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REPORT

Characterizing population vulnerability for 758 species

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Abstract

We investigate relationships between life history traits and the character of population dynamics as revealed by time series data. Our classification of time series is according to 'extinction category,' where we identify three classes of populations: (i) weakly varying populations with such high growth rates that long-term persistence is likely (unless some extreme catastrophe occurs); (ii) populations with such low growth rates that average population size must be large to buffer them against extinction in a variable environment; and (iii) highly variable populations that fluctuate so dramatically that dispersal or some other refuge mechanism is likely to be key to their avoidance of extinction. Using 1941 time series representing 758 species from the Global Population Dynamics Database, we find that, depending on the form of density dependence one assumes, between 46 and 90% of species exhibit dynamics that are so variable that even large carrying capacities could not buffer them against extinction on a 100-year time horizon. The fact that such a large proportion of population dynamics are so locally variable vindicates the growing realization that dispersal, habitat connectedness, and large-scale processes are key to local persistence. Furthermore, for mammals, simply by knowing body size, age at first reproduction, and average number of offspring we could correctly predict extinction categories for 83% of species (60 of 72).

Keywords

Biodiversity database, extinction risk, life history traits, population viability analysis, variation thresholds.

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INTRODUCTION

Population viability analyses are now a standard tool in conservation biology, with goals ranging from providing detailed guidance on management actions (Crouse *et al.* 1987) to simply characterizing the degree of risk faced by populations (Morris *et al.* 1999). Most such evaluations of extinction risk emphasize the importance of stochasticity. For example, Foley (1994) outlines methods for predicting population lifetimes based on knowledge of carrying capacity and environmental stochasticity. However, recent experimental investigations also suggest an unrecognized important role for nonlinear dynamics (Belovsky *et al.* 1999). Nevertheless, for most species and situations we lack the data required for even the crudest PVAs, let alone the detailed datasets advocated for long-term planning (Morris *et al.* 1999; Ruckelshaus *et al.*, in press). Indeed, a recent synthesis found only 21 datasets (19 species) with sufficient data for full PVA assessments (Brook *et al.* 2000). Yet, as we move towards large-scale conservation planning, an urgent need exists to at least categorize species with respect to extinction risk, so that, among other things, we might know how many "representations" or populations of each species might be desirable within a nature reserve system. Such categorization is a key goal of this effort. Rather than enumerate the degree of risk faced by particular populations or even distinguish between "secure" and "at risk" populations, we seek to assess the qualitative character of risks faced by suites of different populations. Such assessment is a component of conservation planning, long before species become federally listed or meet some other criterion reflecting critical risk. In some cases, such as ecoregional planning conducted by The Nature Conservancy (Groves *et al.* 2000; The Nature Conservancy 2000), the most detailed data available constitute time series of population counts, and metrics derived from such time series are used to gauge relative risk among taxa.

When we lack data for finely tuned appraisals of population vulnerability, one possible shortcut is the use of basic information about life history and taxonomic group as a rough indicator of the class of population dynamics and hence extinction risk faced by data-poor species. Beginning with *r*- and *K*-selection theory (Elton 1958; MacArthur & Wilson 1967; Pianka 1970) ecologists have pursued the notion that species life history attributes (e.g. body size, offspring number) are related to aspects of population dynamics such as colonization ability or extinction risk (Terborgh 1974; Diamond 1975; Pimm *et al.* 1988; Gaston & Blackburn 1995; Foufopolous & Ives 1999). Others (e.g. Boyce 1984) have criticized these theories as unduly simplistic. To evaluate empirically whether such a shortcut is possible, we used the Global Population Dynamics Database (hereafter GPDD; Kendall *et al.* 1998; NERC 1999) and analysed the dynamic character of collected time series of population dynamics for each of four taxonomic groups: mammals, birds, marine fish, and lepidopterans.

MATERIALS, METHODS, AND RESULTS

Our approach relies upon characterizing the temporal dynamics of diverse species relative to those of theoretical populations with generic characteristics. Building on previous analyses of extinction risk (Dennis *et al.* 1991; Lande 1993; Mangel & Tier 1993; Foley 1994), Fagan *et al.* (1999) used an array of population growth models to develop relationships between population growth rate at low densities (*r*), the degree of environmental variability (σ) experienced by the population, the population's carrying capacity (*K*), and risk of extinction over a 100-year time period. Although general relationships among these features are known from diffusion approximations of population processes (Dennis *et al.* 1991; Lande 1993), exhaustive numerical work was necessary to define contours of risk for commonly used ecological models (Fagan *et al.* 1999). Here, we emphasize two such models: the Ricker model and exponential growth to a ceiling. Together, these models bracket a wide range of density feedbacks that could occur in real populations, ranging from overcompensatory density dependence (Ricker) to dynamics that are density-independent for all population densities below carrying capacity (ceiling).

Using a process error formulation, the Ricker model is written

$$\frac{N_{t+1}}{N_t} = e^{r(j-N_t/k)} + \text{Error}$$

where N_t is the population size at time *t*, *r* is the intrinsic rate of increase, and *K* is the carrying capacity. We quantify environmental variability using σ, the standard deviation of normally distributed process error [consequently *Error* ∼ N(0, σ)]. Likewise, the ceiling model with process error can be written

$$\frac{N_{t+1}}{N_t} = e^{r} + \text{Error} \qquad \text{for all } N_t < K$$

$$\frac{N_{t+1}}{N_t} = \frac{K}{N_t} + \text{Error} \qquad \text{for all } N_t \geqslant K$$

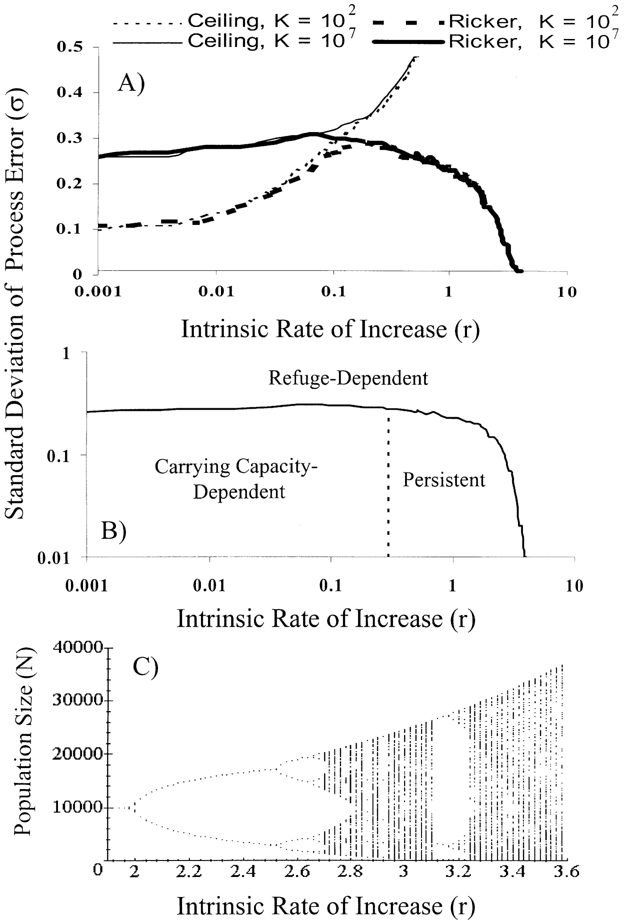


Figure 1 Variation thresholds provide profiles of extinction risk for classical models of population dynamics. Variation thresholds (A), which represent the maximum value of σthat still permits a population with a specified model structure and parameter values to persist ($N_t \geqslant 1$) over a specified time horizon in a certain percentage of runs, are here plotted for 5% chance of extinction in 100 years (based on 1000 replicate simulations). To compare models, we conservatively interpret cessation of *K*-dependence at $r = 0.3$, thereby delineating three categories of extinction risk (shown in B for the Ricker model). In **C**, we plot a bifurcation diagram for the Ricker model ($K = 10\,000$) showing that for fast growing populations, density dependence (specifically overcompensatory dynamics) can generate intrinsic population variability which may be compounded by process error. Density dependence also underlies the qualitative differences between variation thresholds from the ceiling vs. Ricker models in A.

For both these population models (and other similarly structured models, e.g. Hassell, Beverton–Holt), given any combination of r and K, one can identify a "variation threshold" (quantified via σ) above which exists (for example) a greater than 5% chance of going extinct in 100 years (Fig. 1A; Fagan *et al.* 1999). Variation thresholds in life history space (i.e. "r" vs. "K") delineate three classes of species (Fig. 1B). First, we categorize "persistent" species as those that experience such low variability relative to their growth rates that extinction is highly unlikely regardless of carrying capacity. Other species experience such high variability relative to growth rate that extinction seems likely, again regardless of carrying capacity. These species we call "refuge-dependent" because, for them, long-term persistence may hinge upon various kinds of dynamic refugia, such as dispersal that can rescue local populations from extinction (Brown & Kodric-Brown 1977; Hanski 1999). Finally, for our third category of species, habitat size (as reflected by carrying capacity) does make a difference for species with both low growth rates and low variability. In such "carrying capacity-dependent" species, larger populations are better able to withstand higher levels of variability (Fagan *et al.* 1999). For species where extinction risk is not influenced markedly by carrying capacity (both persistent and refuge-dependent species), we can predict whether a single, well-mixed population is likely to be viable over a given time frame simply by knowing its approximate r and σ (Fig. 1B). For fast growing populations, density dependence (e.g. overcompensatory dynamics) can generate intrinsic population variability that may be compounded by process error (Fig. 1C). Such aspects of density dependence also underlie the qualitative differences between variation thresholds from the ceiling vs. Ricker models.

Fagan *et al.* (1999) fitted Ricker models to 15-year time series generated by stochastic simulations of Ricker and Ceiling models, and found that the best-fit Ricker parameters correctly identified the extinction category to which a given time series belonged in more than 75% of the cases for time series generated by the Ricker model. Correctly discriminating among extinction categories proved more difficult when fitting a Ricker model to time series generated by the ceiling model (because the Ricker model assumes density-dependence over a wide range in population size, whereas the ceiling model does not). The reverse pattern was also true: best-fit ceiling parameters were more effective at identifying the extinction category to which time series belonged when the time series were generated by the ceiling model (Meir and Fagan, unpublished data).

Against this theoretical backdrop, we evaluated the temporal dynamics of 1941 time series extracted from the GPDD (NERC 1999), representing 758 species from six continents and two ocean basins. We fitted both the ceiling and Ricker models to N_{t+1}/N_t transitions, and estimated the intrinsic rate of increase (r) and environmental variability (σ) using maximum likelihood techniques under the assumption of normally distributed process error (Hilborn & Mangel 1997). For example, for the Ricker model, r is given by the intercept of the line $\ln(N_{t+1}/N_t) = r - N_t/K$ and σ was estimated as $\sqrt{}(\mathrm{RSS})/(n-2)$ where n is the number of transitions in the time series and RSS is the residual sum of squares. Only time series at least 15 years in length were used; these time series had between 8 and 138 transitions (median = 18). Large σ/r ratios predispose a population to extinction, whereas small σ/r ratios indicate such high resilience relative to environmental variability that persistence is highly likely unless some unforeseen catastrophe ravages the population (Table. 1). Time series included in the database have met minimal requirements for length, completion, accuracy, and other factors, and span a wide range of species, biogeographical regions, and habitat types. We used approximately 90% of the 15 + year time series present in the database as of September 1998; the remaining 10% were not analysed because of repeated 0 counts, conspicuous typos, or because the time series showed no temporal variation and hence contained no information with respect to dynamics. If a species occurred two or more times in the database, we used its average parameter values. Many of the time series in the database represent counts of entire populations. In other cases, the time series represent estimates of population size in an investigator-defined region or habitat block. Because there is no immigration or emigration in our model, we effectively treat all time series as if they represented closed populations.

Overall, very few species in the database exhibit such low growth rates that their persistence is likely to depend on carrying capacity (Fig. 2). Assuming Ricker dynamics, only 6 out of 415 (1.4%) lepidopterans and 8 of 86 (9.3%) mammals fall into this carrying capacity dependent region. Carrying capacity appears more likely to be important for birds (26 of 166, 16%) and for marine fishes (19 of 91, 21%). A second small subset includes species falling in the persistent category, where larger growth rates and moderate variability are indicative of low risks of extinction (unless a catastrophe occurs). In contrast, a staggering majority of species, nearly 90%, fluctuated so much that, in the absence of dispersal or other refuge mechanisms, extinction would be a real possibility over a 100-year time horizon (Fig. 2). Fully 97% of lepidopteran species fall in this refuge-dependent category compared with roughly 80% of birds, 75% of fish, and 88% of mammals. In fact, even if one uses a more stringent threshold of 95% chance of extinction in 100 years, fully

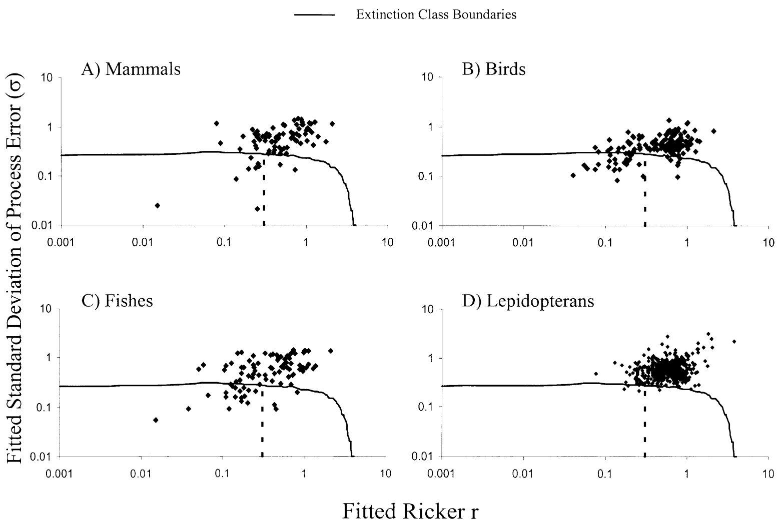


Figure 2 Observed vulnerability profiles from time series for 758 species. Data from Table 1.

Table 1 Key extinction risk parameters for time series from the Global Population Dynamics Database (NERC 1999), assuming Ricker dynamics

	Number of species	σ				σ/*r*			
		Mean	Median	Range	±95% CI	Mean	Median	Range	±95% CI
Mammals	86	0.63	0.61	0.02–147	0.07	1.50	1.15	0.09–14.49	0.35
Birds	166	0.44	0.42	0.08–1.34	0.03	1.16	0.92	0.13–5.13	0.13
Fishes	91	0.62	0.60	0.05–1.44	0.08	2.04	1.36	0.20–12.57	0.43
Lepidopterans	415	0.64	0.57	0.22–3.19	0.03	1.19	1.03	0.20–6.17	0.07

53% of all species (including 60% lepidopterans but only 29% of birds) exhibited sufficient variability to be labelled as refuge-dependent.

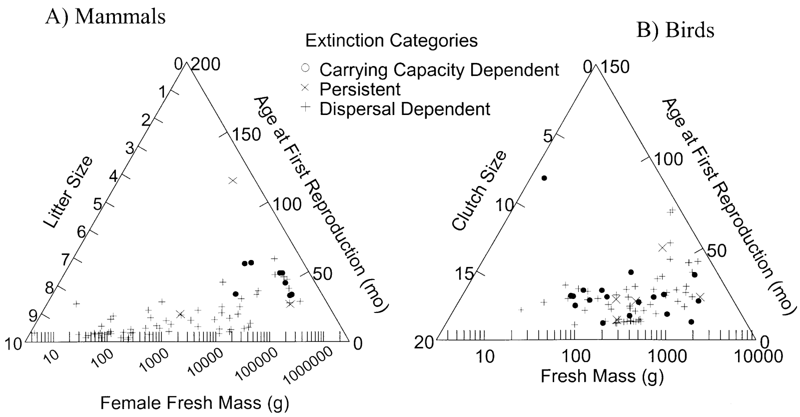
These results are generally robust to our assumptions about population dynamics. For example, if we assume ceiling rather than Ricker dynamics, the percentages of species in different "vulnerability categories" do shift; however, 46% of all of the species analysed still exhibit "refuge-dependent dynamics" (including 53% of mammals, 55% of fish, and 51% of lepidopterans, but only 25% of birds). Hence, our conclusion regarding the magnitude of environmental variability relative to population growth and its implications for local persistence is in many ways robust to the model applied to the data.

To evaluate whether the vulnerability classifications we obtained for species via time series analyses could be anticipated using life history traits, we compiled suites of life history descriptors for each of 72 mammal and 80 bird species in the GPDD. Specifically, we obtained published estimates of adult fresh mass, mean number of offspring, and age at first reproduction (Nowak 1991; Dunning 1993; Hayssen *et al.* 1993; Silva & Downing 1995). Combined in a linear discriminant function analysis, these three traits correctly predicted the Ricker-derived extinction category for 83% of mammal species (Fig. 3A; discriminant function analysis; $P < 0.01$), including all eight carrying capacity-dependent species (e.g. African lion *Panthera leo*, caribou *Rangifer tarandus*, red deer *Cervus elaphus*). Under the assumption of ceiling dynamics, predictability of carrying capacity-dependent mammals remained high (9 of 10 correct), though it proved difficult to use these life history traits to identify persistent species, yielding an overall classification success rate of 50%. Linear discriminant function analysis did a poor job overall of classifying birds with respect to extinction category (at best only 49% of the species were correctly classified) (Fig. 3B; discriminant function analysis; N.S.).

DISCUSSION

From a conservation perspective, species in the carrying capacity-dependent region of our variation threshold plots (Fig. 2) would be especially benefited by large reserves. This argument, that certain species may rely on high carrying capacity (or large reserves) to mitigate extinction risk, derives from an inspection of population dynamics (Fig. 1A). However, it may well be that large reserves confer an additional benefit, one not detected by our

Figure 3 Ternary diagrams delineating the predictive relationship between species' life history attributes and extinction risk profiles assuming Ricker dynamics. Extinction category for each species is derived from the position of points in Fig. 2. Life history attributes were taken from the literature.



analyses. Specifically, large reserves may reduce environmental variability because of a spatial 'averaging process.' It would be interesting to use the approaches we have adopted to investigate whether process error declines as the area inhabited by populations increases. Smallwood & Schonewald (1996) have already quantified such scale-dependence for the average densities of terrestrial mammalian carnivores; it is perhaps not unreasonable to expect scale-dependence in the variability of those densities as well.

Conversely, the pre-eminence of the refuge-dependent category under both density-dependent and density-independent dynamics implies that, for most species, persistence will depend crucially upon some kind of risk-mitigating mechanism, such as dispersal of colonists, seed banks, or other refugia. In the context of conservation planning, establishing multiple representations of species mitigates risk by providing sources of colonists and comprises a hedge against variability even if variability cannot itself be managed (e.g. Harrison & Quinn 1989). Even though carrying capacity per se is not implicated as important for such species, a large reserve area could still contribute to conservation of "refuge-dependent species" because it may provide opportunities for dispersal among collections of animals that are somewhat uncorrelated in their dynamics (Lande *et al.* 1999). This would be especially true for species that are behaviourally reluctant to move through unsuitable habitat [such as grizzly bears, *Ursus arctos horribilis*, and mountain lions, *Felis concolor*, (e.g. Beier 1993)].

We emphasize that our point is *not* that we have confidence that most or even particular sets of the populations we examined really have a high risk of extinction. Rather, these populations, many of which are not closed, exhibit a tendency to fluctuate severely enough relative to their population growth rate that persistence is unlikely without dispersal or some other rescue mechanism. Hence if such populations were to become closed (as happens regularly through human landscape modifications), we would expect their variability to place them at risk. Some of the risk may be due to the potential for intrinsic variability in population transitions stemming from overcompensatory density dependence (Fig. 1C). However, even if one delineates extinction categories using the ceiling model, which lacks density dependence save for an upper limit on population size, roughly 50% of species still fall in the refuge dependent region of a variation threshold plot (100 years, 5% risk of extinction). Hence, whether one envisions real populations as exhibiting mostly density-dependent or mostly density-independent dynamics, variability presents a significant risk for a substantial fraction of species. For many species, spatial processes can mitigate such risk, and we need to keep this point in mind as we struggle with conservation planning.

Assuming density-dependent dynamics, we found that mammal species with high age at first reproduction and small litter sizes have extinction risks primarily dependent on their carrying capacity, whereas species with small masses and low age at first reproduction exhibit refuge-dependent dynamics (Fig. 3A). Furthermore, predictability of the identity of carrying capacity-dependent species from life history traits remained high regardless of the assumptions about density dependence. Thus for mammals it appears possible to use life history attributes to predict whether larger reserve areas are likely to be a fruitful strategy for mitigating extinction risk (as opposed to systems of many smaller reserves). In birds, such clear-cut patterns do not emerge (Fig. 3B). However, this inability to classify birds correctly on the basis of life history traits was not as problematic as it first seems. For instance, if life history attributes led a bird species to be classified as refuge-dependent (31 species were, under the Ricker model), there was a very high likelihood that these species did in fact exhibit refuge-dependent population dynamics (27 of 31, or 87% correctly classified). When birds were misclassified, it was usually because they were incorrectly assigned to the carrying capacity dependent category, whereas their observed population dynamics were far too variable too warrant this classification. Other sources of concern are that the GPDD's mixed bag of breeding bird surveys, flyover counts, and hunting records could obscure dynamic relationships. Another possibility is that patterns for birds may be evident only at finer taxonomic subdivisions than "Aves". For example, within the Piciformes (woodpeckers), the database yielded four carrying capacity-dependent and five refuge-dependent species, and life history traits were sufficient to correctly classify eight of the nine species with respect to extinction category.

Strategies of conservation and reserve design should vary depending on what type of extinction risks a species faces (Belovsky *et al.* 1999). However, for most species, even simple counts of abundance over time (from which one might judge extinction risk) are unavailable. Consequently, conservation efforts on little-studied species would be aided greatly if more easily obtainable descriptors could be used as surrogates for detailed analyses of population dynamics (Pimm *et al.* 1988; Gaston & Blackburn 1995; Foufopolous & Ives 1999). Our analyses highlight the potential utility of such proxies. Unlike previous analyses that have often emphasized the importance of body size, our results suggest that factors affecting reproductive potential (i.e. age at first reproduction, mean number of offspring) could be especially useful surrogates. Of course, life history traits are often highly intercorrelated, and it is difficult to conclude any single life history attribute is more important than another with respect to extinction risk.

There is no substitute for detailed demography, long-term monitoring, and studies of dispersal and behaviour. However, much land-use planning must proceed rapidly, and deal with hundreds of species simultaneously, many of which have never been the focus of such comprehensive studies (Groves *et al.* 2000). Our database analyses – which are intended to complement rather than replace detailed, single-species approaches like PVA – reveal two important features about population fluctuations that may be useful when facing the challenge of conservation planning with a paucity of data. First, the bulk of populations appear to fluctuate so much relative to their capacity for recovery from low densities, that refuge mechanisms, such as dispersal among populations, are likely to be key contributors to long-term persistence. This means we must develop rules of thumb for how many populations are enough and, at the same time, understand better how the spatial configuration of such populations can aid successful dispersal. Second, our findings reinforce the notion that life history traits such as reproductive potential offer some statistical predictive power with respect to the class of population dynamics species exhibit (e.g. Pimm *et al.* 1988; Saether 1997). Hopefully, as we build larger and larger databases, we will be able to generate even more refined predictors of extinction risk, in which taxonomy and life history combine to produce a portrait of 'most likely' population dynamics.

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BIOSKETCH

William F. Fagan's research includes the use of quantitative methods and database approaches to explore key issues in conservation ecology, including the numerical and spatial components of rarity and extinction risk.

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