

What are the best correlates of predicted extinction risk?

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Abstract

Direct estimates of extinction risk are frequently unavailable, so surrogate indicators are used in threatened species categorizations, but there is inadequate information on which best predict vulnerability. We compared the ability of 16 frequently-used factors to predict extinction risk for 45 vertebrate taxa. Median times to extinction were estimated using taxon-specific stochastic population models. Population size (N) and trend were clearly the best correlates of extinction risk in our data set. Stepwise multiple regression with additive and interaction terms identified N , $N \times$ trend, plus taxonomic level, number of sub-populations $\times N \times$ trend, number of offspring (O) and $N \times O$ as predictors, and explained 70% of the variation. Trend was important in large, but not in small populations. Population size is the most important data to collect for threatened species and with trend should be the major focus in endangered species categorization and state of the environment reporting.

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1. Introduction

Earth is currently experiencing a catastrophic loss of biodiversity rivaling the great extinction events in the geological record (see Leakey and Lewin, 1995; Pimm et al., 1995; Lawton and May, 1995). Consequently, we must be able to identify species that are at risk quickly and efficiently. Extinction risk of taxa can be assessed quantitatively by population viability analysis using life-history and other data (Sjögren-Gulve and Ebenhard, 2000; Beissinger and McCullough, 2002). However, for most threatened species there are insufficient data available for reliable models to be built (Coulson et al., 2001). It is not reasonable to delay risk assessment until there are sufficient data, as conservation biology is a crisis discipline where decisions must be made swiftly

(Soulé, 1985; Brook et al., 2002a). Thus, a variety of simple parameters are used frequently as indicators of extinction risk for categorizing taxa (Millsap et al., 1990; Master, 1991; IUCN, 2000; Possingham et al., 2002) and for state of the environment reporting (Saunders et al., 1998; Burgman, 2002).

Data are often incomplete even for threatened species categorization systems that use a limited range of parameters (Mace and Lande, 1991; Harding et al., 2001). For example, Lunney et al. (1996) reported that only 6% of species in New South Wales, Australia had adequate data for assessment under the procedures of Millsap et al. (1990) that were used to generate its endangered species list. Further, resources for collection of data on threatened species are typically limited (Master, 1991; Collar, 1996). Consequently, identifying reliable and easily measured indicators of risk is extremely important (Saunders et al., 1998).

Species are driven to extinction by both deterministic and stochastic factors (Frankham et al., 2002). Typically, population size for species is reduced by the human-associated deterministic threats of habitat loss, over exploitation, the impacts of introduced species and pollution. These reduce population sizes to the point

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where demographic, environmental and genetic stochasticity and catastrophes typically deliver the *coup de grâce*.

What biological parameters of species accurately indicate their likelihood of extinction and could thereby serve as a reliable and easily obtained set of indicators for assessing risk? Parameters commonly linked to extinction proneness include population size, temporal variability of population size, range size, fragmentation of range, body size, and life history specialization (Table 1). A wide range of other parameters has also been linked to extinction risk (see McKinney, 1997; Purvis et al., 2000), but less frequently than those mentioned above. However, no published analyses compare the relative ability of individual parameters to predict extinction risk across a range of taxa where risk has been estimated directly (i.e. not inferred from some other surrogate variable) as a quantitative variable, and where a broad range of parameters are assayed. The best predictors would be expected to encompass indicators of both deterministic and stochastic threats.

The aim of this study was to determine which factors are the best predictors of extinction risk. We examined the empirical relationship between 16 biological parameters assessed for 45 well-studied bird and mammal taxa and identified parameters most strongly correlated with their extinction risk. The parameters assayed were drawn from assessment systems employed by IUCN (IUCN, 2000), NatureServe (Master, 1991; Master et al., 2000), and the Florida Game and Freshwater Fish Commission (Millsap et al., 1990). These three assessment systems are internationally recognized and widely used to prioritize species conservation programs. Based on the collective expertise of these systems' creators, the biological parameters within these systems should be indicators of impending extinction. Hence, the assessment systems are filters of other parameters that are less consistently correlated with extinction risk across a broad taxonomic range (see Purvis et al., 2000).

Risk was estimated via stochastic population models. Stochastic computer models have been used to predict population dynamics for over 35 years (Levins, 1966;

Starfield and Bleloch, 1986) and are established heuristic tools in conservation biology (Shaffer, 1981; Gilpin and Soulé, 1986). Critically, Brook et al. (2000) have shown that such modeling provides an unbiased estimate of extinction risk when based on long-term (>10 years) data. While this paper generated controversy, the controversy related to species with inadequate data (Coulson et al., 2001; Reed et al., 2002), and to the precision of individual estimates of risk (Ellner et al., 2002). Brook et al. (2002a) answered the critics, while Reed et al. (2002) concluded that stochastic population models are valuable tools for examining the relative risks of extinction between taxa. Ellner et al. (2002) concluded that such models are useful heuristic tools for examining trends in extinction risk across large groups of species. Our study used taxa with adequate data and used a large group of taxa.

2. Methods

2.1. Risk factors assessed

Sixteen biological parameters were selected to encompass population numbers and trend, range and fragmentation, ecological specialization, threat/s, and susceptibility to threat/s. These parameters and their originating system are given in Table 2. The parameters values were determined for each taxon for the population for which the population viability analysis was run.

Unless stated otherwise below, each assessment parameter was employed according to the protocols prescribed by the originating system. Where there was a choice of quantitative and qualitative parameters measuring the same attribute, quantitative parameters were used as these provide a more accurate and repeatable estimate of risk than subjective assessments, and are thereby more defensible against challenge (Keith, 1998). When assessing "magnitude of threat" and "immediacy of threat", quantitative thresholds were developed from the qualitative assessment protocols of the NatureServe

Table 1
Biological parameters commonly linked to the extinction risk of taxa

Parameter	References ^a
Body size	Pimm et al., 1988; Gaston and Blackburn, 1995; McKinney, 1997; Owens and Bennett, 2000; Cardillo and Bromham, 2001; Fagan et al., 2001
Fragmentation of range	Terborgh and Winter, 1980; Angermeier, 1995; Newmark, 1996
Life history specialization	Angermeier, 1995; Foufopoulos and Ives, 1999; McKinney, 1997; Terborgh and Winter, 1980
Small population size	Terborgh and Winter, 1980; Goodman, 1987; Pimm et al., 1988; Berger, 1990; Newmark, 1994; Mace and Kershaw, 1997; McKinney, 1997; Belovsky et al., 1999; Foufopoulos and Ives, 1999
Small range size	Terborgh and Winter, 1980; Angermeier, 1995; Newmark, 1996; McKinney, 1997; Purvis et al., 2000; Manne and Pimm, 2001
Variability of population size	Pimm et al., 1988; McKinney, 1997; Belovsky et al., 1999; Vucetich et al., 2000; Fagan et al., 2001

^a McKinney (1997) canvasses a wide literature for these parameters and canvasses other parameters less commonly linked to extinction risk.

Table 2
The parameters measured for the taxa and their originating system

Parameter	Originating system ^a
Change in population size	IUCN
Ecological specialization	FG&FFC
Fluctuation in population size (CV)	IUCN
Fragmentation into sub-populations	IUCN
Generation length	IUCN
Genetic uniqueness of taxon	FG&FFC
Immediacy of threat	NS
Legal protection	FG&FFC
Magnitude of threat	NS
Minimum age at which females first reproduce	FG&FFC
Number of offspring/breeding female/year	FG&FFC
Percentage of taxon in reserve/s	NS
Population size (mature individuals)	IUCN
Range size (area of occupancy)	IUCN
Range reduction (rate of change)	IUCN
Taxonomic level	FG&FFC

^a Abbreviations: IUCN = 2000 IUCN Red List Categorisation System; FG&FFC = Florida Game and Freshwater Fish Commission's system; NS = NatureServe system.

system (Master, 1991; Master et al., 2000). “Immediacy of threat” thresholds “high/moderate/low” was converted to the probability of occurrence per year identified in the information for the most severe threat identified for the specific taxon. “Magnitude of threat” thresholds “high/moderate/low” were converted to the percentage of the taxon killed by the most severe threat identified. Where there were gaps in data for population size trend, statistical interpolation was done using non-linear regression.

To promote normality of the data, the following alterations were made to the nominated parameters:

- “Population reduction” (IUCN, 2000) was modified to incorporate an increase as well as a decrease so that data for taxa with increasing population size were not truncated to 0%. The protocols prescribed for this parameter were otherwise unchanged and the parameter was renamed “percent change in population size” and also referred to as trend.
- “Fluctuation in population size” (IUCN, 2000) was assessed as a coefficient of variation.
- The points assigned by biological variables 7A, 7B and 7C of The Florida Game and Freshwater Fish Commission's system (Millsap et al., 1990) were summed to form one variable viz. “ecological specialization”.

2.2. Stochastic population modeling

Extinction risk for each taxon was determined using stochastic population models based on life-history and other information for the taxon. All models included demographic and environmental stochasticity and catastrophes. The majority of the models (35) were done

using VORTEX, an individual based model that also includes inbreeding depression (Miller and Lacy, 1999), 33 as single populations and two as metapopulations. Of the remainder, six were done with count based *r*-models, two with custom models and two with RAMAS[®] Metapop, as specified for each taxon below. All except four taxa were modeled as single populations, the remaining four being done using metapopulations. An assumption of our study and all such projection studies is that past processes will continue into the future.

Wherever possible, the probability of a taxon's extinction was obtained from a model scrutinized within the literature. Where a study provided different probabilities of extinction in response to a range of scenarios modeled, the probability of extinction generated by the model that the authors deemed most realistic was used. For 10 cases, models were drawn from the study of Brook et al. (2000). In four cases, no published model was found for a taxon, so a model was created based on long-term life history data published for the taxa and using the model development protocols of Ferson (1991), Akçakaya (1996), Miller and Lacy (1999) and Brook et al. (2000). The nature of the model for each taxon is indicated below.

Median time to extinction (MTE) was obtained from the models for each taxon. This was used in preference to probability of extinction as it is a non-constrained variable with better properties for statistical analyses. This was expressed in generations, as MTE and extinction risk scale better to generations than to years (O'Grady, 2002; Reed et al., 2003a). In brief, minimum viable population sizes for 30 well-studied taxa for a 10% probability of extinction over 100 years showed a significant regression on generation length. However, minimum viable population sizes determined for a 10% probability of extinction for 11 generations (the average number of generations in 100 years) showed no significant regression on years. We have shown that catastrophes scale better to generations than years (Reed et al., 2003b), and genetic effects are known to scale to generations (Frankham et al., 2002). Further, Sinclair (1996) has shown that fluctuations in population size in mammals do not differ between small and large mammals when expressed on a per-generation basis.

2.3. Taxa

The study was restricted to mammals and birds, as Brook et al. (2000) have shown that stochastic population models give an unbiased estimate of extinction risk for these taxa. The 45 taxa (30 mammals and 15 birds) were those found for which there were sufficient data to meet the requirements of the study, namely data were available for assessment by the 16 parameters assayed (see Table 2), and data were available for the construction of stochastic population models where no published

risk analysis was found (see stochastic population modeling). Each taxon was a closed system (i.e. $\ll 1$ immigrant/emigrant per year). Hence, in this study the term taxon refers variously to a species, a sub-species, a metapopulation, or a population. The taxa had diverse life histories, and came from a wide geographic range (Europe, Asia, Africa, North and South America, and Australia).

The list of the 45 taxa used follows along with a notation as to the population viability analysis model used (V – VORTEX or its precursors, r – count-based r -models, RM – RAMAS[®] Metapop, or C – custom model), and whether the taxa was a metapopulation and whether a new model was constructed for this study (n): *Alces alces* (r, n), *Amazona vittata* (V), *Babyrousa babyrussa* (V), *Babyrousa babyrussa togeanensis* (V), *Brachyteles arachnoides* (V), *Bubalus depressicornis* (V), *Bubalus mindorensis* (V), *Canis lupus* (V), *Capra species* (V), *Castor fiber* (C), *Cervus elaphus* (V), *Cervus eldi eldi* (V), *Charadrius melodus* (V: metapopulation), *Columba mayeri* (V), *Copsychus sechellarum* (V), *Dendroica kirtlandii* (V), *Dendrolagus matschiei* (V), *Enhydra lutris nereis* (r), two populations of *Gorilla gorilla beringei* (V), *Grus americana* (V), *Gymnogyps californianus* (r, n), *Lasiornis krefftii* (r, n), *Leontopithecus rosalia* (V), *Leucopars rothschildi* (V), *Lichenostomus melanops cassidix* (r), *Lipotes vexillifer* (V), *Lynx pardinus* (V; metapopulation), *Nestor notabilis* (V), *Odocoileus virginianus borealis* (V), *Ovibos moschatus* (r, n), two populations of *Ovis aries* (V), two populations of *Panthera tigris sumatrae* (V), *Perameles gunnii* (V), *Polioptila californica californica* (RM, metapopulation), *Rhinoceros sondaicus* (V), *Strix occidentalis occidentalis* (RM, metapopulation), *Trichechus manatus latirostris* (V), *Tricholimnas sylvestris* (V), *Tympanuchus cupido attwateri* (V), *Ursus arctos* (C), *Ursus arctos horribilis* (V), and *Zosterops lateralis chlorocephala* (V). Further details of the taxa, the populations studied, and the references that provided the data are given in O'Grady (2002), and this information plus the median times to extinction are available from the corresponding author.

2.4. Statistical analyses

Factor analysis with varimax rotation (Child, 1978) was used to identify which parameters correlated best with MTE and thus extinction risk. Forward stepwise multiple regression was used to determine independently which parameters were the best predictors of extinction risk and the relative importance of these variables.

The Akaike Information Criterion (AIC_c) (Burnham and Anderson, 1998) and Mallows's C_p statistics (Draper and Smith, 1981) were used as objective means of selecting the most parsimonious multiple regression model from a set of candidate models of varying complexity (in terms of number of fitted parameters). These methods

help avoid the problem of 'over-fitting' and the subsequent loss of precision of parameter estimates (Burnham and Anderson, 1998).

All statistical analyses were performed using Mini-tab[®] Release 12. In all statistical analyses MTE data were natural logarithm transformed for normality.

3. Results

Population size of mature individuals (N), and trend in population size, were clearly the best predictors of extinction risk (factor analysis, Table 3). As expected, the smaller the population size, and/or the greater the rate of reduction in population size, the shorter the MTE. No other parameters were significantly correlated with extinction risk in the factor analysis. Forward stepwise regression also indicated that population size, and percent change in population size were the best predictors of extinction risk. Both population size and percent change in population size were significantly related to extinction risk (Table 4 (Panel a)). Separately, these parameters explained 23.8% and 23.9% of the variation in time to extinction, respectively, while together they explained 40.2%. No other parameters were significantly related to extinction risk.

We hypothesised that decline in population size, and many other threat factors, would most reliably indicate extinction risk when the population size was already small. As expected, we found that trend had most ex-

Table 3
Factor analysis of the relationship between sixteen biological parameters of mammals and birds and their extinction risk

Biological parameters	Factor loadings
Median time to extinction (generations)	-0.92
Population size (mature individuals)	-0.27
% change in population size (10 years/3 generations)	-0.24
Taxonomic level assessed (species/sub-species/population)	-0.15
Number of offspring per breeding female per year	-0.14
Range reduction	0.13
Variation in population size (CV)	0.09
Range (km ²)	-0.08
Ecological specialization	-0.05
Magnitude of threat	-0.05
Number of sub-populations into isolated sub-populations	0.04
Proportion of total population in reserve	0.03
Generation length	0.02
Age of first reproduction	0.02
Immediacy of threat	-0.02
Number of species in genus	-0.01
Harvest/legal protection	-0.01

Factor loadings with an absolute value below 0.24 are not significant.

Table 4

Multiple regression analyses, using forward stepwise selection, of the relationship between median time to extinction in generations and 16 frequently used variables thought to reflect extinction risk with: analysis of variance – an additive model (Panel a), and the best supported model with both additive and interaction terms (Panel b)

Source	d.f.	SS	MS	<i>F</i>	<i>r</i> ² (%)
<i>Panel a: Additive model</i>					
Regression	2	19.33	9.67	14.09***	40.2
Residual error	42	28.81	0.69		
<i>N</i>	1	11.45			23.8
Trend	1	7.88			16.4
<i>Panel b: Best supported regression model with additive and interaction terms</i>					
Regression	6	33.57	5.59	14.58***	69.7
Residual error	38	14.58	0.38		
<i>N</i>	1	11.45			23.8
<i>N</i> × trend	1	8.12			16.9
Taxonomic level	1	2.19			4.5
Frag × <i>N</i> × trend	1	1.98			4.1
# offspring	1	1.91			4.0
<i>N</i> × # offspring	1	7.91			16.4

*** $p < 0.001$.

planatory power as a $N \times$ trend interaction and that trend had no significant explanatory power in addition to this (data not shown). Consequently, we re-ran the model selection routines to evaluate all other possible interactions with both N and $N \times$ trend (in addition to purely additive terms). This procedure led to four other variables attaining significance, and substantially increased the statistical model's explanatory power over the additive model (Table 4 (Panel b)).

The final regression model containing both additive and interaction terms, explained 69.7% of the variance in extinction risk and had the following form (where MTE = median time to extinction in generations):

$$\ln(MTE) = 1.366 + 0.221 \times \ln(N) + 0.059 \\ \times \ln(N \times \text{trend}) + 0.506 \times \ln(\text{Tax}) + 0.077 \\ \times \ln(\text{Frag} \times N \times \text{trend}) + 2.44 \times \ln(O) \\ - 0.45 \times \ln(N \times O),$$

where N = population size ($t = 3.74$, $p = 0.001$), $N \times$ trend = interaction between population and change in population size ($t = 3.41$, $p = 0.002$), Tax = taxonomic level ($t = 2.32$, $p = 0.026$), Frag × $N \times$ trend = number of sub-populations × population size × change in population size ($t = 2.80$, $p = 0.008$), O = number of offspring per female ($t = 4.93$, $p < 0.001$), $N \times O$ = population size × number of offspring interaction ($t = -4.54$, $p < 0.001$). In the additive plus interactive model, the term $N \times$ trend was superior to just trend, and the inclusion of both terms was not supported. The term $N \times O$ only became important after the O term was first included in the regression model. Once the effects of N and O singly have been removed, taxa with large values of $N \times O$ are at higher risk than those with low values.

This final model was robust to the use of either forward-stepwise or best-subsets multiple regression selection procedures. AIC_c gave 4.4 times more support for the above, six parameter model, than for the next best model (in which Tax was dropped). It also showed that the best additive plus interactive model was 16,829 times more likely than the best purely additive model, which included only N and trend.

For taxonomic level, the “population-level” is most vulnerable and the “species-level” least so. Taxa with large values of number of sub-populations × population size × trend were at less risk than those with low values. Taxa with higher numbers of offspring per female are at less risk of extinction than those with low numbers.

The $N \times$ trend interaction could be due to either (i) trend having most effect when population size is small, or (ii) trend having most effect when N is large, as trend is unimportant in populations already doomed to extinction by small N . To distinguish these hypotheses, we split the data into equal halves with larger ($N = 110$ – 3332) and smaller ($N = 8$ – 102) population sizes and carried out regressions of $\ln(MTE)$ on trend on each of them. The relationship was much stronger in the larger populations ($b = 0.084$, $r^2 = 41.5\%$, $p = 0.0007$) than the small ones ($b = 0.015$, $r^2 = 0.2\%$, $p = 0.84$). Thus, trend is of minor importance relative to stochastic factors when populations are small.

4. Discussion

This study provides the first comparative quantitative assessment of the relative importance of different variables as predictors of a direct estimate of extinction risk. Population size and trend in population size were clearly

the best predictors of extinction risk. Notably, trend in population size predicted best as an interaction with population size, rather than alone. The relationships of all other parameters with risk were comparatively weak in this data set, although some factors indirectly associated with small population size (e.g., taxonomic level, number of sub-populations) or correlated with “slow” life histories (Purvis et al., 2000), such as low reproductive rate, showed some explanatory power. An independent line of evidence for the importance of population size data in predicting extinction risk is that simple count-based population viability analysis models based on mean, trend and variability of population size seem to predict extinction risk as well as more detailed models (Brook, 1999).

Our results provide some conclusions that accord with prior conventional wisdom, and others that conflict with it. There is considerable evidence for an inverse association between population size and extinction risk (MacArthur and Wilson, 1967; Terborgh and Winter, 1980; Diamond, 1984; Goodman, 1987; Pimm et al., 1988; Berger, 1990; Newmark, 1994, 1996; Mace and Kershaw, 1997; McKinney, 1997; Belovsky et al., 1999; Foufopoulos and Ives, 1999; Purvis et al., 2000; Fagan et al., 2001). Evidence relating population growth rate (r) and specifically population decline to extinction risk has been provided by Goodman (1987), McKinney (1997), Mace and Balmford (2000), Brook et al. (2002b), O'Grady (2002) and Reed et al. (2003a).

Taxonomic level, number of offspring per female per year, and number of sub-populations are all supported for inclusion in the multiple regression analysis. Both taxonomic level (where the “population-level” is most vulnerable and the “species-level” least so) and number of sub-populations can be rationalized as representing composite surrogates for a variety of other risk factors, including range size (populations will generally have smaller ranges than species), population size (smaller for populations), level of legal protection and proportion of taxa in a reserve (both less likely for populations), degree of inbreeding (higher in isolated populations), etc. Similarly, low reproductive rate (few offspring) usually signifies “slow-” or “ K -selected” life history strategies, which has previously been correlated with increased extinction risk (McKinney, 1997; Purvis et al., 2000; Cardillo, 2003).

Conversely, other biological variables presumed to be predictors showed no further significant relationship to extinction risk in our data set. Why did not this study find a stronger relationship between these parameters and risk? There are at least six reasons. First, many parameters are often highly correlated with small population size and decline (e.g. large body size, late age of first reproduction, high trophic position, range size, and ecological specialization; reviewed by McKinney, 1997). However, population size and trend effectively collapse

them into an indicator that correlates more strongly with extinction risk than any one of the individual attributes. Second, our sample of taxa may have failed to sample taxa for which these attributes were important. For example, only four of our taxa were metapopulations and this may be a smaller proportion than for threatened species generally. Third, our data set may have lacked power to detect effects for some variables.

Fourth, some of the parameters assayed were measured with coarse resolution. For example, range size was only measured to the nearest 25 km² for some taxa. Fifth, taxa that are legally protected in reserves are not always afforded protection from poaching, as funds for wildlife protection in situ are scarce in developing nations. Both these latter situations add variation to the data. These results do not mean that providing legal protection and/or reserves for endangered species has no influence on extinction risk and need not be attempted or maintained.

Sixth, the influence of deterministic threats may overwhelm the influence of species' intrinsic biological attributes (e.g. ecological specialization, late age of first reproduction, etc.) on their susceptibility to extinction (Duncan and Lockwood, 2001). Many of the taxa in this study have recently been threatened by, and continue to be threatened by, habitat destruction and many also face anthropogenic threats that are reducing their population size.

It is likely that change in population size is most closely correlated with anthropogenic factors (habitat destruction), that current population size correlates with extinction probability through stochastic factors, and the interaction between these terms shows that they operate in tandem (see Caughley, 1994). Consequently, these two factors encompass both deterministic and stochastic threats.

Trend in population size was a significant predictor in an interaction with population size, but not alone when both additive and interaction terms were assessed. While it is logical to expect that trend is a more important indicator of extinction risk when population size is small than when it is large, this was not the case. Decline is not very important in populations that are already doomed by small size, but is most important in populations that are otherwise relatively safe from stochastic factors.

Our results provide strong support for the definitions of IUCN criteria A, C and D (IUCN, 2000). Criterion A concerns only population decline, criterion C uses decline, population size and severity of fragmentation, while criterion D is based solely on population size. While our analyses offer little direct support for range restriction, the primary focus of criterion B, trend or fragmentation might be correlated with range restriction and so capture this variable.

The Florida Game and Freshwater Fish Commission's system (Millsap et al., 1990) and NatureServe both

include population size and trend, but do not have an interaction between them. The Florida system encompasses number of offspring per female and taxonomic level, factors not included in the IUCN system. The NatureServe system also includes a taxonomic level term.

Our study was restricted to mammals and birds. Clearly further studies are required to determine if the same conclusions apply to other taxa, especially invertebrates, plants and fungi. It is also desirable that our conclusions be checked using a sample of vertebrates that samples attributes differently, especially population fragmentation.

Our results have important ramifications for conservation biology. First, priority should be given to collecting time series data for threatened taxa. Second, population size and trend, or other variables that reflect these are the most important data for state of the environment reporting. Population size is usually related to habitat area and this is commonly used in state of the environment reporting (Saunders et al., 1998). Third, they support the practice of using population size and trend in threatened species categorizations, as used in all the major assessment systems.

Improvements and simplifications of threatened species categorization systems may be possible, as population size and trend are sometimes weighted equally with variables that showed less relationship with risk, and our results should aid in such revisions. From a submitted study by O'Grady et al., rank correlations of categorisations with probability of extinction are only 0.368, 0.325 and 0.276 for IUCN, Florida Game and Freshwater Fish Commission's system and NatureServe, respectively, meaning that they are only explaining 13.5%, 10.6% and 7.6% of the variation in probability of extinction. Population size and trend explained 40% of the variation in MTE in our study and our best model explained 70% of the variation.

In conclusion, population size and percent change in population size are the best predictors of extinction risk in our sample of vertebrates. Thus, population size is the most cost-effective data to collect on threatened species. Data on population size and trend, or indicators for them, should have priority in reports on the health of a nation's biological resources.

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