THE ROYAL SOCIETY

Predicting extinction risk in declining species

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What biological attributes predispose species to the risk of extinction? There are many hypotheses but so far there has been no systematic analysis for discriminating between them. Using complete phylogenies of contemporary carnivores and primates, we present, to our knowledge, the first comparative test showing that high trophic level, low population density, slow life history and, in particular, small geographical range size are all significantly and independently associated with a high extinction risk in declining species. These traits together explain nearly 50% of the total between-species variation in extinction risk. Much of the remaining variation can be accounted for by external anthropogenic factors that affect species irrespective of their biology.

Keywords: extinction risk; primates; carnivores; conservation; independent contrasts

1. INTRODUCTION

Studies of past and ongoing extinctions consistently support non-random patterns of species loss across taxa (Raup 1994; McKinney 1997; Russell *et al*. 1998; Purvis *et al*. 2000) and analyses of extant populations and species have identified various factors associated with vulnerability to extinction (Laurance 1991; Gaston 1994; Gaston & Blackburn 1995; Bennett & Owens 1997; Harcourt 1998; Woodroffe & Ginsberg 1998; Foufopoulos & Ives 1999). It is clear that the main processes driving extinction are the 'evil quartet' (habitat loss, over-exploitation, introduced species and chains of extinction) (Diamond 1984). However, statistical tests for differences in extinction vulnerability among species have faced several difficulties, including incomplete information about species' biology, conservation status, phylogeny and the interrelationships between possible predictor variables (McKinney 1997; Woodroffe & Ginsberg 1998). Here, we present, to our knowledge, the first systematic examination of biological attributes associated with high perceived extinction risk among contemporary species that controls for interrelatedness among independent variables, avoids circularity, ensures statistical (phylogenetic) independence across taxa and examines differences between two clades, i.e. Carnivora and Primates. These are arguably the most charismatic mammalian orders and are excellent testing grounds for two reasons: (i) the natural history of many species is known in detail, and (ii) both clades have many species with abundant, widely distributed populations as well as closely related species on the brink of extinction.

Several predictions about attributes of species that correlate with vulnerability to extinction follow from hypotheses commonly found in the literature (for recent reviews see McKinney (1997) and Simberloff (1998)).

(i) Small populations are more likely to die out than large ones: demographic stochasticity, local catastrophes, slow rates of adaptation, 'mutational meltdown' and inbreeding are all more serious for populations with few individuals (Brown 1995; Lande 1999). Small geographical ranges and low population densities are therefore likely to confer an enhanced extinction risk (Gaston 1994).

(ii) Island endemics are very likely to have small geographical ranges and, hence, small populations. In addition, they may have evolved in isolation from predators and competitors (including humans), perhaps making them particularly vulnerable to the effects of introduced species and overexploitation (Pimm 1991).

(iii) Species at higher trophic levels are more vulnerable to the cumulative effects of disturbance to species lower down the food chain (e.g. chains of extinction) (Diamond 1984; Crooks & Soulé 1999).

(iv) Species with 'slow' life histories, i.e. small litters, slow growth rates, late sexual maturity, long gestation and long interbirth intervals, are less able to compensate for increased mortality with increased fecundity and are therefore more vulnerable to population extinction (MacArthur & Wilson 1967).

(v) Species with complex social structures for mating, group foraging or group defence are more vulnerable to extinction because persistence depends upon a larger unit than the individual (Allee effects) (Courchamp *et al*. 1999); in addition, social groups are conspicuous which can lead to increased hunting (Soulé 1983).

(vi) Species where individuals have large home ranges are particularly vulnerable to habitat loss and degradation and, in particular, to edge effects (Woodroffe & Ginsberg 1998).

(vii) Diurnal species show a suite of characteristics that might make them more vulnerable, e.g. large body size, sociality, high predation rates and large home ranges (Gittleman 1985; Fleagle 1999), as well as being easier to hunt.

(viii) Last but not least, large body size correlates with many of the extinction-promoting traits above (McKinney 1997). Larger species tend to have low population densities, slower life histories and larger home ranges. In addition, humans may be less

tolerant of and, thus, more likely to persecute larger carnivores (Weaver *et al.* 1996), and hunters are more likely to target larger primates for food (Cowlishaw & Dunbar 2000).

Although many of these hypotheses are long standing, attempts to discriminate between them systematically have so far been limited. Here we used phylogenetic comparative methods in order to assess the relative importance of many proposed biological factors and adopted a multiple regression approach so that intercorrelated and confounding variables were considered. We found that up to half of the variance in extinction risk could be explained by our models. We then explored the likely importance of extrinsic factors such as anthropogenic disturbance by examining outliers from our regression model—these outliers are species that are perceived to be markedly more or less at risk than expected on the basis of their biology alone.

2. METHODS

The above set of hypotheses was used to select variables for testing against current assessments of species' extinction risks. We collated published data on species' geographical range, island endemicity, body size, life history (age at sexual maturity, gestation length, litter size and interbirth interval) and ecology (home range size, population density, group size, activity timing and trophic level). Continuous variables were logarithmically transformed prior to analysis. Table 1 shows the sample sizes: full details of the data set and sources are available from the authors. The geographical range data were based on present rather than historical distributions, since our interest is in the processes that underpin contemporary risk of decline and extinction rather than those that might have caused historical range contractions.

Assessments of extinction risk came from the 1996 International Union for the Conservation of Nature and Natural Resources (IUCN) Red List (Baillie & Groombridge 1996) which categorizes species as either data deficient (DD), lower risk, least concern (LRlc), lower risk, near threatened (LRnt), lower risk, conservation dependent (LRcd), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW) or extinct (EX). We treated the threat levels identified above as a continuous character, varying from 0 to 5, by combining LRcd species with VU species (as 2) and EW species with EX species (as 5) and excluding DD species. This treatment views the Red List categories as discrete approximations of an underlying continuous spectrum. The IUCN assessments are made using five criteria (A–E), at least one of which must be met for the species to be listed as threatened (VU, EN and CR). Most criteria include measures or correlates of the traits used in our analysis. In order to avoid possible circularity, our analyses (except where indicated) excluded species listed by such criteria from the data set and considered threatened species only if they were listed under subcriterion A1 (recent decline in population size at a specified level); henceforth, we term the species included in these analysis the declining species data set. The results are very similar if all species are included (see § 3).

All statistical tests were performed on phylogenetically independent contrasts (Felsenstein 1985) generated using comparative analysis by independent contrasts (Pagel 1992; Purvis & Rambaut 1995). Such phylogenetic analyses were necessary because of the pseudoreplication and, hence, elevated type I

error rates that result from treating species as independent points when relevant variables show a phylogenetic pattern (Harvey & Pagel 1991). We demonstrate below that non-phylogenetic tests led to a greater number of significant relationships being detected with our data. Hypothesis testing was by regression (or multiple regression) of contrasts through the origin (Garland *et al.* 1992). The phylogenies used (Purvis 1995; Bininda-Emonds *et al.* 1999) were composite estimates including all extant species, with the primate phylogeny modified to match the species recognized in the Red List. The phylogenies are available as supplementary information. Branch length information was needed for scaling the independent contrasts in order to give them common variance. Model criticism (Garland *et al.* 1992) in preliminary analyses showed that homogeneity of variance was more closely approached when branches were all set to the same length than when they were based on divergence times. We therefore used equal branch lengths for all that follows.

We began our analysis of the pooled data set (declining species of both orders) by examining the significance of each predictor separately, as this has been a common approach in testing correlates of extinction risk (Laurance 1991; Harcourt 1998). For comparison, we also performed these tests non-phylogenetically (treating the species as independent). Next, we performed multiple regression analyses of contrasts in order to factor out geographical range (by far the most important variable in the one-predictor models). Finally, because many of the remaining biological traits were intercorrelated, we used multiple regression with model simplification in order to find minimum adequate models (MAMs) for perceived extinction risk within each order. Initially, all variables were included as predictors. The predictor with the lowest marginal reduction in variance was dropped at each step and a fresh set of contrasts generated for remaining variables until all remaining predictors were significant ($p = 0.05$). Because of missing values, removal of a variable often led to an increase in the sample size. Consequently, important variables could be dropped from the model early on. We used two heuristic procedures in order to reduce this risk. First, whenever a variable's removal led to a marked increase in sample size, recently dropped variables were reintroduced. Second, when all remaining predictors were significant, the rest were reintroduced in turn. This multiple regression analysis was performed twice, once for all species and once for the declining species data set.

In order to test the significance of differences between the MAMs for the two orders we conducted a pooled analysis for declining species of both orders. We fitted a model to the combined data using all predictors implicated in either order model, a factor representing order (primate or carnivore) and the order × trait interactions and then used model simplification as before.

3. RESULTS

The first column of results in table 1 shows the traits that were significant correlates of extinction risk assessments in single-predictor phylogenetic analyses of the pooled data set of both orders. Small geographical range and island endemicity were the most important predictors, but there was also support for the hypotheses that slow life history (long gestation and small litters), low population density and diurnal activity each enhance extinction risk. Non-phylogenetic analyses, in which species

Table 1. *Results of one- and two-predictor regressions of independent contrasts for predicting extinction risk in declining species*

(N_s, number of species in pooled analysis; N_c, number of contrasts in pooled analysis. Values in remaining columns are t-statistics. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$ (all tests two-tailed). For island status, $0 = $ not endemic to islands and $1 = $ endemic to islands. For trophic level, $0 = $ herbivore, $1 = $ omnivore, $2 = $ insectivore and $3 = $ vertebrate eater. For activity timing, $0 = $ not diurnal and $1 = $ diurnal.)

variable	N_s	N_c	as sole predictor	with geographical range
geographical range	355	292	-11.73^{***}	—
island status	355	292	3.82^{***}	0.24
body mass	317	266	0.91	2.23^*
gestation length	219	197	2.11^*	2.22^*
litter size	284	245	-3.24^{***}	-1.32
age at sexual maturity	172	156	1.64	0.86
interbirth interval	175	161	0.86	0.93
trophic level	321	270	1.57	1.54
activity timing	327	274	2.10^*	0.77
home range size	197	174	-0.22	1.81
population density	162	147	-2.07^*	-2.82^{**}
group size	237	202	-0.08	0.19

were treated as independent, found further significant correlates: body mass ($t = 2.16$), age at sexual maturity ($t = 2.69$), interbirth interval ($t = 4.68$), trophic level ($t = -3.35$) and group size ($t = 2.17$), though population density was no longer significant ($t = -0.30$).

The pattern of correlation in the phylogenetic analysis changed considerably when multiple regression was used to factor out the effects of the most important single predictor, geographical range (second column of results in table 1). Island endemics are apparently not unusually threatened given their geographical range, suggesting that evolutionary isolation is not the reason for their vulnerability. Litter size and activity timing also lost significance, but large body size was now linked with high perceived risk.

The MAMs for the two orders were quite similar (table 2) when all relevant predictor variables were included and there was little difference between the declining-species and all-species MAMs within either primates or carnivores. Higher extinction risk assessments correlated independently with small geographical range (the most important predictor), high trophic level and low population density in each order. Note that geographical range was the most important predictor even when species listed as threatened on the basis of their small ranges were excluded from the analysis (i.e. when the analysis included declining species only). Trophic level did not emerge as an important factor in the simpler analyses (table 1), but was significant when confounding variables were controlled for. Moreover, this effect was independent of and in addition to the effect of population density, despite the strong interrelationship between abundance and diet across mammals (Damuth 1987). The differences between orders concerned body size (significant only in primates) and life history (significant only in

Table 2. *Multiple regression models predicting extinction risk within each order*

(Values for traits are coefficients. A dash indicates that the predictor was absent from the model. $^*p \leqslant 0.05$, $^{**}p \leqslant 0.01$, $^{***}p \leqslant 0.001$ (all tests two-tailed). The reason for the sample size difference between the two carnivore regressions is that the all-species regression has more predictors so there were fewer species with complete data.)

	primates		carnivores	
	all species	declining	all species	declining
number of species (contrasts)	100 (92)	87 (80)	74 (65)	105 (91)
r^2 (%)	42.5	33.9	59.1	31.9
geographic range	-0.326^{***}	-0.284^{***}	-0.369^{***}	-0.263^{***}
body mass	0.606^{***}	0.360^{**}	—	—
gestation length	—	—	2.520^{***}	0.895^*
age at sexual maturity	—	—	-0.644^*	—[b]
trophic level	0.787^*	—[a]	0.494^{***}	0.232^*
population density	-0.228^*	-0.255^*	-0.205^{**}	—[b]

[a]Values that are near significant ($p = 0.065$) with other predictors remaining significant.
[b]Values that are additionally significant if two contrasts (*Alopex lagopus* versus *Vulpes velox* and *Crocuta crocuta* versus *Parahyaena brunnea*) with abnormally large Studentized residuals ($> \pm 3$) are deleted. Deletion of such contrasts makes no qualitative difference to any of the other models here or in table 3.

Table 3. *Multiple regression model across primates and carnivores predicting extinction risk in declining species*

(Sample size: 120 species and 112 contrasts. The model accounts for 47.6% of the total variance. $^*p \leqslant 0.05$, $^{**}p \leqslant 0.01$, $^{***}p \leqslant 0.001$ (all tests two-tailed). For orders, $0 = $ carnivore and $1 = $ primate.)

predictor	coefficient	t
geographical range	-0.291	-7.65^{***}
trophic level	0.402	4.00^{***}
population density	-0.113	-2.06^*
gestation length	1.590	2.77^{**}
body mass	-0.002	-0.02
order	-0.084	-1.53
body mass × order	0.704	3.33^{***}
gestation length × order	-2.790	-2.80^{**}

carnivores). Table 3 shows that these differences were themselves significant; order (primate versus carnivore) was not significant as a main effect, but interacted significantly with body mass and gestation length.

4. DISCUSSION

(a) *The biology of extinction risk*

Our results indicate that species tend to have a higher risk of extinction if they occupy a small geographical range, occur at low density, occupy a high trophic level in the food chain and exhibit low reproductive rates (although this latter effect can only be inferred from a body size effect in primates, a point we return to in §4(b)). This set of factors emphasizes the overriding importance

of contemporary population size (geographical range and population abundance) and the ability of that population to recover from natural or anthopogenic crashes (reproductive rate) in the global extinction process. However, the fourth factor (trophic level) additionally indicates the importance of a species' dependence on other components of the ecosystem. Hence, even where a species occurs in a large resilient population, it may still be vulnerable to extinction if other species on which it depends do not share such traits.

Island endemics were apparently not at unusually high risk of extinction for their (typically small) geographical ranges. This result may not be expected from theory, but accords with two other recent large- or mesoscale studies. Island endemic New World passerine birds were less likely than continental species of the same geographical range size to be considered threatened with extinction (Manne *et al.* 1999). At a mesoscale, a diverse assemblage of island populations tended to show greater persistence than mainland populations of the same species, notwithstanding their smaller range sizes (Channell & Lomolino 2000). The possibility remains that separate analyses of species on oceanic and landbridge islands might reveal interesting differences.

Our results differ further from those of previous studies of local decline and extinction in that group size, activity timing and, in particular, home range size (Harcourt 1998; Woodroffe & Ginsberg 1998) were not significant predictors in our regression models once other confounding variables were considered. There are at least two possible reasons for the difference. The first is that our analysis was on a different scale, focusing on species-wide decline rather than individual populations. Second, the previous analyses did not control for as many confounding variables as we did: each of these traits was correlated with one or more of the significant predictors and most were significant in simpler regression models (table 1). Further studies on a range of scales should clarify the issue.

Our analysis showed how knowledge of a species' basic biology and natural history alone can provide a prescriptive relative estimate of its vulnerability to extinction, at least compared to related taxa. In fact, our models accounted for up to half the total variance in extinction risk. Surprisingly, even when extinction risk was assessed solely on the basis of population decline, geographical range area alone accounted for 24% of its total variance. A possible explanation is that rates of range decline may be underestimated more in widespread species than in those with narrow ranges, as has been observed for British butterflies (Cowley *et al.* 1999). Another possibility is that a small range indicates habitat specificity, which is likely to affect a species' ability to withstand habitat modification. Whatever the mechanism, our results support the conclusion of recent studies showing that geographical range correlates with perceived extinction risk in birds (Manne *et al.* 1999) and population persistence in a range of taxa (Channell & Lomolino 2000). Moreover, by adding information on life history and ecological variables the explanatory power of our regressions was doubled.

(b) Methodological issues

The multiple regression approach we used is a marked improvement over previous univariate approaches but still not a perfect solution to the problem of intercorrelated predictor variables. The remaining difficulties of interpretation are clearly illustrated by differences between the MAMs for primates and carnivores (table 2). In primates, there was no life-history variable in the MAM, although larger body size, itself associated with lower reproductive rates, was strongly related to higher threat status. One possibility is that this difference simply reflects a greater tendency for exploitation to be size dependent in primates (Cowlishaw & Dunbar 2000). However, distinguishing between the real importance of body size and life history as predictors is likely to be harder in primates than in carnivores because primates exhibit less size-independent variation in life history. When life-history contrasts were regressed through the origin on body mass contrasts in each order separately, the root mean squared error was greater in carnivores than in primates for all four life-history traits (results not shown). It may therefore be that, in primates, body size is a more accurate surrogate for reproductive rate than any of the reproductive variables. This sort of problem has long been recognized in multivariate comparative studies (Economos 1980). A related point worth noting is that gestation length was more significant than other life-history variables. Gestation length is probably our most reliable indicator of a species' position on the fast–slow continuum of life-history strategies (Gittleman 1993) and correlates with late maturity, small litters and long interbirth intervals independently of body size (Harvey *et al.* 1989).

The importance of considering phylogeny was demonstrated by the comparison of the single-predictor, phylogenetic and non-phylogenetic analyses. Treating species as independent led to markedly more significant results than did analysis of independent contrasts. The invalidity of the non-phylogenetic tests was seen most clearly in the apparent negative correlation between extinction risk and trophic level: this result reflects a pseudoreplicated difference between primates (higher average threat and lower average trophic level) and carnivores (lower threat and higher trophic level).

We used IUCN categories as a surrogate measure of extinction risk. Although there is no simple way of validating their use in this way, two arguments suggest that the perceived extinction risk is a reasonable surrogate of the true risk of extinction. First, studies predicting extinction from alternative methods have produced similar estimates to those using the IUCN categories, e.g. species–area relationships (Cowlishaw 1999). Second, the criterion under which declining species are assessed explicitly equates IUCN threat categories to empirically estimated rates of decline in global population size (Baillie & Groombridge 1996).

(c) Anthropogenic factors affecting extinction risk

The models in tables 2 and 3 explain up to half of the variance in the perceived extinction risk of carnivores and primates. In order to investigate the remaining unexplained variation, we used the model for predicting vulnerability in all species for which we had information on the key predictor variables. Plotting our predictions against the categories assigned by the IUCN (figure 1) allowed us to examine the nature of the outliers, species
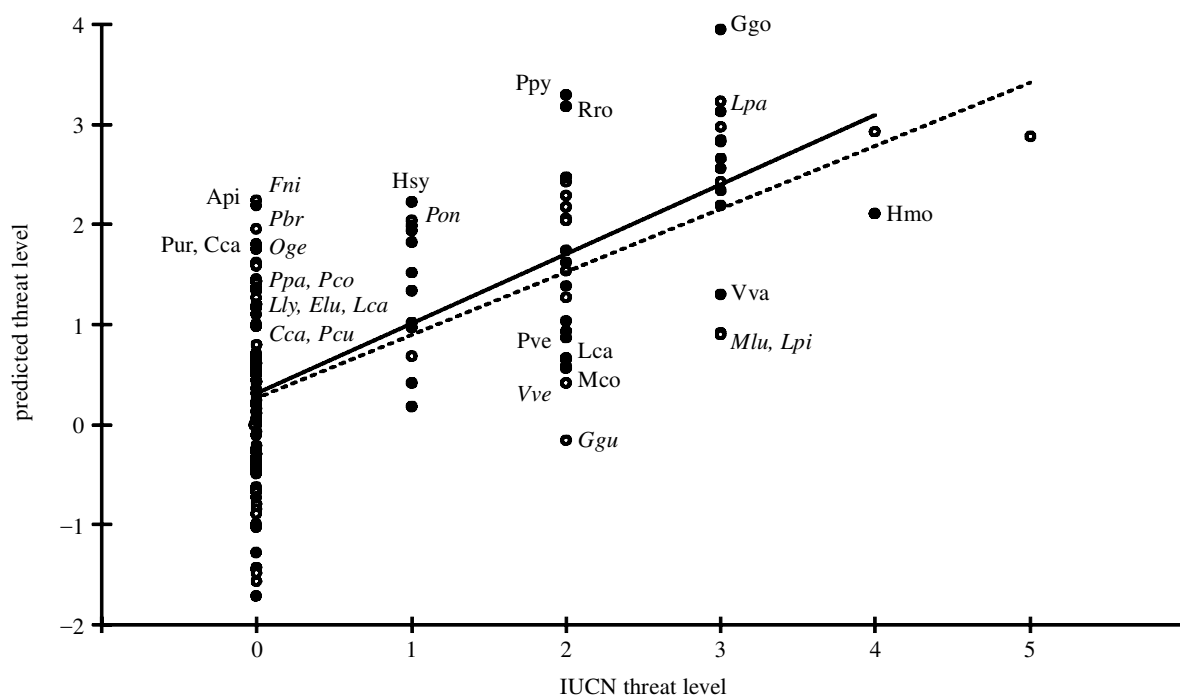
Figure 1. Predictions from order-specific MAMs (table 2, all species) for carnivores (open circles and hatched fitted line) and primates (filled circles and solid fitted line) plotted against IUCN threat categories. The model predictions were standardized in order to have the same means and standard deviations as the IUCN threat codes for each order. The IUCN threat codes were scored as outlined in §2. Lines are least-squares regressions for each order. Species with residuals greater than ± 1.0 are indicated by the first letter of the genus name and the first two of the specific name (carnivores are in italicized text and primates in regular text; see main text for full names). Species classified as LRlc and with negative residuals are not annotated: these residuals have little meaning because there is no subdivision in the IUCN system among non-threatened species.

for which our model provided a poor estimate. We suggest that these outliers reflect the prevalence and magnitude of extrinsic, anthropogenic factors in the extinction of contemporary species.

Among primates, most threatened species for which our model seriously underestimates threat are found in countries where the rates of tropical forest loss have been unusually high (World Resources Institute 1996), such as Java (*Hylobates moloch*) and Madagascar (*Propithecus verreauxi*, *Varecia variegata*, *Mirza coquereli* and *Lemur catta*). These species are relatively biologically robust against extinction, but their habitat is simply disappearing. In contrast, there are a number of primate species whose biological characteristics predict a higher extinction risk than their IUCN category suggests. These either (i) exist in relatively undisturbed regions or habitats, such as north-eastern Amazonia (*Ateles paniscus*), central Borneo (*Pongo pygmaeus*), montane reserves in central China (*Rhinopithecus roxellana*) and desert, savanna and montane habitats (*Papio hamadryas*, *Papio ursinus*, *Theropithecus gelada* and *Hylobates syndactylus*), or (ii) cope relatively well in secondary (disturbed) forest habitats (*Alouatta pigra*, *Cebus capucinus*, *Gorilla gorilla* and *Trachypithecus obscurus*) (Rowe 1996).

As with primates, several carnivores at greater risk than our model predicts have historically experienced (*Vulpes velox*, *Lycaon pictus* and *Mustela lutreola*) or are expected to face (*Gulo gulo*) unusually severe habitat loss, intense commercial overexploitation, persecution or impacts from introduced species. In addition, in common with primates, a number of species for which the model overestimates threat have significant populations in relatively undisturbed habitats in montane, pampas, scrub or desert regions (*Pseudalopex culpaeus*, *Oncifelis geoffroyi*, *Felis nigripes*, *Panthera pardus*, *Caracal caracal*, *Puma concolor*, *Lynx pardinus* and *Parahyaena brunnea*) or in the central Amazon (*Panthera onca*) (see the carnivore action plans listed in Mace & Balmford (2000)). Notably, many of these outliers are felids. In fact, all 17 felids in the analysis are above the line in figure 1. The extinction risk of this clade might be overestimated by our model because of any family-specific trait not in the model that reduces the risk of extinction. Alternatively, the model may be reflecting the fact that felids, as specialist predators of vertebrates, are living on the edge (Carbone *et al.* 1999); such species have short persistence times in the fossil record (Van Valkenburgh 1999). The only other species for which our model markedly overestimates threat, the sea otter (*Enhydra lutris*), is not currently listed as threatened by the IUCN but, on the basis of recent declines (Estes *et al.* 1998), is now recommended for threatened status (J. A. Estes, personal communication).

Conservation biology is faced with describing what species are endangered, identifying why this is so and then prescribing ways of preventing extinction. Our analyses have provided a way of testing between competing hypotheses about species vulnerability to extinction and of identifying species which, while not currently threatened, may need particular conservation attention when human pressure increases. We have highlighted the biological determinants of vulnerability to extinction and also demonstrated how the severity of

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