Drivers of Extinction Risk in Terrestrial Vertebrates

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Keywords
Amphibians; birds; endangerment; invasive species; IUCN Red List; mammals; reptiles.

Abstract
Rising rates of extinction create an urgent need to identify the mechanisms and drivers of endangerment. One critical question is whether major phylogenetic lineages are equally at risk to the same threats. We used the IUCN Red List classification to explore the effect of four major threatening processes (habitat alteration, invasive species, climate change and overexploitation) on 7,441 species in four terrestrial vertebrate classes. As expected, species rated as vulnerable to a higher number of threats were also at greater risk of extinction. However, this pattern differed strongly among classes. Notably, invasive species and climate change were strongly associated with increased risk of extinction in birds but not mammals. These large-scale differences might be artifacts of differing methodologies used by class specialists to classify species vulnerability; or might reflect biological differences. That ambiguity needs to be resolved, because it has strong implications for the assessment and amelioration of threatening processes.

Introduction
Species’ vulnerability to extinction depends upon intrinsic factors (e.g., life-history) combined with external factors (e.g., threatening processes). The most comprehensive listing of species’ extinction risk comes from the IUCN (International Union for the Conservation of Nature), who lists over 7,400 species of terrestrial vertebrates (out of about 26,750 species within the four terrestrial vertebrate classes) as near threatened (NT) or at risk of extinction. The IUCN Red List classification is based on a robust system to evaluate the risk of species extinction (Rodrigues et al. 2006; Mace et al. 2008), and has allowed researchers to identify a range of traits that influence vulnerability (e.g., Bennett & Owens 1997; Cooper et al. 2008; Davidson et al. 2009; Siliceo & Díaz 2010). The IUCN also identifies drivers of extinction for each species. Although this latter listing has been criticized as subjective (e.g., Hayward 2009), it is a first step toward a better understanding of extinction mechanisms. For example, the IUCN list of threatening processes has been used to identify predictors of threat sensitivity (e.g., Owens & Bennett 2000; Gonzalez-Suarez et al. 2013). To our knowledge, however, such attempts have always focused on a single vertebrate class (e.g., Stuart et al. 2004; Schipper et al. 2008; Szabo et al. 2012; Böhmb et al. 2013). Because the current extinction crisis is global, affecting all organisms, we also need to investigate similarities and differences between phylogenetic lineages in their sensitivity to the acknowledged extinction drivers. We provide such an analysis here, considering four out of the five vertebrate classes (amphibians, birds, mammals, and reptiles).

Conservation actions should prioritize threats that (1) affect the most species and (2) have the strongest effects on extinction risk. Most analyses of this topic identify four major threat categories: (1) habitat alteration, (2) invasive species, (3) climate change, and (4) overexploitation, although the relative importance of those threat types at a global scale remains poorly known. Despite consensus that habitat alteration is the most significant cause of extinction, the impact of other threats remains debated (Gurevitch & Padilla 2004; Clavero & Garcia-Berthou 2005).

The four terrestrial vertebrate classes comprise species with very different ecological traits and evolutionary
histories, suggesting that the effects of the main threats may differ across classes. Here, we ask whether the major threat categories differently affect the four vertebrate classes. We compare the proportion of species affected by each threat category among classes, and evaluate whether an increase in the number of threatening processes is associated with an increase in the IUCN rating of “vulnerability to extinction” for that species.

Research effort can affect the number of threats associated with a given species in IUCN listings (more intensively studied mammal species are rated as being subject to more threats: Gonzalez-Suarez et al. 2012). We thus included an index of research effort in our analyses. Although it is difficult to predict patterns a priori, we might expect similarities between birds and mammals (endotherms that attracted detailed research) on the one hand, and amphibians and reptiles (ectotherms, subject to less research; Bonnet et al. 2002) on the other. We thus expect more differences between than within these pairs of classes.

Materials and methods

IUCN data

We extracted data on extinction risk and threat sensitivity from the IUCN website in April 2015. We focused our analyses on species identified as NT or at risk of extinction (vulnerable, VU; endangered, EN; or critically endangered, CR). Extinction risk was coded as an ordinal variable from 1 (NT) to 4 (CR).

In the IUCN threat classification scheme version 3.1, up to 99 different threat types are considered, organized in a hierarchical classification. Our large-scale analyses required combining threats into a few broad categories in order to: (1) limit biases in threat identification due to the timing of a species assessment by the IUCN, or to the data available (Hayward 2009); and (2) obtain categories relevant for all four vertebrate classes. We reclassified the threats into the four main threat categories commonly recognized: habitat alteration/destruction (including pollution); invasive species (including disease); climate change; and overexploitation (see Supplementary Material 1), and constructed a binary variable for each threat category (0 = not affected by the threat, 1 = affected).

Research effort

As a measure of research effort for each species, we used the number of publications referenced in the Zoological Record database between 1978 and 2008 (as done for birds by Ducatez & Lefebvre 2014).

Analyses

Number of threats

We first tested whether the number of threats (from 0 to 4) affecting species at risk of extinction varied across classes, using a linear model with the number of threats as response variable, and class and research effort as fixed effects. We then used Tukey HSD tests to compare each pair of classes. Then, we tested whether the effect of the number of threats on extinction risk differed across classes. We used a cumulative link model fitting extinction risk with a multinomial distribution, in the R package “ordinal.” Research effort, class, threat number and the interaction between class and threat number were included as fixed effects. To test which pairs of classes differed significantly, we then ran the same model on each pair of classes and used Bonferroni corrections. To detail the effects of threat number within each class, we built phylogenetic generalized linear models (PGLMMs) within each class (see Supplementary Material 3), standardizing the fixed effects to a mean of 0 and a variance of 1. This method allowed us to control for phylogenetic nonindependence and to obtain estimates of fixed effects comparable across classes. Because not all species listed by the IUCN are included in available phylogenies, the sample size was different for PGLMMs.

Sensitivity to threats

We then tested whether classes differed in their sensitivity to each threat category, using generalized linear models with a binomial distribution and a logit link. Sensitivity to each threat was included as response variable (we thus built 4 models, one per threat category) with research effort and class included as explanatory variables. We used Tukey HSD post hoc tests. To test whether the effect of each threat category on extinction risk differed across classes, we ran the same models described above, replacing the variable number of threats by the sensitivity to each threat type (testing the interaction between class and each threat type). We included all four threat categories in the same model to ensure that the effects of multiple threat categories were not confounded. Research effort was included as a covariate. We used similar post hoc tests as described above, and we also built PGLMMs within each class. Including geographic range size in the analyses did not affect the results (see Supplementary Materials 4–6), nor did excluding marine mammals. The date a species was last assessed for the IUCN red list was also considered in analyses, but it did not affect our main results (see Supplementary Material 8). We report means ± SE.
Results

Number of threats

The mean number of threats attributed to a given species varied across classes (χ² = 77.94, df = 3, P < 0.001; all post hoc Tukey HSD tests P < 0.001 except birds vs. mammals P = 0.70). The average number of threats per species was highest in birds (1.50 ± 0.20) and mammals (1.47 ± 0.23) followed by amphibians (1.33 ± 0.16) and reptiles (1.03 ± 0.24). Species that attracted more research were adjudged as vulnerable to more threatening processes (χ² = 368.18, df = 1, P < 0.001), but to be at lower risk of extinction (LRT = 6.43, df = 1, P = 0.011). We thus included research effort in our models. The effect of threat number on extinction risk varied across classes (interaction between number of threats and class: LRT = 32.90, df = 3; P < 0.001). After Bonferroni correction, the rate of increase in extinction risk with an increased number of threats was lower in mammals than birds (LRT = 19.88, P < 0.001) or amphibians (LRT = 29.91, P < 0.001), and lower in reptiles than in amphibians (LRT = 8.29, P = 0.024). All other comparisons had P > 0.14. PGLMMs within each class also showed that extinction risk increased with threat number in all classes, but most rapidly in birds, then reptiles, amphibians, and finally mammals (Table 1, see also Figure 1). The negative correlation between research effort and risk of extinction was significant in all intraclass analyses except for mammals (Table 1).

Because these analyses identified mammals as deviating from the patterns seen in other classes, we explored why mammals differ from birds (the group they most resemble in metabolic mode and research effort) in the effect of threat number on extinction risk. Two plausible contenders are the facts that most birds fly, whereas most mammals do not; and that many birds are restricted to islands. We thus separated mammals into flying versus nonflying (Chiroptera versus others) and compared these two groups of mammals with birds. We also separated birds and mammals into insular versus continental species and then compared the four groups obtained. We used the same method as for comparisons across the four classes. Strong differences between mammals and birds remained (see Figure 1b and Supplementary Material 9), although the effect of threat number on extinction risk did not differ significantly between Chiroptera versus birds, nor between mammals (both continental and insular) and continental birds. Insular birds were more imperiled by an increase in number of threats than were continental birds, continental mammals, or insular mammals.

Sensitivity to threats

The classes differed in their sensitivity to each of the four threat categories (all P < 0.001; for details, see Figure 2). Habitat alteration was the most important threat for all four classes (64%–86% of species affected). Although invasive species are often considered as the second most important threat overall, this was only true for amphibians (for which, 27% of species were affected). The proportion of threatened species affected by invasive taxa was lower in mammals and reptiles (16% in both classes) than in birds (23%). Birds were highly affected by climate change (24%; see Figure 2). Finally, direct overexploitation affected mammals (42%) and birds (30%) more than reptiles (15%).

We then tested for between-class differences in the effect of each threat category on extinction risk. The effects of all four threat categories on extinction risk differed among classes (all interactions P < 0.001). Post hoc analyses show that invasive species had less effect on extinction risk in mammals than in the three other classes (Table 2, Figure 3), whereas habitat alteration had more effect on amphibians than on reptiles or mammals (Figure 3). Climate change increased extinction risk in
birds and amphibians, but not in mammals or reptiles (Figure 3, Table 2). Finally, overexploitation increased extinction risk at similar rates in mammals, birds and reptiles, but had no significant effect in amphibians (Figure 3). Intraclass PGLMMs supported these conclusions, with all four categories of threat additively affecting extinction risk in birds and amphibians (except that overexploitation did not affect extinction risk for amphibians). However, mammals were only affected by habitat alteration and overexploitation, and reptiles by invasive species and overexploitation (with a marginal effect from habitat alteration: Table 3).

Again, the difference between mammals and birds, especially in response to invasive species, might be due to differences in either flight or insularity. We thus tested whether the effects of invasive species on extinction risk differed between Chiroptera, non-Chiroptera mammals and birds on one side, and continental and insular birds and mammals on the other. The effect of invasive species was similar in birds and Chiroptera. In contrast, it was stronger on insular birds than on the three other groups (insular mammals and continental birds and mammals; see Supplementary Materials 9 and 10). The greater effect of invasive species on extinction risk for birds than mammals was thus mostly due to the vulnerability of insular birds to invaders.

Discussion

The IUCN red list provides the most extensive database describing species endangerment, with the current version (2015-4) covering over 59,000 animal and 20,700 plant species. It thus provides a powerful tool to investigate endangerment processes. Backed by substantial research and financial investment, this database is
Drivers of extinction risk in vertebrates
S. Ducatez & R. Shine

Figure 2 Proportion of near-threatened and threatened species affected by each of the four threat categories used in the current analysis (habitat alteration, invasive species, climate change, overexploitation). Data are shown separately for mammals, birds, reptiles and amphibians. Letters indicate the significance of differences between classes within each threat category.

Table 2 Post hoc tests of between-class differences in the effect of four types of threatening processes (habitat alteration, invasive species, climate change, overexploitation) on extinction risk in four vertebrate classes. P-values are given after Bonferroni corrections. All four types of threat were included in each model, and the LRT test depicts the effect of the interaction between a given threat and class identity (significant effects are in bold type).

| Threat Category | Class       | LRT    | P-value |
|-----------------|-------------|--------|---------|
| Habitat alteration and destruction | Birds       | LRT = 4.883; P = 0.163 | – |
|                  | Mammals     | LRT = 10.492; P = 0.006 | – |
|                  | Reptiles    | LRT = 8.082; P = 0.027 | – |
| Invasive species | Birds       | LRT = 4.411; P = 0.214 | – |
|                  | Mammals     | LRT = 14.457; P < 0.001 | LRT = 29.551; P < 0.001 |
|                  | Reptiles    | LRT = 0.183; P = 1 | LRT = 0.925; P = 1 |
| Climate change   | Birds       | LRT = 0.005; P = 1 | – |
|                  | Mammals     | LRT = 31.385; P < 0.001 | LRT = 36.171; P < 0.001 |
|                  | Reptiles    | LRT = 13.102; P = 0.002 | LRT = 13.884; P < 0.001 |
| Overexploitation | Birds       | LRT = 25.881; P < 0.001 | – |
|                  | Mammals     | LRT = 15.066; P < 0.001 | LRT = 2.975; P = 0.510 |
|                  | Reptiles    | LRT = 8.877; P = 0.017 | LRT = 2.588; P = 0.646 |

used internationally to guide political decisions affecting species conservation. Understanding its strengths and limits is thus important. Our comparative analysis reveals major divergences across vertebrate classes in the IUCN listings of identified threats, and in the relationship between those threats versus vulnerability to extinction. Either these patterns are biologically meaningful, and/or they result from differences in how species from different classes have been assessed by the IUCN’s experts. Understanding the roles of those two processes is important in ensuring rational decision-making for international conservation efforts.

First, the mean number of threats identified in the IUCN listing differs among classes, even at the same level of extinction risk. For example, a reptile species is rated as being at risk from about 30% fewer threats than a bird or mammal (Figure 1). This pattern partly reflects differences in research effort, but remains obvious even after correcting for this factor. Similarly, species listed as subject to more threats also are ranked as at higher risk of extinction, but that relationship differs among classes. In birds, more threats translate into a much higher risk of extinction—whereas in mammals, the relationship is weak. Knowledge base is unlikely to explain this
Drivers of extinction risk in vertebrates

S. Ducatez & R. Shine

Figure 3 Effects of each IUCN threat type [habitat alteration (a), invasive species (b), overexploitation (c), climate change (d)] on the IUCN rating of extinction risk for species in four vertebrate classes. Letters indicate the significance of slope differences between classes. They refer to post hoc tests made on models including all threat categories. NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered. Note that the y-axis scales differ across panels because of important differences in the average proportion of species affected by each threat category.

difference between birds and mammals, as both classes were attributed similar mean numbers of threats. The similarity in the “threats versus risk” relationship between flying mammals (Chiroptera) and continental birds suggests that mobility may strongly influence vulnerability, but the broader paradox of the differences between birds and mammals remains.

Habitat alteration was the threat affecting the most species in all four classes. Although frequently cited as the second most important threat overall, invasive species had this rank only in amphibians (reflecting the impact of disease organisms such as chytrid fungus and ranaviruses: Hof et al. 2011). In contrast, exposure to invasive species did not increase the IUCN rating of a species’ vulnerability in mammals or continental birds (although for insular birds, invasive species were a major risk). The overall discrepancy between mammals and birds in their vulnerability to invaders thus reflects the greater ability of birds to colonize insular habitats, where invaders can be devastating. The globally lower effect of invasive species on mammals may depend on scale, with Australian mammals particularly sensitive to invasive species (Woinarski et al. 2015). Reanalysis focusing on Australian species revealed similar effects of invasive species on all four classes in Australia (see Supplementary Material 11). The strong global pattern we observe can thus vary locally, depending on the environment and the history of human colonization.

Our analysis of IUCN data identified climate change as an important driver of endangerment for birds, whereas mammals and reptiles were less affected by this threat. Although amphibians affected by climate change were at higher risk, this threatening process was identified as important for relatively few amphibians (Figure 2). Assessing a species’ vulnerability to climate change is difficult; predicting future impacts requires substantial data on a species’ life history, physiology and ecology (Pearson et al. 2014). Birds are a model group for the study of climate change effects (e.g., Barbet-Massin et al. 2011; Barbet-Massin & Jetz 2015), probably explaining why they have been classified so differently from the other classes in their vulnerability to this threat. Unsurprisingly, given that most endotherms are much larger than most ectotherms (Pough 1980), and thus provide more meat, hides, etc., overexploitation was rated as a greater threat for mammals and birds (and to a lesser extent reptiles) than for amphibians.

The patterns above could be confounded by several variables, including phylogenetic nonindependence within classes, differences in geographic range size,
Table 3 Phylogenetic generalized linear mixed models testing for the (additive) effect of four types of threatening processes (habitat alteration, invasive species, climate change, overexploitation) on extinction risk in threatened and near-threatened species of four vertebrate classes. We used the MCMCglmm R package and included phylogeny and biogeographic area as random factors and research effort as a fixed effect (significant effects are in bold type).

| Class | Explanatory variable | Prm   | CI               | pMCMC |
|-------|----------------------|-------|------------------|-------|
|       |                      |       |                  |       |
|       | Research effort      | -0.093| [-0.192; -0.011] | 0.030 |
|       | Habitat alteration   | 0.215 | [0.135; 0.285]   | <0.001|
|       | Invasive species     | 0.163 | [0.067; 0.256]   | <0.001|
|       | Climate change       | 0.248 | [0.174; 0.335]   | <0.001|
|       | Overexploitation     | -0.034| [-0.124; 0.060]  | 0.452 |
| Birds | Research effort      | -0.123| [-0.208; -0.042] | 0.002 |
|       | Habitat alteration   | 0.136 | [0.060; 0.224]   | <0.001|
|       | Invasive species     | 0.302 | [0.220; 0.377]   | <0.001|
|       | Climate change       | 0.299 | [0.231; 0.372]   | <0.001|
|       | Overexploitation     | 0.189 | [0.104; 0.265]   | <0.001|
| Mammals| Research effort    | -0.029| [-0.143; 0.088]  | 0.629 |
|       | Habitat alteration   | 0.173 | [0.067; 0.275]   | <0.001|
|       | Invasive species     | 0.052 | [-0.057; 0.162]  | 0.366 |
|       | Climate change       | 0.061 | [-0.036; 0.160]  | 0.250 |
|       | Overexploitation     | 0.226 | [0.098; 0.364]   | 0.002 |
| Reptiles| Research effort   | -0.145| [-0.292; 0.019]  | 0.086 |
|       | Habitat alteration   | 0.141 | [0.024; 0.278]   | 0.070 |
|       | Invasive species     | 0.454 | [0.264; 0.641]   | <0.001|
|       | Climate change       | 0.111 | [-0.060; 0.242]  | 0.164 |
|       | Overexploitation     | 0.156 | [0.002; 0.293]   | 0.024 |

Differences in threat exposure across biogeographic realms, or even depend on the way threats were categorized. However, controlling for these variables did not change any of our basic conclusions. Similarly, the year in which a species was assessed, although it influenced the extinction risk and the number of threats attributed, did not explain the discrepancies among classes. We thus propose three hypotheses, not necessarily exclusive, to explain our results. First, biological differences between the four classes are important. For example, the difference between mammals and birds in response to invasive species was mostly due to the high proportion of island-dwelling birds that are threatened by invasions. Other biological phenomena may also be important. Second, the taxon-specific IUCN specialists who constructed these rankings may be influenced by the traditions and practices of their disciplines. Although the IUCN rankings are based on quantitative and consistent criteria, different workers may interpret those criteria differently (a problem exacerbated by differences in data availability and in comprehensiveness of assessment). Finally, an apparently consistent criterion (e.g., range size) may translate differently into extinction risk in different classes: a population of tigers requires a larger geographic area than a population of salamanders. Similar population numbers or geographic range sizes may have different consequences for organisms from different classes, a complexity that is difficult to include objectively in IUCN red-list procedures.

The huge IUCN red-list dataset is exactly the kind of database we need in order to prioritize conservation actions; but in order to do so, we need to be clear and consistent about how and why we rank species of all classes. How can we improve the accuracy and across-class consistency of IUCN threat assessments? First, we need to develop quantitative indices based on objective criteria to assess threat impacts. Second, we suggest that when developing these new indices, or reviewing extinction risks and threat levels for species within a given class, the people tasked with these jobs should include at least one expert on a different class, or people whose expertise covers more than one class (to maintain among-class consistency). The critical question to ask after classifying a species’ threat level is “based on the available data, would we have arrived at a different categorisation if this animal was a frog and not a rodent?” Progress is already evident. The IUCN recently developed a new threat assessment and scoring protocol based on quantitative criteria that should facilitate more accurate IUCN threat assessments. Nonetheless, unconscious “taxonomic chauvinism” (Bonnet et al. 2002) will remain a threat: we need to carefully consider potential biases in threat assessments across taxonomic groups. Finally, it is important to keep in mind that even the most accurate and comparable
indices will always have limits, especially at large taxonomic scales. Even when quantitative thresholds are in place for threat evaluation, divergent biological features of major lineages will inevitably generate divergences in (for example) the relationship between range size and threat level. No single set of criteria will ever be perfect, but we need to recognize, understand and respond to the imperfections of existing schemes if we are to most effectively frame global conservation plans.

Acknowledgments
We thank the IUCN, and all the experts whose work has allowed the construction and open access to the IUCN Red List database. Our research was supported by the Australian Research Council (ARC).

Supporting Information
Additional Supporting Information may be found in the online version of this article at the publisher’s web site:

**Supplementary Material 1.** Methods: threat reclassification.

**Supplementary Material 2.** Supplementary Table: number of species within each extinction risk and threat category.

**Supplementary Material 3.** Methods: Phylogenetic generalised linear mixed models (PGLMM).

**Supplementary Material 4.** Methods: Geographic range size.

**Supplementary Material 5.** Supplementary Table: Effects of the number of threats on extinction risk within each Class including geographic range size as covariate.

**Supplementary Material 6.** Supplementary Table: Effects of each threat category on extinction risk within each Class including geographic range size as covariate.

**Supplementary Material 7.** Supplementary Material: Effects of threats categorization method - using the 12 IUCN threat categories instead of a reclassification into 4 categories.

**Supplementary Material 8.** Supplementary Analyses: effects of IUCN assessment year.

**Supplementary Material 9.** Supplementary Table: flight ability, insularity and the effect of threat aggregation on extinction risk in birds and mammals.

**Supplementary Material 10.** Supplementary Figure.

**Supplementary Material 11.** Supplementary analyses: focus on Australia.

**Supplementary Material 12.** Supplementary Figure.

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