How species respond to multiple extinction threats

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It is well established that different species vary in their vulnerability to extinction risk and that species biology can underpin much of this variation. By contrast, very little is known about how the same species responds to different threat processes. The purpose of this paper is therefore twofold: to examine the extent to which a species' vulnerability to different types of threat might covary and to explore the biological traits that are associated with threat-specific responses. We use an objective and quantitative measure of local extinction risk to show that vulnerability to local population decline in primates varies substantially among species and between threat types. Our results show that a species' response to one threat type does not predict its response to others. Multivariate analyses also suggest that different mechanisms of decline are associated with each type of threat, since different biological traits are correlated with each threat-specific response. Primate species at risk from forestry tend to exhibit low ecological flexibility, while those species vulnerable to agriculture tend to live in the canopy and eat low-fruit diets; in further contrast, primates at risk from hunting tend to exhibit large body size. Our analyses therefore indicate that a species' vulnerability to local extinction can be highly variable and is likely to depend on both threat type and biology.

Keywords: extinction risk; hunting; habitat disturbance; primates

1. INTRODUCTION

Patterns of global extinction risk have now been studied in a range of taxa, including birds (Bennett & Owens 1997), carnivores and primates (Purvis *et al.* 2000), freshwater fish (Duncan & Lockwood 2001) and bats (Jones *et al.* 2003). These comparative studies have shown that extinction risk varies markedly across taxa and that species' biological characteristics can be an important determinant of this variation. Nevertheless, our understanding of the mechanisms that link species biology with vulnerability to extinction is still relatively poor. This is because extinction is not a unitary phenomenon but rather arises from a variety of different processes, such as habitat loss and hunting. Recent research has begun to investigate this heterogeneity with considerable success (Owens & Bennett 2000), demonstrating that those species endangered by one threat process have different biological traits from those endangered by another. However, despite such progress, very little is known about how the same species responds to different threat processes, and how these patterns of multiple response can vary between species. This is a question of fundamental importance, since differential patterns of vulnerability across multiple threats must play a central role in determining the overall pattern of global extinction risk for many species.

Accordingly, our intention in this paper is to explore patterns of vulnerability between species and threat types. We therefore present data from multiple localities on local variation in species abundance that is attributable to known threats. We also investigate, in a multivariate framework, the species' biological characteristics that are related to these patterns. We use primates as a model system for this analysis since they are diverse, their biology and phylogeny are well known, and their local responses

to a range of human impacts are exceptionally well documented (Cowlishaw & Dunbar 2000). Across the primates, we examine three anthropogenic threats, namely two types of habitat disturbance, *forestry* (selective logging) and *agriculture* (shifting cultivation), and *hunting* (usually for wild meat). We would expect that variation in the responses to these threats reflects a variety of biological processes underlying extinction risk. We explore the mechanisms most commonly proposed to explain this variation (Johns & Skorupa 1987; Harcourt 1998; Cowlishaw & Dunbar 2000) through the analysis of six species traits that are related to these mechanisms. Some of these traits have been specifically associated with global extinction risk in primates (Jernvall & Wright 1998; Purvis *et al.* 2000). We examine the same traits at intraspecific levels and in relation to more detailed mechanisms of threat. Our hypotheses can thus be summarized as follows.

(i) *Home range area*. Species with large home ranges will be more vulnerable to extinction from habitat disturbance since a large home range reflects high resource demands (Oates 1987) and vulnerability to edge effects (Woodroffe & Ginsberg 1998). By contrast, species with small home ranges will be most susceptible to hunters, since a restricted ranging area makes their movements more predictable (Kuchikura 1988).

(ii) *Diet*. Strongly frugivorous species are dependent on scarce and patchy food resources. This makes such species more vulnerable to habitat disturbance (Terborgh & Winter 1980; Johns & Skorupa 1987; Jones *et al.* 2001). In addition, these species will be more susceptible than folivores to hunting, since their dependence on fruiting trees makes their ranging behaviour more predictable (Hill & Padwe 2000).

(iii) *Sociality*. Large groups require more food resources, so species that live in such groups will be more

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vulnerable to the loss of food patches associated with habitat disturbance (Fimbel 1994). Larger groups also tend to be more conspicuous and therefore an easier target for hunters (Struhsaker 1999).

(iv) *Ecological flexibility.* Species with poor ecological flexibility will be less tolerant of habitat disturbance since they will be less able to adapt to changes in the forest structure (Harcourt 1998; Vazquez & Simberloff 2002). Such species might also be more vulnerable to hunting, since their ability to change their ecological habits to reduce exposure to hunters (e.g. switching diets or ranging patterns) will be more limited (Cowlishaw & Dunbar 2000).

(v) *Habit.* Canopy-dwelling species will be more susceptible to habitat disturbance because they are less able to cope with disruption to the forest canopy from tree felling (Harcourt 1998). In addition, such species will be more vulnerable to hunters since movement through the canopy is noisy and conspicuous (Oates 1996) and some projectile weapons become less effective as the attack trajectory approaches the horizontal (Kuchikura 1988).

(vi) *Body size.* Species' body size tends to correlate with several of the preceding biological traits (Fleagle 1999). Once the potential effects of these are accounted for in multivariate analyses, larger-bodied species may respond better to habitat disturbance since their lower metabolic requirements and higher energy reserves allow them to survive periods of reduced food availability (Lindstedt & Boyce 1985). Conversely, larger-bodied species are usually more heavily targeted by human hunters owing to their higher profitability and conspicuousness (Cowlishaw & Dunbar 2000).

In addition to these six biological traits, we also tested for an effect of local population size and reproductive rate. These traits have frequently been implicated as drivers of extinction risk through small-population processes (Pimm *et al.* 1988; Bennett & Owens 1997; Courchamp *et al.* 1999; Owens & Bennett 2000; Purvis *et al.* 2000; Johnson 2002; Reynolds 2003). However, we would not expect them to be directly associated with species' responses to the declining-population processes in this study. Rather, small population size and slow recovery rate should exacerbate declines brought about by the mechanisms described above.

Our analysis begins with a description of how individual primate species tend to respond to different threat processes, and an examination of the covariation between the threat-specific response patterns obtained. We then use multivariate statistics to distinguish among the above hypotheses and reveal the primary traits associated with vulnerability to each threat type.

2. MATERIAL AND METHODS

To obtain a measure of species' vulnerability to local extinction, we collected data from a wide variety of studies reporting species abundance in threatened areas and matching non-threatened areas. In each threatened area, species were exposed to one of the three threat types: forestry, agriculture or hunting (where two or more threat types were involved, the data were

discarded). In each non-threatened area, these and other threats (e.g. fragmentation) were absent. Using these matched-pair data we calculated vulnerability on the basis of the response ratio, r, as

$$\frac{\text{abundance in threatened area}}{\text{abundance in non-threatened area}}.$$

The response ratio is a flexible statistic (Johns & Skorupa 1987; Hedges *et al.* 1999) that permits direct comparison of data between studies even when abundance is measured in different units (e.g. individuals km^{-2}, groups km^{-1}) and different methods (e.g. fixed-width transects, distance sampling). It is also a quantitative and objective measure of changes in abundance. A value of $r = 1.0$ indicates that abundance is the same in both threatened and non-threatened areas, i.e. that the threat has no impact. For all other values, the magnitude of r above or below 1.0 indicates the extent to which species do better or worse in threatened areas, while $r = 0$ corresponds to local extinction.

The full dataset contains 293 response ratios to forestry (across 66 species at 38 sites), 72 response ratios to agriculture (44 species, 19 sites) and 204 response ratios to hunting (54 species, 32 sites) (see electronic Appendix A). Out of these, 25 species had recorded responses to all three anthropogenic threats, 27 had responses to two and 35 had responses to only one. Since there were occasions when multiple data were available for each species, we collapsed the variation into a single response to each threat for each species. The species' response ratios were calculated through a procedure of nested medians, as follows. (i) The value for each matched pair of areas was calculated as the median of all available repeated measures for that pair (i.e. when the areas were surveyed multiple times). (ii) The value for each study site was calculated as the median of the matched-pair area values at that site. (iii) The species value was calculated as the median of the site values. Nesting the data allowed repeated measures to be appropriately treated as pseudoreplicates, rather than as independent estimates of the threat response. Medians were preferred to means to reduce the effect of extremely high response ratios. In addition, several sources present data from a single site where multiple threatened areas were sampled. In these cases, a response was calculated for each species in each threatened area with reference to a single matching non-threatened area. Owing to the nested nature of our calculations, we used a simulation method (based on 1000 bootstrap replicates) to estimate the variance associated with each median species' response ratio.

To test the proposed hypotheses that link species biology with vulnerability, we also collated information on a range of biological traits, with species defined according to Corbet & Hill (1991). Data were collected from a variety of sources on species' home range area (ha), group size (individuals), frugivory (percentage of daily feeding time eating fruit and seeds), terrestriality (percentage of time spent at or below 5 ± 2 m in the canopy) and female body mass (henceforth body mass, kg). We indexed each species' ecological flexibility using the annual temperature range (°C) and rainfall seasonality (proportion of rainfall in the wettest quarter) that the species is typically exposed to (i.e. recorded near the centre of the species' range, following Cowlishaw & Hacker (1997)). We used population density (individuals km^{-2}) and gestation period (days) as indices of population size and reproductive rate, respectively (following Purvis *et al.* 2000). All predictor variables were log-transformed to obtain normal distributions, except for frugivory and rainfall

Table 1. Summary of response ratio data for forestry, agriculture and hunting.

(Tolerant and susceptible species are those with a median response in excess of and below unity, respectively; p(sign test) is the two-tailed p-value of the binomial test, against the null hypothesis that species are as likely to be tolerant as susceptible.)

	forestry	agriculture	hunting
median response	0.75	0.41	0.53
tolerant species	23	12	11
susceptible species	42	32	43
p(sign test)	0.025	0.004	< 0.001

Table 2. Minimum adequate models of responses to forestry, agriculture and hunting.

(b, t and p are the slope, t-score and p-value of the regression.)

threat and predictor	b	t	p
forestry ($r^2 = 0.10$, $n = 66$)			
temperature range	0.77	2.72	0.0084
agriculture ($r^2 = 0.37$, $n = 28$)			
frugivory	0.080	2.31	0.029
terrestriality	0.081	2.81	$\leqslant 0.01$
hunting ($r^2 = 0.14$, $n = 53$)[a]			
body mass	−0.11	−2.94	0.005
hunting ($n = 49$)[b]			
body mass	−0.23	−2.42	0.020

[a] Species values: one influential species (*Saguinus oedipus*) removed.
[b] Independent contrasts: one comparison (apes versus gibbons) removed to satisfy the assumption of constant variance.

seasonality, whose distribution was already close to normal. The raw data and full bibliography can be found in electronic Appendix A.

Once our data were collated, our analysis took place in two stages. First, we explored the basic patterns of response-ratio variation between species and threat type. Second, we investigated which of our proposed hypotheses best explained the interspecific response-ratio variation for each threat type. To test our hypotheses, we generated a Minimum Adequate Model (MAM) for each threat process using GLMSTAT 5.7 (Beath 2001). Initially, all nine predictors were included in the model. This maximal model was simplified in a stepwise procedure by removing the variable with the lowest explanatory power (following Purvis *et al.* 2000). This continued until all remaining terms in the model were significant ($p \leqslant 0.05$). Unfortunately, the data matrix contains many missing values. This could lead to important variables being omitted from the MAM. We guarded against this possibility by reintroducing recently discarded variables whenever the removal of a term caused the sample size to increase by more than five species. Finally, we reintroduced each discarded parameter into the MAM in turn to see if it explained any additional variance. We tested the robustness of our MAMs using the Shapiro–Wilks test to check that residuals from the model were normally distributed. We found that this was most easily attained when the species' response ratios were square-root transformed. We also examined the scatter plots of our putative relationships and present models in which influential outliers have been removed.

We also tested whether species' response ratios are independent with respect to phylogenetic history, using the λ statistic (Pagel 1999; Freckleton *et al.* 2002), which varies between 0

(phylogenetic independence) and 1 (species covary in proportion to their shared evolutionary history). We found that closely related species do not respond similarly to either type of habitat disturbance (forestry or agriculture; MLE$\{\lambda\}$ = 0 in both cases). However, there was evidence of a phylogenetic effect in species' responses to hunting (MLE$\{\lambda\}$ = 0.52). Accordingly, we repeated our analysis of species' responses to hunting using independent contrasts (Felsenstein 1985) calculated from Purvis's primate phylogeny (Purvis 1995), implemented by CAIC v. 2.6.9 (Purvis & Rambaut 1995). We found that the underlying assumptions of the model were best fitted using equal branch lengths and when the species' values of the response ratio were square-root transformed.

All statistical tests are two-tailed.

3. RESULTS

The pattern of vulnerability shows a great deal of variation between both species and threat type. Figure 1 illustrates the range of variation for those species with response ratios recorded for all three threat processes. Some species show a similar degree of vulnerability to each of the three threat types; for example, *Ateles belzebuth* (white-bellied spider monkey) always goes locally extinct. However, most species display a distinctive response to each threat type, for example, *Procolobus verus* (olive colobus) is one of the few species tolerant of hunting ($r > 1$), yet has one of the lowest responses to agriculture. Out of the 52 species with responses to more than one threat type, 24 are tolerant to one threat and susceptible ($r < 1$) to another. Moreover, seven species have responses in the lower quartile for one threat and in the upper quartile for another. The distinctiveness of each species' response to different types of threat is highlighted by the finding that a species' vulnerability to one threat process does not predict its vulnerability to another: across species, the response to hunting does not correlate with the response to forestry or agriculture (Pearson correlation: $p > 0.4$ in both cases). Although the response ratios to forestry and agriculture are correlated, this relationship disappears after the influential *Callicebus cupreus* (red titi monkey) point is removed ($p > 0.8$). This species has the highest response ratio for both threat types.

Despite the intraspecific variation in vulnerability to the different threat types of forestry, agriculture and hunting, the general trend is for all three threat processes to reduce local species abundance (sign test: $p < 0.05$ in each case; table 1). Across all species, abundance is reduced, on average, by 25% in areas of forestry, by 47% in areas of hunting, and by 60% in areas of agriculture. Nevertheless, there are also species that are not strongly affected by a
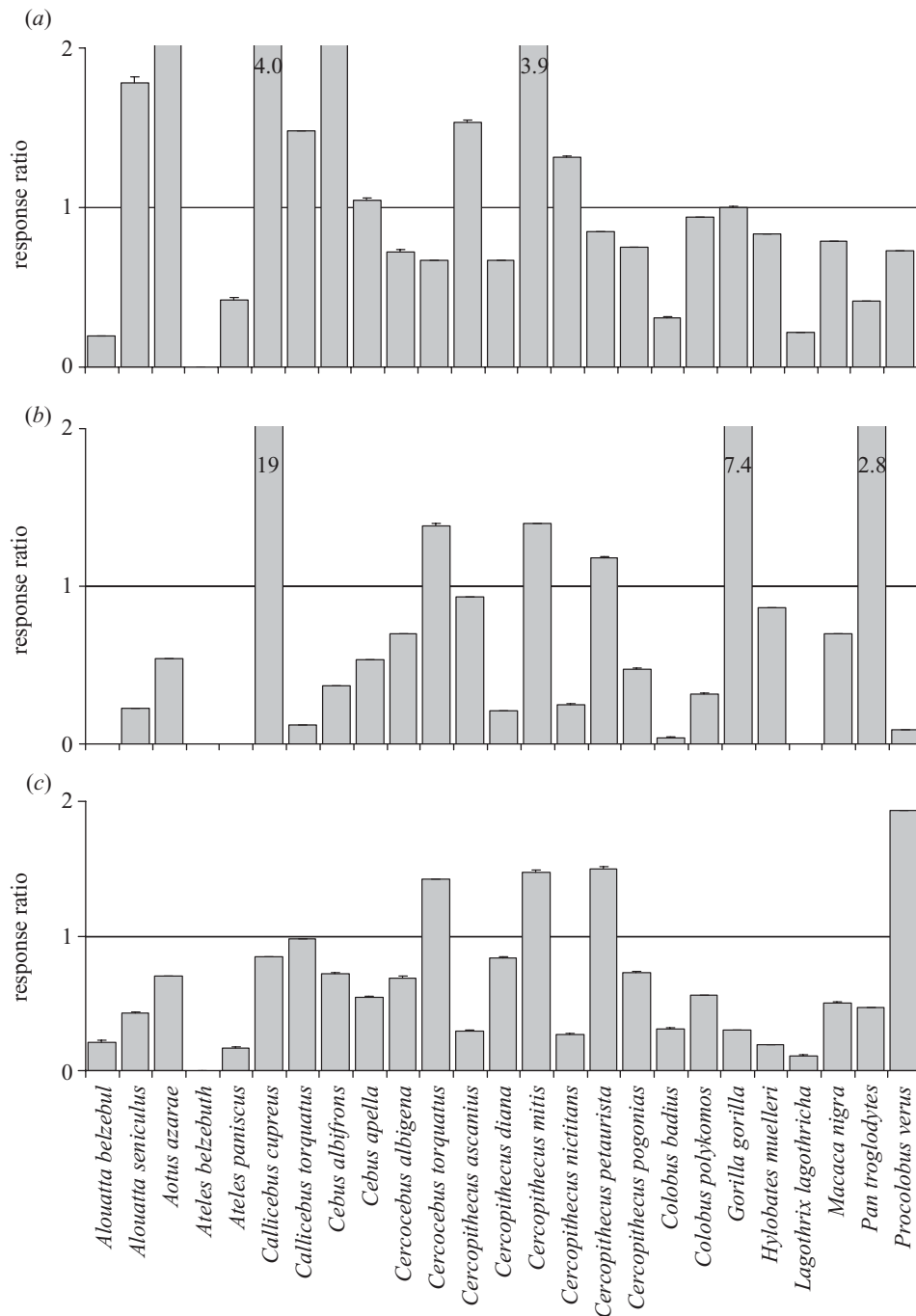
Figure 1. Interspecific variation in response ratio for (*a*) selective forestry, (*b*) agriculture and (*c*) hunting. Only species with responses to each of three threat types are shown. Error bars are standard errors generated from 1000 bootstrap replicates. These are extremely small in most cases, and are not correlated with the number of responses for any of the three threat processes.

given threat process ($0.8 < r < 1.2$: $n = 9$ species for forestry, 5 for agriculture and 7 for hunting) or can actively benefit from it ($r > 1.2$: $n = 19$, 9 and 9).

Our tests of the proposed mechanisms that link species' biology and vulnerability yielded a different MAM for each of the three threat processes (table 2). MAMs for forestry and hunting contain a single parameter, whereas the agriculture MAM contains two. None of the nine predictor variables is correlated with responses to more than one threat type. Therefore, our most important finding from these tests is twofold: species biology is linked with vulnerability for each threat process, but different traits

are associated in each case. In the case of forestry, species' response ratios increase with the annual temperature range associated with the geographical range of that species distribution: i.e. species with low ecological flexibility are more vulnerable to forestry. In the case of agriculture, species' response ratios are positively correlated with terrestriality and frugivory: i.e. species are better able to survive in areas of shifting cultivation if they are adapted for movement on the ground and a diet of fruit and seeds. Finally, in the case of hunting, species' response ratios decline with increasing body size: i.e. larger species are more vulnerable to hunting. This effect is equally strong

regardless of whether species values or independent contrasts are used (table 2).

4. DISCUSSION

Our analyses show that not only do species vary in their vulnerability to a given anthropogenic threat (see also Pimm *et al.* 1988; Cowlishaw & Dunbar 2000; Reynolds 2003), but single species can show widely divergent patterns of vulnerability to different threat types. For example, species' response ratios to agriculture are lower, on average, than those to forestry. This is not surprising in itself because the impact of agriculture on forest structure is typically more severe (Rijksen 1978; Van Gemerden *et al.* 2003). However, species' responses to forestry and agriculture are not reliably correlated despite the fact that both are forms of habitat disturbance. This demonstrates that even within apparently homogeneous threat processes there may be a great deal of heterogeneity in species response. It also emphasizes that different mechanisms are associated with patterns of species vulnerability to each threat type. Further scrutiny of our results, in the context of the hypotheses under test, provides some indication of the most important mechanisms that are likely to be operating.

First, species with high ecological flexibility tend to do better in areas of selective logging than others. This finding is corroborated by the observation that the geographical ranges of primate species that survive well in logged forests extend into more variable environments, i.e. exhibit higher maximum latitudes (Harcourt 1998). The importance of ecological flexibility, and the lack of diet and terrestriality effects, suggest that it is general modification of the habitat rather than any specific alteration (such as loss of food trees or disruption to the canopy) that is the primary driver. The fact that our first measure of ecological flexibility (based on annual temperature range) correlates, whereas our second measure (based on rainfall seasonality) does not, suggests that changes to the thermal environment might have a predominant effect. Logged forests are known to experience much greater temperature extremes, which are likely to cause thermal stress (heat loading during the day, cold stress at night) to the remaining wildlife (Greiser Johns 1997). Previous studies of comparative primate responses to selective logging have also identified other traits of biological importance, such as body size and diet (Johns & Skorupa 1987; Harcourt 1998), but on the basis of smaller and often simplified datasets.

Second, terrestrial frugivorous primate species are best able to cope with the impact of shifting cultivation. The effect of terrestriality is consistent with the tendency for shifting cultivation to largely eliminate the forest canopy (Rijksen 1978). The effect of frugivory is contrary to our general prediction for habitat disturbance. However, it is consistent with the fact that those trees that remain following disturbance tend to produce more fruit as a result of increased insolation (Johns 1988, 1991; Ganzhorn 1995). The reason why this pattern of species response is seen in only agricultural areas, and not logged areas, may be related to the fact that cultivators tend to actively retain useful fruiting trees in their fields and also plant new fruiting trees among their crops (Johns 1991). The superior

ability of frugivorous primates to survive in areas of shifting cultivation has also been reported from a case study in Sierra Leone (Fimbel 1994).

Third, large primate species are most vulnerable to hunting. Several previous studies have also reported that animals of large size are more susceptible to overhunting (Jennings *et al.* 1998; Owens & Bennett 2000; Purvis 2001; Denney *et al.* 2002; Alroy 2003). In this case, however, the absence of an effect of gestation period indicates that primate vulnerability to hunting is driven more strongly by hunter preferences than by population recovery rates (cf. Purvis *et al.* 2000; Johnson 2002). The observation that some species actively benefit from hunting ($r > 1$) requires additional explanation. This phenomenon is most likely to reflect competitive release for some smaller species as their larger competitors decline in abundance (Peres & Dolman 2000). A similar process of competitive release might also be partly responsible for those species that benefit from habitat disturbance.

Several species traits were unrelated to species responses for any of our three disturbance types. The lack of a home range effect might be attributed to the fact that it is a relatively crude measure of both habitat resource use (C. Carbone, G. Cowlishaw, N. J. B. Isaac and J. Rowcliffe, unpublished data) and predictability of location to hunters. By contrast, the absence of a group size effect corroborates existing evidence that primate social behaviour is extremely adaptable. Large groups may fragment into subgroups in disturbed areas to circumvent the high resource demands they normally experience (Struhsaker 1997), and also adopt higher levels of vigilance to compensate for their increased conspicuousness to predators (Cowlishaw 1997), including hunters. In the case of initial population size and reproductive rate we did not expect a direct effect: species that exist in small populations and exhibit low reproductive rates may be more vulnerable to spontaneous population decline through intrinsic small-population processes, but there is no reason why they would be more likely to respond badly to extrinsic anthropogenic forces. We therefore expected these traits to have a significant effect only in association with other traits, i.e. in exacerbating an ongoing decline. The absence of such an effect suggests that the observed changes in local abundance are driven so strongly by declining-population processes that any effects of stochastic small-population processes are relatively trivial (cf. Fisher *et al.* 2003).

One outstanding issue is whether the patterns of vulnerability explored in this paper reflect birth–death processes or immigration–emigration processes. For example, are frugivorous species more abundant in cultivated areas because an increase in fruit availability leads to higher birth rates or to higher rates of immigration? In fact, both types of process might operate. For example, larger species may be less common in hunted areas because they experience higher mortality rates and migrate to surrounding areas (where hunting pressure is lower). However, limited opportunities for immigration and emigration, owing to the spatial scale at which these widespread anthropogenic activities operate, are likely to make changes in fecundity and mortality schedules more important. This conclusion is supported by those field studies that describe resident rather than transient animal populations following habitat disturbance (e.g. Johns 1986), and poor body condition

(Olupot 2000) and elevated infant mortality (Grieser Johns & Grieser Johns 1995) in those populations. In either case, the emergent pattern of local extinction risk, as measured by the response ratio, remains the same: if a species declines in a threatened area it is at greater risk of extinction in that area, regardless of whether the decline is the result of mortality or emigration.

Our analyses demonstrate that a species' vulnerability to local extinction is highly variable depending on the anthropogenic activity that threatens it. This marked threat specificity provides a cautionary lesson about the dangers of making broad generalizations about species vulnerabilities to extinction. Our results also show that the link between species biology and vulnerability is threat specific, even when two threats of a similar nature (agriculture and forestry, both forms of habitat disturbance) are involved. These findings therefore also serve to emphasize the importance of incorporating extrinsic anthropogenic forces in comparative analyses of species extinction risk (see also Owens & Bennett 2000; Fisher *et al.* 2003). Finally, our approach elucidates the extent to which different anthropogenic threats affect a multitude of primate species, and the mechanisms that might be responsible for mediating such effects. In light of the fact that approximately half of all primate species are threatened with global extinction (Cowlishaw & Dunbar 2000), this information should help us to gain a deeper understanding of the processes that underpin this global pattern, and therefore ultimately prevent such global extinctions from taking place.

REFERENCES

Alroy, J. 2003 Megafauna died from big kill, not big chill. *Science* **300**, 885–885.

Beath, K. J. 2001 *GLMSTAT: generalised linear modelling software*. Berkeley, CA: Kagi.

Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. Lond.* B **264**, 401–408. (DOI 10.1098/rspb. 1997.0057.)

Corbet, G. B. & Hill, J. E. 1991 *A world list of mammalian species*. London: Natural History Museum Publications.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999 Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410.

Cowlishaw, G. 1997 Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**, 667–686.

Cowlishaw, G. & Dunbar, R. I. M. 2000 *Primate conservation biology*. University of Chicago Press.

Cowlishaw, G. & Hacker, J. E. 1997 Distribution, diversity, and latitude in African primates. *Am. Nat.* **150**, 505–512.

Denney, N. H., Jennings, S. & Reynolds, J. D. 2002 Life-history correlates of maximum population growth rates in marine fishes. *Proc. R. Soc. Lond.* B **269**, 2229–2237. (DOI 10.1098/rspb.2002.2138.)

Duncan, J. R. & Lockwood, J. L. 2001 Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biol. Conserv.* **102**, 97–105.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Fimbel, C. 1994 Ecological correlates of species success in modified habitats may be disturbance-specific and site-specific—the primates of Tiwai Island. *Conserv. Biol.* **8**, 106–113.

Fisher, D. O., Bloomberg, S. P. & Owens, I. P. F. 2003 Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc. R. Soc. Lond.* B **270**, 1801–1808. (DOI 10.1098/rspb.2003.2447.)

Fleagle, J. G. 1999 *Primate adaptation and evolution*. New York: Academic Press.

Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726.

Ganzhorn, J. U. 1995 Low-level forest disturbance effects on primary productivity, leaf chemistry and lemur populations. *Ecology* **76**, 2084–2096.

Greiser Johns, A. 1997 *Timber production and biodiversity conservation in tropical forests*. Cambridge University Press.

Grieser Johns, A. & Grieser Johns, B. 1995 Tropical forest primates and logging: long-term coexistence? *Oryx* **29**, 205–211.

Harcourt, A. H. 1998 Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In *Behavioral ecology and conservation* (ed. T. M. Caro), pp. 56–79. Oxford University Press.

Hedges, L. V., Gurevitch, J. & Curtis, P. S. 1999 The meta-analysis of response ratios in experimental ecology. *Ecology* **80**, 1150–1156.

Hill, K. & Padwe, J. 2000 Sustainability of Ache hunting in the Mbaracayu Reserve, Paraguay. In *Hunting for sustainability in tropical forests* (ed. J. G. Robinson & E. L. Bennett), pp. 79–105. New York: Columbia University Press.

Jennings, S., Reynolds, J. D. & Mills, S. C. 1998 Life history correlates of responses to fisheries exploitation. *Proc. R. Soc. Lond.* B **265**, 333–339. (DOI 10.1098/rspb.1998.0300.)

Jernvall, J. & Wright, P. C. 1998 Diversity components of impending primate extinctions. *Proc. Natl Acad. Sci. USA* **95**, 11 279–11 283.

Johns, A. D. 1986 Effects of selective logging on the behavioral ecology of west Malaysian primates. *Ecology* **67**, 684–694.

Johns, A. D. 1988 Effects of 'selective' timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* **20**, 31–37.

Johns, A. D. 1991 Forest disturbance in Amazonian primates. In *Primate responses to environmental change* (ed. H. O. Box), pp. 115–135. London: Chapman & Hall.

Johns, A. D. & Skorupa, J. P. 1987 Responses of rain-forest primates to habitat disturbance—a review. *Int. J. Primatol.* **8**, 157–191.

Johnson, C. N. 2002 Determinants of loss if mammals species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc. R. Soc. Lond.* B **269**, 2221–2227. (DOI 10.1098/rspb.2002.2130.)

Jones, K. E., Barlow, K. E., Vaughan, N., Rodriguez-Duran, A. & Gannon, M. R. 2001 Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. *Anim. Conserv.* **4**, 59–66.

Jones, K. E., Purvis, A. & Gittleman, J. L. 2003 Biological correlates of extinction risk in bats. *Am. Nat.* **164**, 601–614.

Kuchikura, Y. 1988 Efficiency and focus of blowpipe hunting among Semaq Beri hunter–gatherers of peninsular Malaysia. *Hum. Ecol.* **16**, 271–305.

Lindstedt, S. L. & Boyce, M. S. 1985 Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* **125**, 873–878.

Oates, J. F. 1987 Food distribution and foraging behaviour. In *Primate societies* (ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 197–209. University of Chicago Press.

Oates, J. F. 1996 Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Aust. J. Ecol.* **21**, 1–9.

Olupot, W. 2000 Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conserv. Biol.* **14**, 833–843.

Owens, I. P. F. & Bennett, P. M. 2000 Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl Acad. Sci. USA* **97**, 12 144–12 148.

Pagel, M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884.

Peres, C. A. & Dolman, P. M. 2000 Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* **122**, 175–189.

Pimm, S. L., Jones, H. L. & Diamond, J. 1988 On the risk of extinction. *Am. Nat.* **132**, 757–785.

Purvis, A. 1995 A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond.* B **348**, 405–421.

Purvis, A. 2001 Mammalian life histories and responses of populations to exploitation. In *Conservation of exploited species* (ed. J. D. Reynolds, G. M. Mace, K. H. Redford & J. Robinson). Cambridge University Press.

Purvis, A. & Rambaut, A. 1995 Comparative-analysis by independent contrasts (CAIC)—an Apple-Macintosh application for analyzing comparative data. *Comput. Applic. Biosci.* **11**, 247–251.

Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond.* B **267**, 1947–1952. (DOI 10.1098/rspb. 2000.1234.)

Reynolds, J. D. 2003 Life histories, population dynamics and conservation. In *Macroecology: concepts and consequences* (ed. T. M. Blackburn & K. J. Gaston), pp. 195–217. Oxford: Blackwell Scientific.

Rijksen, H. D. 1978 *A field study of Sumatran orang-utans (Pongo pygmaeus abelii, Lesson 1827): ecology, behaviour and conservation.* Wageningen: H. Veenan & Zonen, BV.

Struhsaker, T. T. 1997 *Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation.* Gainesville, FL: University Press of Florida.

Struhsaker, T. T. 1999 Primate communities in Africa: the consequences of long-term evolution or the artefact of recent hunting? In *Primate communities* (ed. J. G. Fleagle, C. H. Janson & K. E. Reed), pp. 289–294. Cambridge University Press.

Terborgh, J. & Winter, B. 1980 Some causes of extinction. In *Conservation biology: an evolutionary–ecological perspective* (ed. M. Soule & B. A. Wilcox), pp. 119–133. Sunderland, MA: Sinauer.

Van Gemerden, B. S., Shu, G. N. & Olff, H. 2003 Recovery of conservation values in Central African rain forest after logging and shifting cultivation. *Biodiv. Conserv.* **12**, 1553–1570.

Vazquez, D. P. & Simberloff, D. 2002 Ecological specialization and susceptibility to disturbance: conjectures and refutations. *Am. Nat.* **159**, 606–623.

Woodroffe, R. & Ginsberg, J. R. 1998 Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.