

Doomed to die? Predicting extinction risk in the true hawks Accipitridae

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Abstract

One of the most important tasks in conservation biology is identifying species at risk from extinction and establishing the most likely factors influencing this risk. Here, we consider an ecologically well-defined, monophyletic group of organisms, the true hawks of the family Accipitridae, which are not only among the most studied, but also contain some of the rarest bird species in the world. We investigate which intrinsic and extrinsic factors, covering morphology, life history and ecology, covary with International Union for the Conservation of Nature and Natural Resources threat status, as well as global population size and geographic range size. By decomposing threat status into population size and range size, we test whether any factors are generally important: we found that species with less habitat specialization, a larger clutch size and more plumage polymorphism were associated with lower extinction risk and larger population and range sizes. Species with special habitat requirements might be less capable of dealing with habitat transformation and fragmentation, while species with small clutch sizes might not be able to reverse population declines. Plumage polymorphism might indicate the size of the species' gene pool and could be a good marker of extinction risk. The analyses also emphasized that no single factor is likely to be sufficient when predicting the threat of extinction.

Introduction

The rate at which species are currently going extinct is as rapid as at any time in the geological past (Regan *et al.*, 2001). Accumulating evidence suggests, however, that extinction risk is non-randomly distributed among taxa, being typically clustered within closely related species (Purvis *et al.*, 2000; Fisher & Owens, 2004). These may share many attributes, and so certain traits may predispose species to extinction. As Brown (1995) emphasized, extinction is predictable.

The International Union for the Conservation of Nature and Natural Resources (IUCN) assesses species systematically and assigns them to a threat category according to their perceived risk of extinction. The IUCN uses five quantitative criteria to assess the risk of extinction: population size, geographic range size, population reductions, continuing population declines and the level of population and habitat fragmentation. The result is the Red List of Threatened Species, which has proved to be a useful catalyst for conservation action (Fuller *et al.*, 2003). However, the IUCN categories alone tell us little about what actually drives species towards extinction. Consequently, many studies have attempted to elucidate the factors which predict these threat categories (e.g. Purvis *et al.*, 2000; Jones, Purvis & Gittleman, 2003; Cardillo *et al.*, 2006).

Much variation in threat status is often explained by differences in population size and range size (Long *et al.*, 2007). Low population size means an increased likelihood that genetic variation within a species will diminish, resulting in a reduced chance of long-term survival (Schonewald-Cox *et al.*, 1983). A small geographic range may decrease the likelihood of a population persisting when faced with the problems resulting from demographic stochasticity, local catastrophes and inbreeding (Purvis *et al.*, 2000). Comparing the biology of rare versus common and localized versus widespread taxa is central to our understanding of the differential success of species, and hence to understanding influences on biodiversity (Fisher, Blomberg & Owens, 2003). Given that population size and geographic range size are two of the important criteria used by the IUCN to assign threat status, several studies have excluded species with small population size and/or small range size when assessing the risk of extinction (Purvis *et al.*, 2000; Fisher *et al.*, 2003; Jones *et al.*, 2003). However, the interrelationships between factors influencing IUCN threat status, population and range size should be explicitly studied. Furthermore, when direct estimates of extinction risk are unavailable, surrogate indicators are often used to categorize threatened species; with population size and range size two of the most commonly used (O'Grady *et al.*, 2004). It is therefore important to consider what factors influence population size

and range size (Owens & Bennett, 2000), and to investigate whether they are similar to those influencing IUCN threat categories.

To investigate successfully which traits result in a higher threat status and/or smaller population and range sizes requires a data set of macroecological scope and an evolutionarily well-defined group of species, to minimize noise due to opposing factors and to control for phylogenetic non-independence (Gaston & Blackburn, 1996; Fisher & Owens, 2004). Carnivores (Purvis *et al.*, 2000), primates (Purvis *et al.*, 2000; Harcourt, Coppeto & Parks, 2002), bats (Jones *et al.*, 2003), marsupials (Fisher *et al.*, 2003) and wildfowl (Gaston & Blackburn, 1996) have, for example, been studied in this way. The family Accipitridae (true hawks) provides another excellent opportunity in this regard (Krüger, 2000). Furthermore, because raptors are one of the most intensively studied groups of organisms, detailed information on a variety of different traits is available for almost every species. This minimizes the problem of missing data points in comparative analyses (see Ackerly, 2000) and enables both the search for general correlates of extinction risk and a species-specific understanding of extinction risk, which is ultimately needed to guide conservation efforts (Fisher & Owens, 2004). Investigating potential indicators of extinction risk in the Accipitridae is important from a conservation perspective because the family contains some of the rarest bird species in the world, with <100 wild breeding pairs of, for example, the white-collared kite *Leptodon forbesi*, the Madagascar fish-eagle *Haliaeetus vociferoides* and the Philippine eagle *Pithecophaga jefferyi* (BirdLife International, 2000). The threatened accipitrid species are listed predominantly under criteria A, C and D (Table 1), indicating that population declines and small and restricted populations lead to a species being included in the IUCN threat categories.

Many researchers have considered how population and range sizes are influenced by intrinsic factors (i.e. those that relate to the biology of the species in question), such as body size, life history and trophic group (e.g. Brown, 1995; Gaston & Blackburn, 1996; Purvis *et al.*, 2000). However, it is also important to include extrinsic factors, that is, environmental characteristics such as habitat productivity, latitude and altitude, to maximize the amount of variation explained (Blackburn & Gaston, 2002; Fisher *et al.*, 2003). Here, we consider the relationship between a variety of

intrinsic and extrinsic factors and three indices of rarity (IUCN threat category, small global population size and small geographical range size) within the Accipitridae. Specifically we test the following predictions:

(1) Large-bodied species, commonly having longer generation times, lower reproductive rates and lower population densities (McKinney, 1997), are prone to extinction because of human perturbations and persecution (Owens & Bennett, 2000). Hence, body weight should be correlated positively with threat status and negatively with population size.

(2) Variables such as reproductive rate and clutch size describe the potential of a species to bounce back from population crashes, whatever the cause (MacArthur & Wilson, 1967). Reproductive rate and clutch size should therefore be correlated negatively with threat status and positively with population size and range size.

(3) The size of prey commonly caught by a species, as well as the share of mammals and birds in the diet, reflect its potential for conflict with humans who see it as a competitor, and hence they can serve as meaningful surrogates for persecution (Thiollay, 1994). Therefore, prey size and the share of mammals and birds in the diet should be positively correlated with threat status. In addition, because species at higher trophic levels are more vulnerable from ecosystem disturbance (Diamond, 1984), they should correlate negatively with population size.

(4) Species occupying broad niches tend to be abundant and widespread (Brown, 1984). Hence, the number of breeding habitats occupied by a species should be correlated negatively with threat status, but positively with population size and especially range size.

(5) The degree of prey specialization and the hunting method used indicate the breadth of a species' prey base. Because prey specialists are more prone to extinction because of their narrow food niche (Owens & Bennett, 2000), prey specialization and hunting method are predicted to correlate positively with IUCN threat status and negatively with population size and range size.

Materials and methods

Data collection

We collected data on the 237 species in the family Accipitridae from the literature (mainly Thiollay, 1994; Krüger,

Table 1 Breakdown of threat levels and the IUCN criteria used for the family Accipitridae

Threat category	Criterion used to assign threat category				
	A	B	C	D	E
Near threatened	11	3	18	5	0
Vulnerable	2	0	16	6	0
Endangered	0	1	5	1	0
Critically endangered	2	1	4	1	0

Criteria are defined by the IUCN as follows: A, reduction in population size; B, small geographic range size; C, small population size and decline; D, population size small and restricted; E, quantitative analysis of extinction risk. Note that some species are listed under several criteria. IUCN, International Union for the Conservation of Nature and Natural Resources.

Table 2 Explanatory variables and their description

Variable	Variable type	Description
Body weight	Morphology	Log body weight (g)
Body size	Morphology	Body size from tip of bill to tip of tail (cm)
Wingspan	Morphology	Wingspan (cm)
Wing length	Morphology	Wing length (cm)
Tail length	Morphology	Tail length (cm)
Sexual size dimorphism	Morphology	Male wing length over female wing length, ratio then cubed to reflect overall bulk Ferguson-Lees & Christie (2001)
Sexual plumage dimorphism	Morphology	Scored from 0 (no difference) to 4 (completely different plumage) Krüger & Davies (2002)
Plumage polymorphism	Morphology	Number of plumage morphs described in Ferguson-Lees & Christie (2001)
Display behaviour	Life history	1 = ground display, 2 = aerial non-acrobatic display, 3 = aerial acrobatic display, 4 = very acrobatic display
Breeding system	Life history	-1 = polygyny, 0 = monogamy, 1 = polyandry
Reproductive rate	Life history	Mean number of chicks fledged/pair and year
Egg volume	Life history	Log estimated egg volume (mL)
Clutch size	Life history	Mean clutch size
Clutch volume	Life history	Egg volume × clutch size
Incubation time	Life history	Mean incubation time (days)
Fledging time	Life history	Mean fledging time (days)
Population density	Ecology	Number of breeding pairs per 100 km ²
Prey size	Ecology	1 = fruits, 2 = insects, 3 = snails, 4 = frogs, 5 = lizards, 6 = snakes, 7 = fish, 8 = rodents, 9 = birds, 10 = small carrion, 11 = mammals, 12 = large carrion
Mammal and bird prey	Ecology	Occurrence of mammals and birds in the diet: 0 = never, 1 = rare, 2 = common, 3 = exclusively
Prey specialization	Ecology	Scored from 1 (generalist) to 4 (extreme specialist) Krüger (2000)
Hunting method	Ecology	1 = only searching, 2 = searching and handling/killing, 3 = attacks on prey that has low defence or escape potential, 4 = attacks on prey that has high defence or escape potential
Habitat productivity	Ecology	Productivity in g carbon m ² per year Reichle (1970)
Breeding habitat diversity	Ecology	Number of habitats in which a species breeds (tropical forest, subtropical & temperate forest, woodland, freshwater habitats, coastline, marsh, savannah, grassland, mountain, semi-desert)
Migration pattern	Ecology	Scored from 0 (sedentary) to 4 (long-distance migrant) Krüger & Davies (2002)
Breeding latitude	Ecology	Median breeding latitude (°)
Breeding altitude	Ecology	Median breeding altitude above sea level (m)

Extrinsic variables are in bold.

2000; Ferguson-Lees & Christie, 2001). Threat categories were taken from the IUCN (2006) and scored as follows: least concern = 0; near-threatened = 1; vulnerable = 2; endangered = 3; critically endangered = 4. No accipitrid species has gone extinct since 1600 (Thiollay, 1994), so the threat categories 'extinct in the wild' and 'extinct' were not represented in the data. Only the chestnut-shouldered goshawk *Erythrotriorchis buegersi* is classified as 'data deficient' and had to be excluded from the analyses. Threat categories were treated as categorical in the cross-species analysis and as a continuous variable in the contrast analyses (Purvis *et al.*, 2000).

A global population size for each species was obtained from BirdLife International (2000), where available, and from Ferguson-Lees & Christie (2001) in the remainder of cases. The cited figure for a particular species was sometimes simply the product of local abundance estimates and the geographic range size for that species. This will most likely overestimate population sizes because populations are always patchy to some degree. Although such global population-size estimates become increasingly crude with

increasing abundance, most birds of prey are now either sufficiently rare (75% of species are believed to number fewer than 100 000 individuals) and/or well-studied to provide useful estimates (Ferguson-Lees & Christie, 2001).

The geographic range size (in km²) for a species was also taken from Ferguson-Lees & Christie (2001). The ranges of those few species for which a figure was not given were estimated by superimposing distribution maps on a world map. Given the difficulties inherent in their estimation, these figures must be treated as an approximation only. Nonetheless, they should be adequate for broad interspecific comparisons, especially because geographic range sizes vary by six orders of magnitude.

We also collected data on 26 predictor variables, covering morphological, life history and ecological aspects of each species (Table 2). All data was scored by one author (O. K.) and scoring was done blind to the threat status. Data were not available for all variables from all species, especially some tropical rainforest ones, so sample sizes vary (Table 2). We included so many variables because we wanted to capture as much information about a species' biology as

possible. Our definitions of variables such as breeding habitat, prey size and prey specialization are admittedly broad, but this allowed us to score these variables reliably for most species. We preferred this approach to one in which we focussed on a small number of species for which very detailed information exists. Moreover, the broadly defined variables we used have been shown to be meaningful in previous comparative analyses (Krüger & Davies, 2002, 2004; Fowle & Krüger, 2003; Krüger, 2005).

When data were provided for more than one population of a particular species, means were calculated. If a range of values was provided, the midpoint of that range was taken. Morphometric data are mean values for adults of both sexes. Because many raptor species are sexually dimorphic in size, a measure of this was also included. Egg volumes were estimated from egg length and breadth measurements in Schönwetter (1967–1992) and the approximation for egg volume provided by Hoyt (1979), where egg volume = $0.51 \times \text{egg length} \times \text{egg breadth}^2$. The variable 'hunting method' was included to reflect the energetic cost of hunting and the aerial skill level needed. All other variables in Table 1 are either self-explanatory or have been described in more detail elsewhere (Krüger, 2000, 2005; Krüger & Davies, 2002; Fowle & Krüger, 2003).

Data analysis

We started by performing a cross-taxa analysis at the species level, treating each taxon as an independent data point, to show the overall correlation pattern. We used ordinal response models for the analysis of IUCN categories and the non-parametric Spearman's rank correlation for the other two analyses, with sequential Bonferroni's adjustment to correct for multiple testing. Because half and quarter values were assigned in some categorical variables (e.g. a species feeding on lizards and snakes in similar proportions would be given the prey-size value 5.5), they were treated as continuous in each analysis.

To test for phylogenetic signal in the data, we used the randomization test developed by Blomberg, Garland & Ives (2003) and implemented with their MATLAB code PHYSIG. The test randomly distributes tip trait values along the phylogeny and tests whether the given tree better fits the tip trait data compared with the same tree but with tip trait data randomly permuted across the tips of the tree.

We calculated phylogenetically independent contrasts using the method of Felsenstein (1985), as implemented in the computer program CAIC (Purvis & Rambaut, 1995), and we also checked for heterogeneity of variances in CAIC. Variables that did not meet this assumption were excluded from the analysis. The comparative analysis was based on a composite phylogeny of 172 species (73% of the family, available from the authors on request), formed by combining several published phylogenies (Holdaway, 1994; Wink & Sauer-Gürth, 2000, 2004; Gamauf & Haring, 2004; Helbig *et al.*, 2005). Branches were assumed to be of equal length because of the composite nature of the phylogeny.

We developed three separate, forward-stepwise regression models in SPSS to produce minimum adequate models assessing the importance of the predictor variables (Table 1) for IUCN threat status, global population size and geographic range size. At each step, the variable with the lowest *P*-value associated with its *F*-statistic was entered. To check for model robustness, we also performed a backwards elimination procedure (Hair *et al.*, 1995). In comparative analyses, missing data can cause problems (Ackerly, 2000; Fisher *et al.*, 2003), especially when multivariate models are developed. We dealt with this issue in the following ways. A regression equation was calculated between the variable in question and the one with which it had the highest correlation coefficient, and used to derive estimates for missing data points. Correlation coefficients were always above 0.9, so they are likely to give reliable estimates. Between 0 and 15% of data points had to be estimated, with the exception of reproductive rate (30%). We are aware that this approach increases the degrees of freedom of our analyses. However, we also checked whether results remained qualitatively the same with missing data excluded from multivariate analyses (which they did in all cases). To address multicollinearity, we analysed tolerance levels and only included variables above 0.1 tolerance (Hair *et al.*, 1995), thus controlling for significant correlations between different independent variables. Contrast models did not include an intercept and were only considered valid if residuals were distributed approximately normally as assessed by Kolmogorov–Smirnov tests with Lilliefors correction.

Finally, we used the most general predictor variables in a multiple ordinal regression to predict threat status across the family, and thus identify whether any species currently considered safe are predicted threatened using our correlates (see Cardillo *et al.*, 2004, 2006 for a similar approach).

Results

Threat status

Of the 236 species in the family which have a threat status, 172 are categorized as least concern, 29 as near-threatened, 22 as vulnerable, six as endangered and seven as critically endangered. Hence, 14.8% of the species in the family are considered threatened to some degree; 27.1% if the near-threatened category is included.

Threat status covaried significantly with six variables (body weight, body size, plumage polymorphism, egg volume, incubation time, fledging time) across species (Table 3) and showed significant phylogenetic signal ($P < 0.05$). The independent-contrast analysis indicated that threat status increased with increasing body weight and decreased with increasing plumage polymorphism, reproductive rate and display behaviour (Table 4). The multiple regression model was highly significant ($F_{4,167} = 7.27$, $P < 0.001$) and explained 14.8% of the variation in threat-status contrasts.

Table 3 Cross taxa analysis without phylogenetic correction, showing the slope of an ordinal response model for the analysis of IUCN threat status and non-parametric correlations for the other analyses

Variable	<i>n</i>	Status	Population size	Range
Body weight	196	1.811**	-0.207*	0.118
Body size	236	0.025*	-0.114	0.187
Wingspan	231	0.007	-0.034	0.260**
Wing length	231	0.021	-0.035	0.263**
Tail length	231	0.064	-0.117	0.134
Size dimorphism	231	-0.704	0.060	0.115
Plumage dimorphism	236	-0.286	0.138	0.162
Plumage polymorphism	236	-1.087*	0.259**	0.236**
Display behaviour	180	-0.615	0.206*	0.196
Breeding system	236	-0.328	-0.125	-0.162
Reproductive rate	115	-1.408	0.271*	0.032
Egg volume	163	3.108**	-0.330**	0.075
Clutch size	190	-0.412	0.250*	0.023
Clutch volume	160	0.052	0.113	-0.009
Incubation time	148	0.078*	-0.336**	0.008
Fledging time	141	0.023**	-0.397**	-0.060
Population density	145	-0.021	0.308**	0.015
Prey size	236	0.161	-0.093	0.106
Prey specialization	236	0.229	-0.049	-0.043
Mammal and bird prey	236	-0.093	0.033	0.045
Hunting method	236	0.126	-0.125	0.012
Habitat productivity	236	0.001	-0.276**	-0.294**
Breeding habitat	236	-0.277	0.382**	0.447**
Migration pattern	236	-0.385	0.315**	0.352**
Breeding latitude	236	-0.003	0.088	0.146
Breeding altitude	236	0.001	-0.026	-0.044

P-values have been adjusted for multiple testing using sequential Bonferroni's correction.

P*<0.05; *P*<0.01.

IUCN, International Union for the Conservation of Nature and Natural Resources.

Population size

Population size was significantly correlated with 12 explanatory variables across species (Table 3) and showed highly significant phylogenetic signal ($P < 0.01$). The independent-contrast analysis indicated that population size increased with increasing breeding habitat number, clutch size, plumage polymorphism and display behaviour (Table 4). The multiple regression model was highly significant ($F_{4,167} = 21.91$, $P < 0.001$) and explained 34.4% of the variation in population-size contrasts.

Range size

Range size was significantly correlated with six explanatory variables across species (Table 3) and showed significant phylogenetic signal ($P < 0.05$). The independent-contrast analysis indicated that range size increased with breeding habitat number, clutch size, plumage polymorphism and breeding altitude (Table 4). The multiple regression model was highly significant ($F_{4,167} = 19.79$, $P < 0.001$) and explained 32.2% of the variation in range size contrasts.

Species predicted to become threatened

The most general correlates of extinction risk identified across all three response variables were body weight, clutch size, breeding habitat number and plumage polymorphism. Together, they explained 22% of the variance in IUCN threat status across species in an ordinal regression model which was highly significant ($\chi^2 = 34.93$, d.f. = 4, $P < 0.001$). While the model failed to predict a number of threatened species and classified them as least concern instead, it identified three species whose biology predicted them to be a case for concern. Bearded vultures *Gypaetus barbatus*, Himalayan griffons *Gyps himalayensis* and the harpy eagle *Harpia harpyja* are all predicted by their intrinsic biology to be potential cases for the IUCN category 'vulnerable'.

Discussion

Threat status

In 2006, 14.8% of the Accipitridae were considered globally threatened, which is comparable to the figure of 12.4% for all bird species (IUCN, 2006). As predicted, raptor species

Table 4 Multiple regression models examining predictors of independent contrasts in IUCN threat status, population size and range size for Accipitridae ($n=171$)

Variable	β	SE	t	P	R^2	Collinearity
<i>Threat status</i>						
Plumage polymorphism	-0.379	0.103	3.675	0.001	0.074	0.992
Reproductive rate	-0.354	0.122	2.901	0.004	0.103	0.919
Display behaviour	-0.266	0.109	2.431	0.016	0.126	0.967
Body weight	0.784	0.372	2.104	0.037	0.148	0.913
<i>Population size</i>						
Plumage polymorphism	0.494	0.091	5.429	0.001	0.168	0.954
Breeding habitat diversity	0.211	0.043	4.874	0.001	0.277	0.911
Clutch size	0.422	0.136	3.114	0.002	0.325	0.974
Display behaviour	0.215	0.096	2.234	0.027	0.344	0.939
<i>Range size</i>						
Plumage polymorphism	0.387	0.080	4.854	0.001	0.153	0.953
Breeding habitat diversity	0.189	0.037	5.103	0.001	0.246	0.951
Clutch size	0.392	0.117	3.337	0.001	0.295	0.993
Breeding altitude	0.468	0.184	2.549	0.012	0.322	0.992

The overall se of the three model estimates are 0.488, 0.423 and 0.370, respectively, and residuals are approximately normally distributed ($P=0.038, 0.058$ and 0.200 , respectively). The collinearity column shows the redundancy of explanatory variables in the model, with 0 indicating that a variable is completely redundant and values close to 1 indicating high explanatory power independent of other variables in the model.

IUCN, International Union for the Conservation of Nature and Natural Resources.

with larger body weights and slower reproductive rates were more threatened. Such species might be more at risk because they are less able to tolerate any additional mortality inflicted upon them as a consequence of direct persecution or habitat transformation and loss. A high reproductive rate is an effective buffer against population crashes and allows populations to bounce back more quickly. This might be an increasingly critical factor determining extinction risk because human-induced population crashes have been documented for many raptor species (Thiollay, 1994). An example of such species under threat would be the Indian vulture species *Gyps indicus* and *Gyps bengalensis* where populations have recently crashed (Green *et al.*, 2006) and their low reproductive rate might severely constrain their ability to recover.

Threat status also decreased with increasing plumage polymorphism, which might be a marker for the size of the species' gene pool (Fowle & Krüger, 2003), and was also a consistent correlate for both population size and range size. Finally, species with an acrobatic display behaviour were less threatened than species without such displays. We believe that display behaviour most likely captures residual variation not accounted for by any of our other variables, rather than species being able to somersault themselves out of extinction risk; we do not have a clear causal explanation for why the display behaviour should influence extinction risk directly.

Population and range sizes

Variables from all three complexes (morphology, life history and ecology) were found to be important predictors of both a small population size and a small range size in the Accipitridae. As predicted, high habitat specialization limits

population size. Assuming the number of breeding habitats reflects available resources, species occupying broad habitat niches should be better able to survive and/or rear offspring more quickly, thus explaining why species with few breeding habitats have smaller population sizes. Species which can breed in a variety of habitat types also have larger ranges; ecological specialization correlates with a small range size. As mentioned before, the number of breeding habitats likely reflects the overall ability of a species to deal with environmental change and this seems to be of paramount importance when it comes to extinction risk.

Also as predicted, there was a strong positive correlation between clutch size and both population and range size. Developmental-rate variables, such as clutch size, have been shown previously to have strong and consistent relationships with abundance (Gaston & Blackburn, 1996). Species with larger clutch sizes are more effectively buffered against population crashes and should be able to recover from them more quickly (Thiollay, 1994). Clutch size should also affect range size, because habitat fragmentation and alteration leave many scattered and small populations and so stochastic events play an important role. A larger clutch size enables small populations to persist for longer by providing a buffer against both environmental and demographic stochasticity.

Another consistent correlate of both population size and range size was plumage polymorphism: more polymorphic species being associated with larger population and range sizes. Larger populations have a larger genetic variability (Frankham, 1996), which can give rise to polymorphism. Hence, plumage polymorphism might serve as an indicator of a species' gene pool (Fowle & Krüger, 2003); we do not propose here that polymorphism causes larger population sizes, just that it is associated with them. Additionally, it might indicate that a species occupies a large and potentially

heterogeneous habitat, which is often associated with polymorphism (Ferguson-Lees & Christie, 2001). Polymorphism (or rather the lack of it) might therefore act as a potentially useful marker to identify species at risk when more detailed biological information is scarce or absent.

Contrary to our predictions, we found no negative effect of body weight on population size. Several previous studies have found no significant relationship between abundance and body size when considering entire taxonomic assemblages in particular geographic areas (e.g. Blackburn & Lawton, 1994). However, we have used global population sizes for almost all species within a well-studied taxon. As in Gaston & Blackburn's (1996) study of waterfowl, therefore, we have avoided at least two potential criticisms (see Blackburn & Lawton, 1994): first, rare species are well represented in the analyses and, second, the abundances of rare species are represented relatively accurately. We therefore believe our result to be biologically valid and not the consequence of a statistical artefact.

Two further predictions were not supported by our analyses. First, prey size was not found to be an important correlate of global population size. Either the measure we used was too crude or it might be that many raptor species are opportunistic foragers and some species that normally feed on large prey can subsist on much smaller alternative prey (Thiollay, 1994). Second, there was no significant association between geographic range size and indicators of foraging specialization (e.g. hunting method and prey specialization). This contrasts with the negative relationship found in a variety of other taxa (see Harcourt *et al.*, 2002) and might again be because raptors are more opportunistic foragers than reflected by our variables.

Wider issues and implications

In general, macroecological patterns seem particularly vulnerable to data inadequacies, especially in the case of analyses on a global spatial scale (see Gaston, 1994; Gaston & Blackburn, 1996). However, the Accipitridae represent one of the best-known and most intensively studied monophyletic groups of organisms. Although the level of knowledge is poorer for rainforest raptors than it is for temperate ones, we do not believe that this difference generated the qualitative results presented.

In line with many other studies (Gaston & Blackburn, 1996; Blackburn & Gaston, 2002, but see Purvis *et al.*, 2000; Cardillo *et al.*, 2004; Thomas, Lanctot & Szekely, 2006), we found that the amount of variation explained in threat status was low (15%). Nevertheless a few general correlates of extinction risk have emerged and variables such as body weight, reproductive rate, breeding habitat diversity and breeding altitude have been found to be significant correlates of extinction risk in other groups of birds such as wildfowl, shorebirds and Neotropical birds in general (Gage *et al.*, 2004; Thomas *et al.*, 2006; Long *et al.*, 2007). Thomas *et al.* (2006) also emphasized the importance of a multitude of factors influencing extinction risk, rather than any mono-causal explanation.

Decomposing the abstract threat status into population size and geographic range size allowed us to analyse vital contributing variables to threat status, but even the inclusion of extrinsic variables did not result in >35% of the variation being explained for either measure. We believe a crucial factor that we did not manage to include meaningfully is human persecution. Cardillo *et al.* (2004) used human population density to explain extinction risk in carnivores, but found that the amount of variation explained by it (0.5%) was tiny compared with the variation explained by a species' biology (44%). With the true hawks, it is not human population density, but a species' scope for conflict with humans and local attitudes towards a species that are likely to be important (Thiollay, 1994). We believe future comparative research should try and translate this complex interplay between socioeconomic factors and attitudes into candidate variables and this should significantly increase the predictive power of multivariate models.

For a conservation biologist, studying the distribution and abundance of organisms acquires a special meaning: identification of those attributes that predispose species to extinction would help predict future scenarios and facilitate proactive conservation efforts (Fisher & Owens, 2004). We have identified three species that might be predisposed entirely by their biology to be a cause of concern. The bearded vulture has undergone dramatic population declines over most of its range (Ferguson-Lees & Christie, 2001) and is already a threatened species in many countries (Carrete, Donazar & Margalida, 2006). Our knowledge about the Himalayan griffon is particularly scarce and it is unknown how much the species has suffered population crashes due to diclofenac poisoning, as other Asian vulture species have done (Ferguson-Lees & Christie, 2001; Green *et al.*, 2006). Finally, there should be increased concern about the fate of the harpy eagle, the world's most powerful eagle species. It is currently listed as near-threatened, and there is accumulating evidence of further drastic population declines in Central America and also in many parts of South America (Vargas *et al.*, 2006). It is the case for all three species that, while their biology predicts them to be a cause of concern, they live in relatively undisturbed habitats over at least part of their range, which might well explain the difference between our model and the formal IUCN assessment (see also Purvis *et al.*, 2000 for a discussion of this issue).

Different taxa may be put at risk of extinction through different mechanisms (Diamond, 1984; Pimm, Jones & Diamond, 1988; Owens & Bennett, 2000; Blackburn & Gaston, 2002). Our analyses showed that a variety of variable types influence extinction risk and highlight the increasing likelihood that a comprehensive explanation for why some species are common while others are rare will not be dominated by a single factor, either extrinsic or intrinsic. Instead, there will be a need to integrate the small effects of a large number of independent variables.

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