

Figure 4. The relationship between population variability (PV) and extinction rate (ER) for 5000 simulated populations. Population variability is the standard deviation in log-transformed population size (σ_n) calculated from each simulated trajectory. Extinction rate is the inverse of the time to extinction (T_e). Notice the cluster of points for PV = 0 and ER = 1 (as in Fig. 2). The correlation coefficient for this data set is −0.18. The inset shows the predicted positive relationship between PV and ER (predicted from equation 8 of Foley 1994), and a smoothing spline of the simulated data illustrates the observed negative relationship between PV and ER for populations with relatively small PV.

and $\log(\sigma_r^2)$ are strongly positively correlated $(r^2 = 0.79,\ n = 138$ animal population time series; data available from authors upon request; Vucetich & Waite 1999).

The simulated relationship between PV and ER resembled empirical observations relating PV and ER (compare Figs. 2 & 4). For example, a cluster of points occurred in the upper left corner of both graphs, where PV = 0 and ER = 1. Also, numerous points for ER = 0.5 were shifted to the left. For these points, σ_n was calculated from only two population counts and was thereby typically underestimated. Observations where ER = 1 and PV > 0 (upper panel, Fig. 2) superficially represent important deviations from the similarities between Figs. 2 and 4. In all cases, these observations represent islets where extinction occurred within a survey interval and where recolonization subsequently occurred. The PV of these recolonizing populations (each exhibiting ER = 1) was inappropriately characterized as >0 (PV was calculated as variability in size among the independently founded populations for each islet). In reality, these observations also represent cases where PV = 0 and ER = 1.

In contrast to the empirical data (Fig. 2), approximately 10% of the 5000 simulated trajectories yielded $\sigma_n > 1.0$. Such levels are rarely observed in nature. For example, only two of 202 trajectories of naturally regulated animal populations exhibited $\sigma_n > 1.0$ (Pimm 1991). Thus, our simulations apparently included some unrealistically high underlying levels of variation (σ_r^2). Because knowing the exact range of underlying variation is impossible, we considered the relationship between σ_n and ER both for the full data set (5000 points) and for a truncated data set (4268 points) from which points with $\sigma_n > 1.0$ were excluded.

The correlations between σ_n and ER were −0.07 for the full simulated data set and −0.30 for the truncated data set. According to bounded diffusion theory, the process that generated the simulated data, the expected relationship between σ_r^2 and ER is a straight line with a y-intercept of zero and a positive slope (inset, Fig. 4). A spline-smoothing curve suggests, however, that ER was highest for low values of PV (inset, in Fig. 4).

We conducted bootstrap analysis on the simulated data to estimate the frequency distribution for the correlation between σ_n and ER. We created 10,000 bootstrap samples, each sample containing 10, 20, or 40 randomly chosen values. For each sample, we calculated Pearson's correlation coefficient (r) for the relationship between σ_n and ER. We then generated the frequency distributions of r. This analysis revealed that correlations were more likely to be negative than positive (Fig. 5). Moreover, because convergence on the pattern in Fig. 3 occurred with increasing sample size, the probability of observing a statistically significant, positive slope decreased with increasing sample size. (These patterns held for both the full and truncated data sets.) Specifically, the power of the correlation analysis in a sample
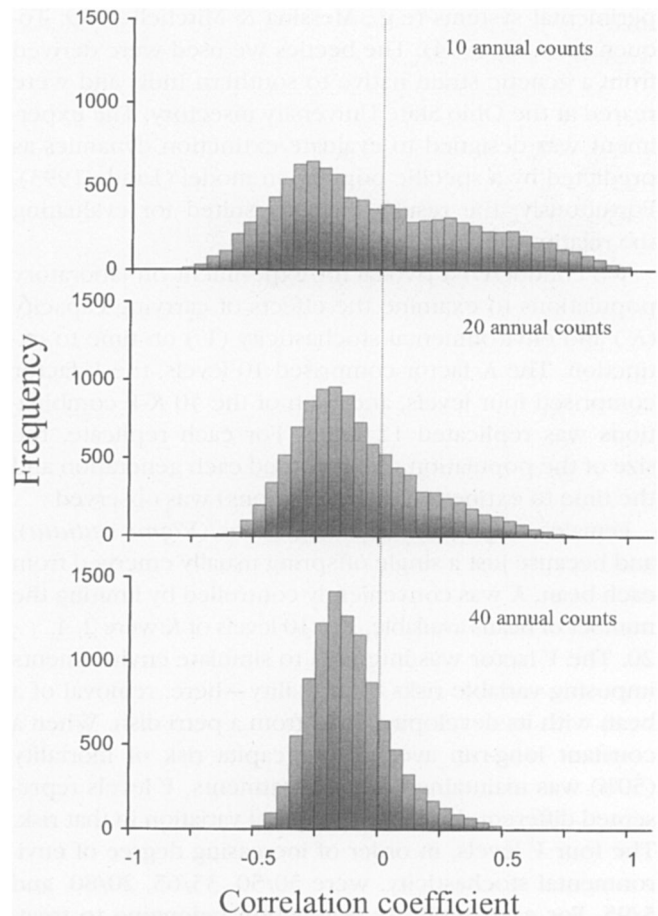
Figure 5. Estimated frequency distributions for the correlation coefficient (r) for the relationship between population variability and extinction rate, based on 10,000 bootstrap samples. Each bootstrap sample is the r calculated from 10, 20, or 40 data points drawn at random from the truncated data set. (Patterns for the full data set were similar.)

of 40 observations (Fig. 5) was probably no more than 0.20 (estimated from the full data set) and perhaps as low as 0.03 (truncated data set).

The chance of detecting a positive relationship between PV and ER, if one exists, may be improved by restricting the analysis to statistically meaningful data. Considering only those data characterized by low ER (high T_e) tended to minimize the underestimation of PV and thereby increase the power of the test for a positive relationship. Correlation and bootstrap analyses showed that the probability of detecting a positive relationship between σ_n and $1/T_e$ increased dramatically as the ER threshold for data inclusion decreased. For ER thresholds of <1/(6 years), the power approached an asymptotic maximum (Table 1).

Experimentation with *Callosobruchus* Populations

The bean beetle (*Callosobruchus maculatus*), an important pest species, has been used extensively in model ex-

perimental systems (e.g., Messina & Mitchell 1989; To-quenaga et al. 1994). The beetles we used were derived from a genetic strain native to southern India and were reared at the Ohio State University insectory. The experiment was designed to evaluate extinction dynamics as predicted by a specific population model (Lande 1993). Fortuitously, the results are well suited for evaluating the relationship between PV and ER.

We conducted a two-factor experiment on laboratory populations to examine the effects of carrying capacity (K) and environmental stochasticity (V) on time to extinction. The K factor comprised 10 levels, the V factor comprised four levels, and each of the 40 K-V combinations was replicated 12 times. For each replicate, the size of the population was recorded each generation and the time to extinction (in generations) was observed.

Females oviposited on mung beans (*Vigna radiata*), and because just a single offspring usually emerged from each bean, K was conveniently controlled by limiting the number of beans available. The 10 levels of K were 2, 4, . . ., 20. The V factor was intended to simulate environments imposing variable risks of mortality—here, removal of a bean with its developing larva from a petri dish. When a constant long-run average per capita risk of mortality (50%) was maintained across treatments, V levels represented different degrees of temporal variation in that risk. The four V levels, in order of increasing degree of environmental stochasticity, were 50/50, 35/65, 20/80, and 5/95. For each replicate population belonging to treatment X/Y (e.g., 35/65), either X or Y percent chance of mortality (35% or 65%) was applied to all larvae. The chance of larval mortality was assigned independently to each bean. With equal probability, the value X or Y was assigned randomly to each replicate in each generation.

This experiment provided strong evidence that T_e was shorter for larger V or smaller K. A Cox proportional-hazards regression analysis (Fox 1993) revealed that both V (slope $\beta = 0.32$, $p < 0.0001$) and K ($\beta = -0.12$, $p < 0.0001$) were significant predictors of T_e. Examining the effect of V for each level of K revealed two patterns. First, nine of the 10 slopes for V were positive (i.e., $\exp[\beta] > 1$). The quantity $\exp[\beta]$, when > 1, indicated the increased relative risk of extinction for a one-level increase in experimental factor V (Table 2). (Values of $\exp[\beta] < 1$ indicated a decreased relative risk.) Second, each regression coefficient increased both as the proportion of data where ER ≤ 0.2 increased and as K increased (Table 2; Fig. 6).

In addition to analyzing the effect of underlying population variability (i.e., the V factor) on T_e, we also examined the relationship between observed population variability (σ_n) and T_e across all K-V factor combinations. Four of the 10 Cox regression coefficients were negative (i.e., $\exp[\beta] < 1$), and only one indicated a significant positive relationship (Table 2). Spearman's rank correlation coefficients (r_s) indicated a similar pattern (Table 2; Figure 7), in which eight of 10 correlations were negative and none of the 10 was significantly positive. Thus, consistent with our simulation results, the measured relationship between population variability and extinction risk was typically negative, despite an underlying positive relationship.

Reanalysis of British Island Bird Data

A positive relationship between PV and ER, if one exists, should be detectable for British island bird populations

Table 2. Cox regression results for the relationship between population variability and extinction risk (ER = inverse of time to extinction) in laboratory populations of *Callosobruchus maculatus* for which the dependent variable is either the underlying or the observed population variability.[a]

K	Proportion of data for which ER ≤ 0.20	Underlying variability[b] exp(β)[d]	Observed variability[c] exp(β)[d]	r_s (p)[e]
2	0.00	0.83 (0.210)	0.02 (0.005)	−0.71 (0.000)
4	0.25	1.33 (0.029)	0.05 (0.017)	−0.17 (0.248)
6	0.40	1.02 (0.870)	1.73 (0.590)	−0.11 (0.468)
8	0.10	1.38 (0.016)	0.63 (0.065)	−0.27 (0.063)
10	0.25	1.61 (0.002)	4.25 (0.180)	−0.02 (0.863)
12	0.15	1.62 (0.002)	0.43 (0.430)	−0.25 (0.082)
14	0.23	1.65 (0.000)	3.15 (0.230)	−0.03 (0.847)
16	0.29	1.58 (0.004)	2.75 (0.340)	−0.03 (0.834)
18	0.38	1.94 (0.000)	3.19 (0.250)	0.01 (0.960)
20	0.65	1.85 (0.000)	16.20 (0.007)	0.17 (0.240)

[a] *Two-tailed p values are in parentheses.*

[b] *Analyses in which time to extinction (T_e) is the dependent variable and the underlying population variability (i.e., V, the four experimental levels of environmental stochasticity) is the independent variable.*

[c] *Analyses in which T_e is the dependent variable and the observed population variability for each replicate (measured as σ_n) across experimental treatments is the independent variable.*

[d] *The relative per-generation risk of extinction for each increase in experimental treatment for population variability, as estimated by Cox regression, is given by $\exp(\beta)$.*

[e] *Spearman's rank correlation (r_s) between σ_n and ER for each replicate population is shown.*
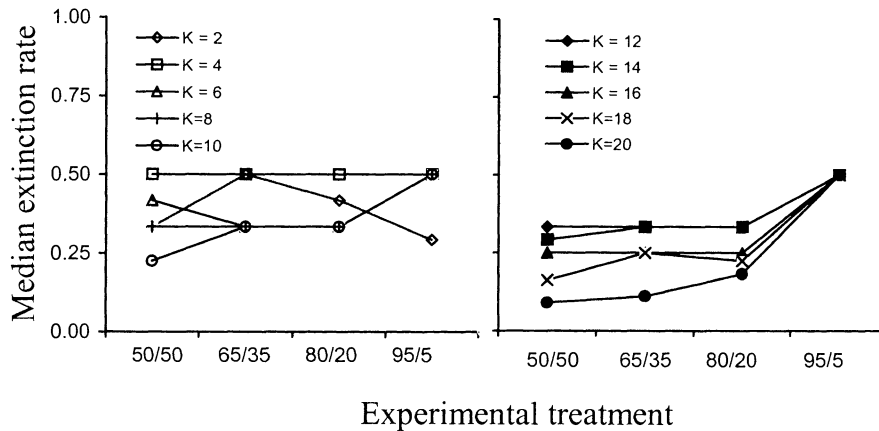
Figure 6. Experimental treatments of environmental stochasticity (V) and their effect on the median extinction risk $(1/T_e)$ for laboratory populations of C. maculatus with various carrying capacities (K). Each median is based on 12 replicate populations. The V was manipulated by varying mortality rates.

(Pimm et al. 1988), considering that 97% of the (114) PV estimates were based on >6 years of data (i.e., ER threshold <1/6). Nevertheless, analyses to date have provided controversial findings. The analysis by Pimm et al. (1988) suggests a positive relationship, but Tracy and George (1992) used the same statistical procedure on the same data and obtained a nonsignificant result (see empirical relationships). Tracy and George then performed a putatively more appropriate analysis. Using $\log(T_e)$ as the independent variable in a Cox proportional-hazards regression model, they failed to detect a significant relationship between PV and ER (but see Diamond & Pimm 1993). A resolution of this debate over analysis and interpretation would be valuable, especially because this data set represents one of the best available for examining PV-ER relationships.

We used an appropriate method of analysis and present a presumably sound interpretation. Although Cox regression is an appropriate model, transforming T_e with a logarithm function (Tracy & George 1992) is unnecessary and inappropriate. Therefore, we performed Cox regression on untransformed data (Appendix in Pimm et al. 1988), with T_e as the dependent variable and with number of pairs of birds, coefficient of variation in number of pairs (CV), and body size as independent variables. In contrast to the analysis by Tracy and George (1992) and the conclusions of Pimm et al. (1988), we found that body size ($p = 0.22$) was not a significant predictor of T_e (but for discussion of potentially complex interactions between body size and other ecological variables, see Tracy & George 1992). More important, our analysis showed that both the number of pairs ($\beta = -0.49, p = 0.0001$) and the CV ($\beta = 2.54, p = 0.03$) were significant predictors of T_e. Extinction risk was thus negatively associated with population size and positively associated with variability in population size.

Population Variability and Quasiextinction Risk

Count data for 48 naturally regulated animal populations indicate a strong positive relationship between σ_n and

time to quasiextinction (T_{qe}). Each population is represented by, and each estimate of σ_n is based on, at least 18 annual population estimates. The sample represents a variety of taxa (24 mammalian, 6 avian, and 18 invertebrate species) and spans the range of population variability observed in nature (Vucetich et al. 1997). None of the 48 populations went extinct during the period of observation. Therefore, we operationally defined T_{qe} as the time to first decline to <10% of median population size. This definition has several desirable properties. First, we expected T_{qe} to be independent of population size. Second, in the context of conservation, quasiextinction is often more relevant than actual extinction (Burgman et al. 1993). Finally, defining T_{qe} as a proportion of the median rather than the mean is desirable because occasional population explosions may cause the distribution of population size to be highly skewed. If so, quasiextinction might occur too frequently to be meaningful if it were defined as time to the first decline to 10% of the mean population size. Of the 48 populations we analyzed, 17 never exhibited quasiextinction. A Cox regression analysis confirmed that median population size was independent of T_{qe} ($\beta = -8.4 \times 10^{-5}, p = 0.14$) and revealed that σ_n was a significant predictor of T_{qe} ($\beta = -4.65, p = 3.5 \times 10^{-11}$). Thus, quasiextinction risk was higher for populations that were more variable (see also Ludwig 1999).

Discussion

Standard population viability models predict increased extinction risk with increased population viability (Fig. 1), yet some published empirical studies have reported a negative relationship between PV and ER (Schoener 1991; Schoener & Spiller 1992; Lima et al. 1996). Through simulation, we have shown that negative-measured relationships may be the byproduct of a statistical artifact. The mismeasurement of the relationship between PV and ER arises from underestimating PV in populations with short persistence (Figs. 2 & 3). This bias
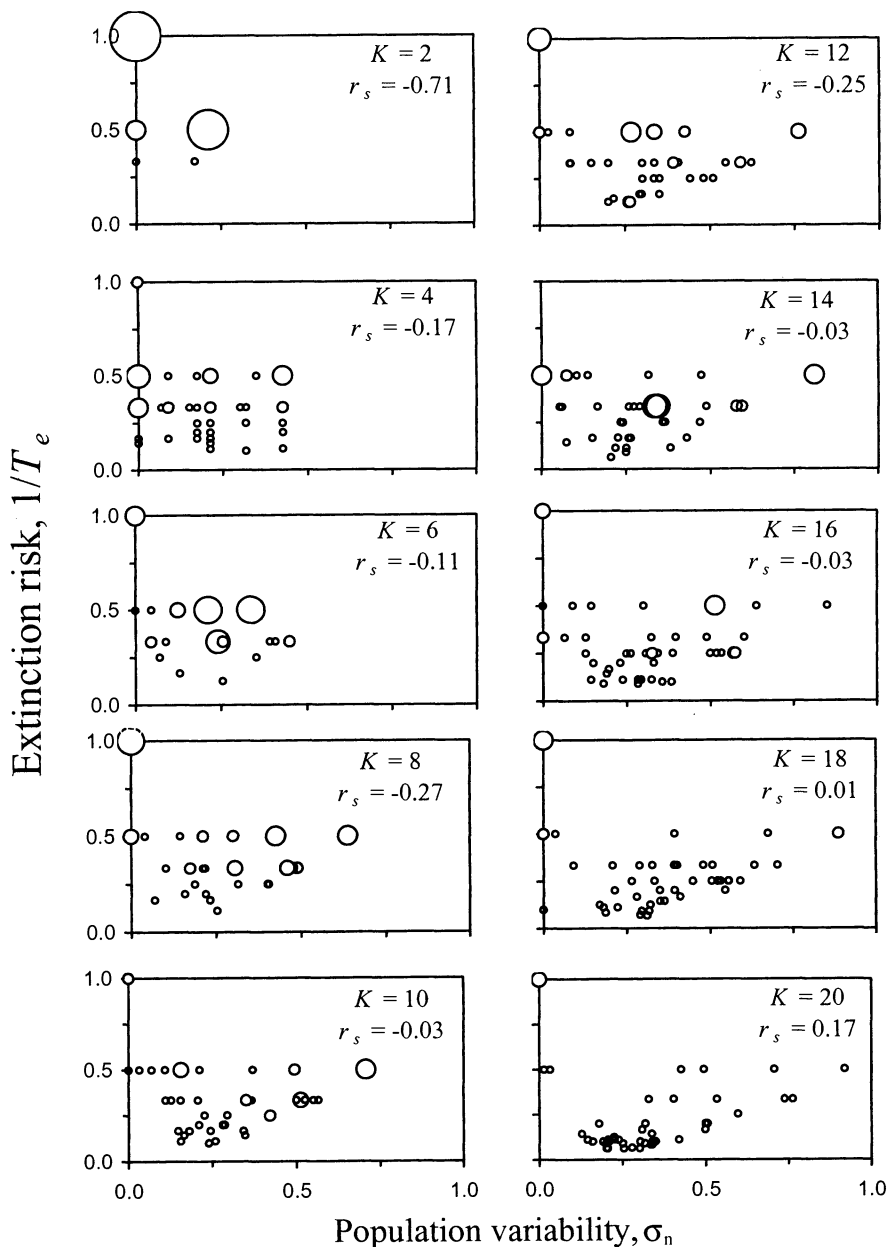
Figure 7. Observed correlations between population variability (σ_n) and extinction risk ($1/T_e$) for laboratory populations of C. maculatus with various carrying capacities (K). Spearman's rank correlation coefficient (r_s) is given for each K. The size of each symbol indicates the number of overlapping data points.

may produce a negative-measured relationship between PV and ER despite an underlying positive relationship (Figs. 4 & 5). For a meaningful test, data with high values of ER should be excluded from analysis (Table 1). Given this guideline, the controversial data set on extinction in British island birds should permit a meaningful test. Using a Cox regression analysis, we found support for the predicted positive relationship between PV and ER. Likewise, our experimental data on extinction in *C. maculatus* populations provide clear support for this prediction (Table 2; Figs. 6 & 7), and our analysis of data on 48 naturally regulated animal populations reveal a positive relationship between PV and quasiextinction risk. Overall, our analyses have explained and eliminated

previous discrepancies between theory and data. In confronting the theory with statistically meaningful data (sensu Hilborn & Mangel 1997), we have provided strong evidence that population variability is an important contributor to extinction risk.

Pimm (1993) recognized that a high extinction rate imposes low variability on small populations. In fact, he suggests that count data for populations whose average size exceeds eight should be useful for testing the relationship between PV and ER. Because N and T_e covary (equivalently, K and ER; see Fig. 6), our recommendation to limit count data to those with small ER is deceptively congruent with Pimm's recommendation to limit count data to those with large N. Our analysis of experi-

mental data from *C. maculatus* populations confirmed that positive correlations between PV and ER are more likely to arise in data sets with larger K (Figs. 6 & 7) and smaller ER (Table 2). Simulated bivariate data (σ_n and T_e), however, indicated that a negative-measured correlation is likely for populations with average sizes up to 15, even though the underlying relationship is positive (result not shown). According to Pimm's criterion, meaningful analysis of bird populations (σ_n typically <0.5) could be accomplished simply by excluding from the data set those populations whose average size is ≤ 2 (see Statistical Considerations). Clearly, this is no restriction at all. Regardless of the average population size, if the British island bird data had consisted of numerous populations that went extinct within 5 years, the detection of a positive relationship between PV and ER would have been unlikely.

The refinement of population viability analysis depends, in part, on meaningful evaluation of fundamental predictions derived from the theory of extinction risk. One such prediction, the focus of this paper, is that extinction risk increases with increased population variability. Obtaining empirical data to test this prediction has proven difficult. Performing proper analysis of such data has proven difficult as well. We have shown that count data will often be unsuitable for testing the prediction. We have provided a general guideline for the proper analysis of count data: exclude data with large ER. Unfortunately, the availability of appropriate data is limited. The recognition that a short time series of population counts tends to yield misleading evidence for the influence of population variability on extinction risk reinforces the common plea for additional long-term population studies. Given the current rarity of long-term data sets, however, we also promote experimentation as useful for evaluating the relationship between population variability and extinction risk. Beyond conducting proper analysis of count data, future efforts to refine our understanding of this fundamental relationship should include experimental tests using a variety of systems.

Acknowledgments

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