
Incorporating Evolutionary Measures into Conservation Prioritization

DAVID W. REDDING* AND ARNE Ø. MOOERS

Simon Fraser University, Burnaby BC V5A 1S6, Canada

Abstract: *Conservation prioritization is dominated by the threat status of candidate species. However, species differ markedly in the shared genetic information they embody, and this information is not taken into account if species are prioritized by threat status alone. We developed a system of prioritization that incorporates both threat status and genetic information and applied it to 9546 species of birds worldwide. We devised a simple measure of a species' genetic value that takes into account the shape of the entire taxonomic tree of birds. This measure approximates the evolutionary history that each species embodies and sums to the phylogenetic diversity of the entire taxonomic tree. We then combined this genetic value with each species' probability of extinction to create a species-specific measure of expected loss of genetic information. The application of our methods to the world's avifauna showed that ranking species by expected loss of genetic information may help preserve bird evolutionary history by upgrading those threatened species with fewer close relatives. We recommend developing a mechanism to incorporate a species' genetic value into the prioritization framework.*

Keywords: birds, evolutionary worth, global avifauna, IUCN Red List, phylogenetic diversity, threatened species

Incorporación de Parámetros Evolutivos a la Definición de Prioridades de Conservación

Resumen: *La definición de prioridades de conservación está dominada por el estatus de amenaza de la especie candidata. Sin embargo, las especies difieren marcadamente en la información genética compartida que contienen, y esta información no es tomada en cuenta si las especies son priorizadas solo por el estatus de amenaza. Desarrollamos un sistema para priorizar que incorpora tanto el estatus de amenaza como la información genética y lo aplicamos a 9546 especies de aves a nivel mundial. Diseñamos una medida simple del valor genético de una especie que toma en cuenta la forma del árbol filogenético completo de las aves. Esta medida se aproxima a la historia evolutiva que contiene cada especie y se agrega a la diversidad filogenética de todo el árbol taxonómico. Posteriormente combinamos este valor genético con la probabilidad de extinción de cada especie para crear una medida especie-específica de la pérdida de información genética esperada. La aplicación de nuestros métodos a la avifauna mundial mostró que la clasificación de especies por la pérdida de información genética esperada puede ayudar a preservar la historia evolutiva de las aves al elevar la categoría de aquellas especies amenazadas con menos parientes cercanos. Recomendamos el desarrollo de un mecanismo para incorporar el valor genético de una especie al marco de definición de prioridades.*

Palabras Clave: aves, avifauna global, diversidad filogenética, especies amenazadas, Lista Roja IUCN, valor evolutivo

Introduction

The most widely recognized system to determine the threat status of a species is the IUCN (World Conserva-

tion Union) Red List (Gärdenfors et al. 2001). The IUCN Red List provides scientific decision-making guidelines with which to assign species into categories of threat based on threshold values of population parameters, such

*email dredding@sfu.ca

Paper submitted September 8, 2005; revised manuscript accepted April 18, 2006.

as range of occurrence and population decline (Mace & Lande 1991). The categories, indicating decreasing risk of extinction, are critically endangered (CR), endangered (EN), vulnerable (VU), lower risk/conservation dependent (LR/cd), lower risk/near threatened (LR/nt), and least concern (LC). Although it was not intended as a prioritization metric, the lack of a globally accepted alternative means that the IUCN Red List status or other threat status measures are often seen as being synonymous with conservation priority (Possingham et al. 2002; Avise 2005). Categorizations used in this way assume that all species are of equal worth except for their threat status.

Species differ substantially in the amount of unique genetic information they embody (May 1990; Vanewright et al. 1991; Faith 1992; Crozier 1997). Several metrics have been developed to capture genetic variation (reviewed in Diniz 2004). If species were ranked for conservation purposes based on these metrics, resources would be preferentially allocated to those species that embody disproportionately large amounts of unique genetic information above those with many close relatives.

May (1990) discusses the genetic value of species in relation to the conservation of tuataras (*Sphenodon* spp.). He cites a study by Daugherty et al. (1990) that suggests that there are two species of tuatara within the suborder Rhynchocephalia, the sister group to Squamata (the snakes, lizards, and amphisbaenians, a group containing over 6000 species): these two tuatara species are thought to represent 0.3–7% of the unique genetic information found in both suborders (Vanewright et al. 1991). Until 1990 all tuatara were considered a single species (*Sphenodon punctatus*) that was “neither rare nor endangered” (Williams & Given 1981). Prior to its recognition as a full species, the Cook Island Tuatara *S. guthberi* became extinct in one of only two sites where it occurred (Daugherty et al. 1990). The IUCN now ranks *S. guthberi* as vulnerable. There are, however, 100 species in Squamata and Rhynchocephalia with the same threat rank and 65 that are deemed more threatened.

Nevertheless, if a prioritization system that explicitly incorporated genetic distinctness had been applied earlier to this species, it is likely that the taxonomic uncertainty would have been resolved, perhaps preventing the loss of key populations. We propose and evaluate a potential prioritization system.

Meffe and Carroll (1997) suggest that evolutionary and ecological value should be the key components of any system that assigns conservation priority. Evolutionary importance, however, is difficult to quantify because of problems such as difficulties in determining what constitutes “evolutionarily significant units” (e.g., Erwin 1991) and the relationship between phenotypic and genetic variation (e.g., Diniz 2004). In our heuristic analysis, we applied the precautionary principle and sought to maximize genetic distinctness.

Promoting species for conservation priority based solely on high levels of genetic information would fail, in the opposite way from that which led to *S. guthberi*'s demise, by potentially ignoring those species in greatest peril (Possingham et al. 2002). Nevertheless, by calculating the expected loss of genetic information for a group of species, which is the product of the probabilities of extinction and a value of genetic diversity, the two approaches can be combined (Witting et al. 1994). We applied this thinking to the bird species on the IUCN Red List.

Little is known about how threat status and measures of genetic diversity are related. Previous work suggests that species with high levels of unique genetic information are more likely to be threatened (e.g., Purvis et al. 2000). This suggests that prioritization based solely on threat status may also capture genetic uniqueness, but the overlap between ranking species for their genetic value and by threat has yet to be quantified. Therefore, we carried out a comparative assessment to determine whether threat status and expected loss of genetic information produce similar rankings of taxa. We asked whether species in higher threat categories embody more genetic uniqueness and how the rankings of bird species are different if they are ranked by a prioritization metric that combines statutes and genetic value, as suggested by Witting et al. (1994), as opposed to one based on their threat status alone.

Methods

Study System and Evolutionary Tree Considerations

Following von Euler (2001), we used Monroe and Sibley's (1993) 13-level taxonomy of 9702 bird species to estimate the shape and branch lengths of the evolutionary tree for the global avifauna. Node ages were estimated using a calibration factor of $\Delta TH_{50} 1.0 = 4.7$ million years (MY) (Sibley & Ahlquist 1990), which is consistent with a hypothesized Eoaves-Neoaves split at approximately 130 MY (Cooper & Fortney 1998; for alternative dates see, e.g., Feduccia [1995]). The tree was produced from a manual analysis of the taxonomy (see Crozier et al. [2005] for advances in automating this step). Because this is a heuristic analysis, we considered a tree based on Monroe and Sibley appropriate due to its relative simplicity and wide taxonomic coverage.

Each species in the tree was allocated a threat-status category from the IUCN Red List (downloaded from www.redlist.org). We used only the major threat categories, with the three LR/cd and all LR/nt species condensed into the lower-risk category, which left us with five categories in total: CR, EN, VU, LR, and LC. We designated any species classified as CR, EN, or VU as threatened and any LR or LC species as unthreatened. We used Avibase (Lepage 2005) as a reference to resolve categorization disputes due to name changes. Species

from the 9702 in the Monroe and Sibley taxonomy that were extinct, extinct in the wild, data deficient, or taxonomically uncertain (156 species) were excluded from the analysis, and the final data set contained 9546 species, of which 1090 were categorized as threatened.

Assigning Extinction Probabilities to Threat Categories

The threshold probability of extinction (criterion E) can be used, under the IUCN Red List Guidelines, to assign species to the three threatened species categories (IUCN 2001). Species that have a predicted probability of extinction $p_e > 0.5$ in 10 years are designated CR, those with $p_e > 0.2$ in 20 years are designated EN, and those with $p_e > 0.1$ in 100 years are designated VU. Ideally, extinction probabilities are estimated for each species based on a standardized approach, such as population viability analysis (PVA). In anticipation of future precision and to allow quantitative comparisons among species in the absence of such data, we used the criterion E value to assign p_e values to each bird species.

To do this, we first extrapolated the extinction probabilities to a common time scale (here, 100 years). Because such extrapolations are problematic (Kindvall & Gärdenfors 2003), we also calculated values of p_e for categories CR and EN based on published p_e data derived from full PVAs (O'Grady et al. 2004). We compared these values to our extrapolations. There were an average of 12 bird-species values for the CR and EN categories, always at the 100-year time frame. For the EN category the p_e value was qualitatively very similar to the extrapolated p_e calculated by assuming extinction risk remains constant over 100 years (mean 0.315 vs. extrapolated 0.328). For CR the mean value of probability of extinction suggested that a lower score was more appropriate (mean 0.786 vs. extrapolated 0.999). The category VU has a designated criterion E value of 0.1 over a 100-year period, so there was no need to extrapolate.

For LC species there is no associated p_e value in the IUCN guidelines. Therefore, we hypothesized that approximately 0.01% or 7 out of the approximately 7000 LC species will go extinct within 100 years. This seems a reasonable estimate because over the next century the extinction rate could be 10 times higher than the current rate (Pimm et al. 1995) and because over the previous 100-year period approximately two previously abundant species became extinct (*Ectopistes migratorius*, *Conuropsis carolinensis*).

Finally, we fit a power curve ($y = 0.007x^{4.1234}$, $r^2 = 0.999$) to these four probability measures to interpolate a p_e for the LR category, which assigned LR species a p_e of 0.02. Our measures are heuristic only; the approach we apply below can be used for any set of species with associated p_e values. It is also possible to perform a sensitivity analysis to measure the effect of assigning different probability values to the categories. This would be an im-

portant step if a system, such as the one we suggest, were put into practice.

Assigning Species Genetic Distinctness Values

Based on the average age of each taxonomic level (Sibley & Ahlquist 1990), the global evolutionary tree of avifauna contains approximately 79.9×10^9 years of evolutionary history (EH; Nee & May 1997). We apportioned this history among all the species, based on their position in the tree, with an equal-splits approach:

$$ES = \sum_{j=1}^r \frac{B_j}{\prod_{k=1}^j (d(k) - 1)}, \quad (1)$$

where j is the internal node on direct path from i to root (r), B_j is the edge length from internal node j to $j - 1$, and $d(k)$ is the degree (three for bifurcation) at node k .

The equal-splits approach divides the evolutionary time represented by a branch equally among its daughter branches. The sum of the equal-splits value from every taxonomic level is the estimated amount of evolutionary time each species embodies (Fig. 1). This measure reflects how evolutionarily isolated a species is and therefore approximates how genetically distinct it is from the other species in the tree.

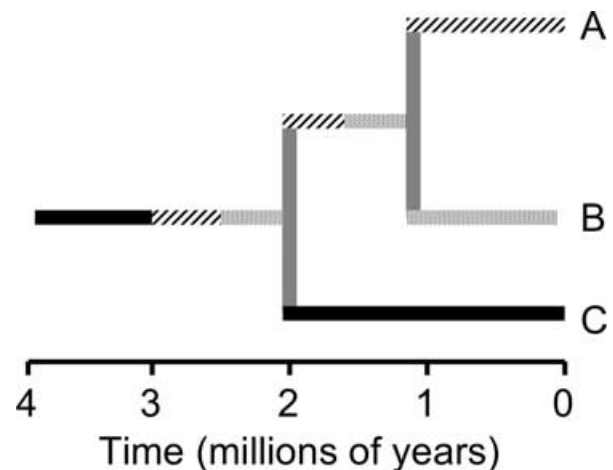


Figure 1. The equal-splits approach is used to apportion the total EH (Nee & May, 1997) of this tree (8 million years) among the three constituent species in the tree (A, B and C). The branch that represents the common ancestor to all three species from 4 MY to 2 MY ago is divided equally among clade (AB) and clade C, and therefore each group is awarded 1 MY. The branch for the common ancestor of (AB) is divided equally between A and B, awarding each 0.5 MY. Summing these with their individual branch lengths, the equal-splits value for species A is 2 MY, for species B, 2 MY and for species C, 3 MY. The sum of these values equals the total EH of the clade.

Our measure differs from calculating PD (Faith 1992) and genetic diversity (Crozier 1992) for a single species. A PD value for a species is calculated either as the distance from the species to the root, which is the same for all species, or its age, or pendant edge value (Altschul & Lipman 1990) (i.e., the length of the branch from the tip to where it joins the tree). Our measure distributes the entire tree among all its constituent species. Under a simple model of tree production (Hey 1992), equal-splits values are positively correlated with pendant edge scores (Spearman's correlation coefficient, $\rho = 0.71$, $p < 0.05$; 100, 16-taxa trees). This correlation is not perfect and shows that these two measures incorporate different information. Clearly, where the species joins the tree is a key factor in determining its equal-splits score, but the value also depends on the length of all branches between it and the root and the number of species that share those branches with the focal species at each node.

Indeed, this is its strength. More of the total evolutionary history of the clade is apportioned to those taxa that have long pendant edges, are members of species-poor clades, and that diverged from the tree near its root. The equal-splits measure captures more information about how isolated that species is on the tree, weighing more isolated species more highly. In this way, it takes into account the evolutionary redundancy present in the surrounding tree, giving greater value to species whose genetic history is not shared with many other species. The measure also apportions the entire tree uniquely among its tips, such that the sum of the equal-splits measure across the tips equals the total PD of the tree (Pauplin 2000; Semple & Steel 2004). For the global avifauna the distribution of equal-splits scores is highly skewed and could not be normalized with any common transformation. Therefore it was used in this analysis in an untransformed state.

Relationship between Equal Splits and Probability of Extinction

To test how genetic distinctness and threat are related, we used Monte Carlo simulation, a nonparametric approach that uses resampling with replacement (in the Poptools program; Hood 2004). We created a distribution, based upon 10,000 random samples from all 9,546 bird species, of the summed equal-splits values from 1,090 species to estimate the population mean μ and variance σ^2 . This group size corresponds to the total number of species from the categories CR, EN, and VU. The null hypothesis is that any difference between the sum of the equal-splits values observed in the 1090 IUCN threatened bird species and the estimated population mean is due to chance. Therefore, the number of samples taken that exceeded the observed total seen in threatened species, can be divided by the number of replications (in this case

10,000) to give a "true" probability of the likelihood of the observed value occurring by chance.

We also modeled the distribution of species within the threatened (VU and worse) and nonthreatened (LR and LC) categories by applying a logistic regression with equal splits as the covariate (see Purvis et al. 2000). This was done to test whether a logistic model containing equal splits adequately described whether a species was designated as threatened or not, thus assessing the strength of the relationship between threat status and genetic distinctness.

We then created five more distributions (again $n = 10,000$) for total equal splits in groups of species with the same size as each of the five IUCN categories (158, 291, 641, 716, 7740). Using the same assumptions, we calculated how many samples exceeded the observed amount of summed equal-splits values, seen in each threat category, with the null hypothesis that any variation was due to chance.

Relationship among Equal Splits, Family Species Richness, and Probability of Extinction

To see how equal splits compared with a measure previously used to assess the relationship between genetic distinctness and threat (family species richness; Purvis et al. 2000), we compared our results from the above tests to those based on family species richness. We first tested for a correlation between equal splits and family species richness and then repeated the resampling tests above with family species richness instead of equal-splits values.

We created a null distribution, with 10,000 samples, of the average size of families to which 1,090 randomly drawn species belong, reapplying the Monte Carlo method we used for the equal-splits measure. From this distribution we determined how often values that are the same as or greater than the average family species richness for all 1090 threatened species occurred, therefore determining the probability of this value occurring by chance. We then modeled the distribution of species within the threatened and nonthreatened categories with a logistic regression, this time with family species richness as the covariate (Purvis et al. 2000).

Finally, we created five additional distributions ($n = 10,000$) for average family species richness in groups the same size as each of our categories (158, 291, 641, 716, 7740) and used the same assumptions tested to see if family species richness in each of the individual categories was significantly different from the estimated mean.

Incorporating Evolutionary Values into Conservation Prioritization

The species-specific expected loss of evolutionary history (EL) was calculated using an equation modified from the one used to determine expected loss of evolutionary

history for groups of species (Witting et al. 1994; Weitzman 1993, 1998):

$$EL = ES_i \cdot Pe_i, \quad (2)$$

where ES_i is the evolutionary history embodied by species i and Pe_i is the probability that the species i will become extinct within the time frame of interest.

All species were then ranked by expected loss and again separately by IUCN threat category. We compared the two rank orders to determine the percentage of overlap in species at five different points in the rank sequences. These points were the first 158, 449, 1090, and 1806 species, corresponding to the group sizes of CR, CR, and EN, all threatened species, and threatened and LR species. Finally, we used two cumulative distributions of evolutionary history values (expected loss and threat) to determine the difference in history captured at the same five points in the ranking sequence.

Results

The avian tree is highly imbalanced (von Euler 2001), and as a result species-specific PD was highly skewed, with 73% of species having values lower than the mean (Fig. 2). The mean was 8.319 MY (SD = 4.79 MY). *Strutho camelus* (Southern Ostrich) had the highest value, 92.31 MY, due to its basal and monotypic status.

Threatened species embodied more evolutionary history than expected by chance (Monte Carlo, $n = 10,000$, $p < 0.001$). This relationship did not seem to be influenced specifically by any of the threat categories (i.e., CR, EN, VU; Monte Carlo for the three subsamples $n = 10,000$, all $p > 0.05$).

Equal splits significantly but poorly predicted whether a species was threatened or not (logistic regression, pseudo $r^2 = 0.01$, $p < 0.05$). Although there was more evolutionary history embodied by threatened species than expected in a group size, the difference only represented a 3.8% increase over the population mean or 348 MY (0.4% of the PD of the entire tree) more evolutionary history in threatened species than expected.

As a point of comparison, if the most threatened species were also the most distinct, giving a perfect positive correlation between level of threat and evolutionary history embodied, then there would be 20,939 MY more evolutionary history in the 1,090 threatened species (a 229% increase over the mean) than evolutionary history in 1,090 species chosen at random.

Family species richness was a different but related measure to equal splits (Spearman's correlation coefficient, $\rho = 0.196$, $p < 0.001$). The weak positive correlation suggests the two measures captured different information. Family species richness also significantly but poorly predicted whether a species was threatened or not, yielding

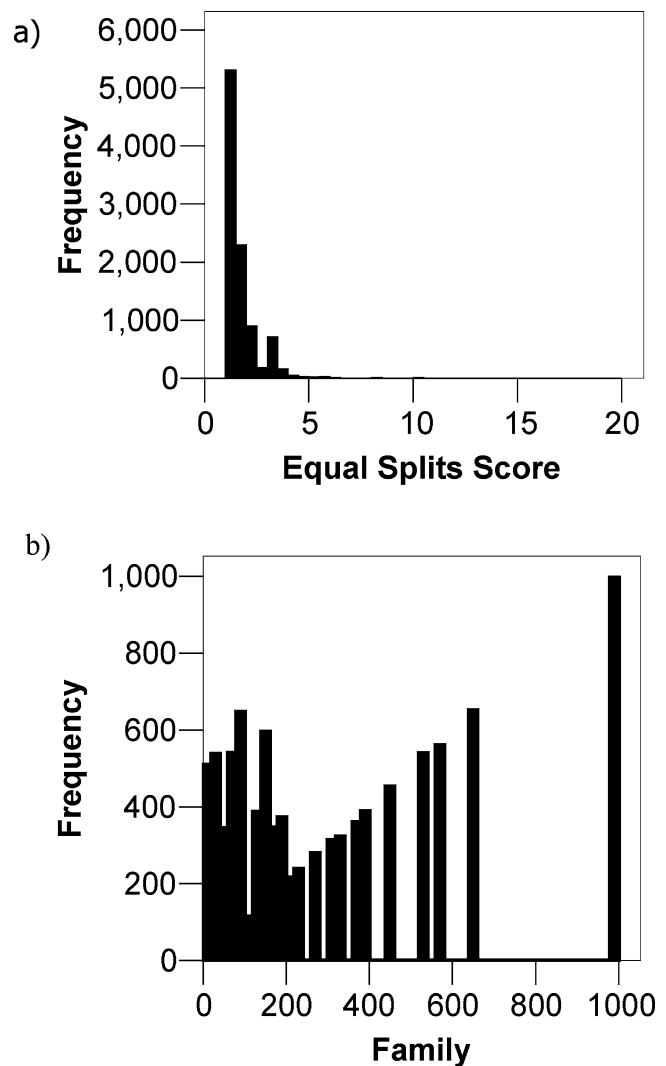


Figure 2. Frequency distributions of (a) the equal-splits scores and (b) family species richness for 9546 bird species. The y-axis for both graphs is \log_{10} transformed endangerment ranking.

qualitatively similar results to equal splits (logistic regression, pseudo $r^2 = 0.01$, $p < 0.05$). Threatened species came from smaller families (Monte Carlo, $n = 10,000$, $p < 0.001$) and again this was not influenced by any particular threat category (Monte Carlo, $n = 10,000$, all $p > 0.05$).

Because ranking by expected loss incorporated IUCN threat status, the two systems identified broadly similar sets of species. Of the 1090 threatened species, 1086 were captured in the first 1090 species ranked by equal splits (the missing taxa were the vulnerable species *Nectarinia thomensis*, *Turdus celaenops*, *Turdus feae*, and *Turdus menachensis*).

Ranking by expected loss did, however, order species differently. The addition of equal splits was expected to create a large difference if the correlation was weak, and

equal splits had reasonable variance. Indeed, there were only 68 species common to both the first 158 species ranked by threat (the CR species) and the first 158 ranked by expected loss. Ranking by expected loss chose 40% more total evolutionary history in the first 158 species, but only 2% more in the first 1090 species (Fig. 3).

Discussion

We considered how to incorporate a value of worth into conservation prioritization to help direct conservation action toward important species. An example of a potentially important species is the Plains Wanderer (*Pedionomus torquatus*). This species and 270 others are considered the 159th most important for conservation action according to the IUCN Red List. As the sole member of the family Pedionomidae, however, its equal-splits score was 53.6 MY of evolutionary history (compared with the average 8.139 MY). When this species' evolutionary history "value" was incorporated in the prioritization approach with the expected-loss calculation, the species moved up 140 places to the 19th species most in need of conservation action.

Ranking species by the expected loss of genetic distinctness incorporated 40% more evolutionary history in the first 150 species when compared with ranking by the expected loss of species (i.e., the IUCN Red List). The two ranking approaches shared 99.6% of the first 1090 species, meaning that ranking by expected loss changed only the order of the threatened species. Importantly, conservation efforts will still be concentrated on largely the same cohort of species if they are applied based on our rankings.

Although threat and genetic distinctness are related, there was a large increase in the amount of genetic information captured in the first 150 species when prioritizing all species with a metric that included genetic distinctness and threat, as opposed to the one that contained only threat. This occurred because only an estimated 1% of the variation in the distribution of species within threat categories was explained by equal-splits values or species per family. This means threat is a poor surrogate for conserving genetic information and needs to be considered as a separate component when prioritizing species.

Measures of Genetic Distinctness

The U.S. Fish and Wildlife Service is one of few prioritization bodies that already assess species genetic distinctness when allocating resources. They use a system that, after a species has been awarded a score based on its threat status, gives a secondary score of 1 point to members of monotypic genera, 0 points to full species, and minus 1 point to subspecies. The final result is an overall species listing score that determines where each taxon will enter

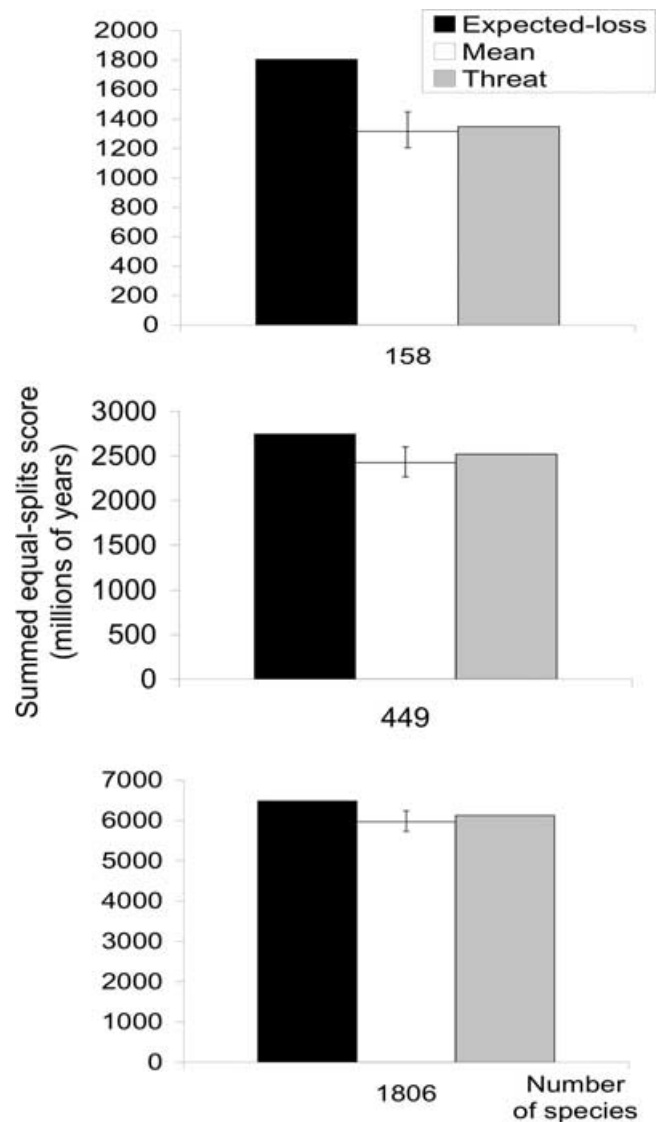


Figure 3. Total evolutionary history represented based on different endangerment ranking metrics. Results for the top 158 (critically endangered [CR] species), 449 (critically endangered plus endangered [EN]), and 1,806 (CR plus EN plus vulnerable and lower risk/near threatened) ranked species out of 9546 total bird species are shown. Black bars represent the summed equal-splits scores, a measure of embodied evolutionary history, of the top species when species are ranked by their expected loss of evolutionary history. Gray bars represent the summed equal-splits scores of the top species when species are ranked by how threatened they are, with the most threatened first. White bars represent the average summed equal-splits scores of the same number of species (i.e., 158, 449, 1,806) chosen at random from the total pool, from 10,000 resamples with replacement. Error bars represent 95% confidence limits.

the Endangered Species List relative to the others already listed (Fay & Thomas 1983).

This measure is designed to be simple to apply (Andelman et al. 2004) and is essentially a categorical estimate of a taxon's pendant edge value. Thus, this score is influenced by the shape of the tree toward the tips and does not take into account how close to the base of the tree the taxa are rooted. This distinction can be seen in the kiwi family (Apterygidae), which with three species, is not monotypic. Under the U.S. system, they would not receive any increased priority, despite the fact that they are genetically (and phenotypically) distinct from the majority of other bird species (May 1990).

Family species richness, as considered in this study, is another simple measure of evolutionary isolation. It offers more differentiation than the U.S. system, but again the overall shape of the family subtree, or its position relative to the root, has no impact on an individual species' score. If all 9546 bird species were ranked by their family species richness in ascending order, the 3 kiwi species and 10 other taxa would rank as the 108th most evolutionarily isolated.

The equal-splits measure we propose captures different evolutionary "information" than family species richness, and although correlated, it has the potential to take into account the shape of the entire tree. With the equal-splits measure each kiwi species receives an evolutionary history value of 28.34 MY; equal to the 61st highest equal-splits value out of all species. The equal-splits score also has the advantage that it can be widely applied across taxonomic groups because it is measurable for both phylogenies and taxonomies. It is, however, measured from a particular root (here the root of the bird clade) and therefore is relative to the other species being considered, rather than being an absolute value.

Results of several studies show how measures of genetic distinctness respond to tree shape. These measures, when independently applied to the same clade, yield different levels of interspecies variation and contrasting weights to "basal" species and "pendant" species (Pavoine et al. 2005; A.O.M. et al., unpublished data). Rao (1982) states that the key properties of distinctness measures are their straightforward calculation and applicability to less-studied groups. Studies are needed to investigate the properties of such measures and how these correspond to the needs of the conservation community.

Combining Genetic Distinctness and Threat

In many countries (e.g., Canada's Species at Risk Act, United Kingdom's Wildlife and Countryside Act) there is strong link between threatened species lists and conservation legislation (Possingham et al. 2002). Therefore, either the individual listing procedures used in such legislation need to be altered in scope to incorporate other

values deemed important by the scientific community, as the U.S. system adjusts a species listing priority number by its degree of taxonomic isolation, or a widely adopted approach of prioritizing species needs to be developed and put into practice.

A prioritization system (analogous to the U.S. approach) that builds on the framework of the widely used IUCN threat-listing protocols, could use a threshold of expected loss as one of many criteria to assign species to categories of conservation importance. This would ensure that species with more than an acceptable level of expected loss would be entered into priority categories above the level assigned by population parameters alone.

A key implementation problem of using an approach with broad categories, as in the U.S. system, is that there are only a few levels of conservation concern and therefore large numbers of species with equal priority. Another potential drawback is that this prioritization system would only increase the number of species considered worthy of protective measures and not downgrade those species with many close relatives.

The quantitative approach we used to create a prioritization metric (expected loss) is separate from but integrates threat status. It has the functional benefit that it reflects the true distribution of the input variables (i.e., highly distinct species receive much greater priority than moderately distinct species). It also produces a ranked order of species, rather than several groups with equal priority, and the combined quantitative values create understandable units (millions of years of evolutionary history that are expected to be lost in 100 years) rather than just a combined rank score, such as the listing-priority number.

By reflecting the distribution of the input variables accurately, expected loss is highly sensitive to the shape of a variable's distribution, unlike the listing system used by the U.S. Fish and Wildlife Service. Our results showed that most species with high equal-splits values were in the LC and LR categories (85.3% of the upper 10th percentile), but only a few of these moved above the rank of any threatened species. This is because the LC, LR, and VU categories were, coincidentally, given p_e values with approximately the same difference in magnitude as between the highest and lowest equal-splits scores for all species. Therefore, ranking by expected loss as we have implemented it can only affect the intercategory order for most species within LC and LR. Whether this is a desirable characteristic is uncertain, and more work is needed in assigning p_e values to individual species.

Unlike this analysis, previous example systems to combine threat and genetic distinctness measures (Weitzman 1993; Avise 2005) were based on very small groups of species (15 and 4, respectively) for which large amounts of detailed information was available. Avise (2005) suggests a mechanism which sums, for each species, the

weighted ranks of five different criteria (rarity, distribution, ecology, charisma, phylogeny), and Avise (2005) and Weitzman (1993) both advise that prioritization measures take into account the economic feasibility of conserving chosen species. These studies offer a possible path to development of our prioritization measure; however, it is important that such measures are simple enough to be applicable to data-poor species groups to ensure the widest taxonomic relevance.

Conclusion

Our study represents an initial step toward developing and incorporating a value of evolutionary importance into a species prioritization approach. We showed how threat status can be used, not as the only measure of conservation importance, but as a way to focus conservation attention on the important species we identified.

However it is incorporated, and whichever measure is used, it is imperative that this accessible and valuable information be included in conservation prioritization efforts. It seems inadvisable to risk the loss of large amounts of genetic information by waiting until valuable species have become highly threatened before conservation action occurs. Conservation scientists are working hard to understand the betting odds but also need to consider the value of chips being held.

Acknowledgments

We thank F. von Euler for supplying the initial taxonomic data, A. Mimoto, R. Vos, and M. Steel for valuable discussion, the fab* lab at Simon Fraser University for a stimulating environment, and A. Purvis and several anonymous reviewers for useful comments on this work.

Literature Cited

- Altschul, S. F., and D. J. Lipman. 1990. Equal animals. *Nature* **348**:493–494.
- Andelman, S. J., C. Groves, and H. M. Regan. 2004. A review of protocols for selecting species at risk in the context of US forest service viability assessments. *Acta Oecologica* **26**(2):75–83.
- Avise, J. C. 2005. Phylogenetic units and currencies above and below the species level. Pages 76–101 in A. Purvis, J. L. Gittleman, and T. Brooks, editors. *Phylogeny and Conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Cooper, A., and R. Fortey. 1998. Evolutionary explosions and the phylogenetic fuse. *Trends in Ecology & Evolution* **13**:151–156.
- Crozier, R. H. 1992. Genetic diversity and the agony of choice. *Biological Conservation* **61**:11–15.
- Crozier, R. H. 1997. Preserving the information content of species: Genetic diversity, phylogeny, and conservation worth. *Annual Review of Ecological Systematics* **28**:243–268.
- Daugherty, C. H., A. Cree, J. M. Hay, and M. B. Thompson. 1990. Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). *Nature* **347**:177–179.
- Diniz, J. A. F. 2004. Phylogenetic diversity and conservation priorities under distinct models of phenotypic evolution. *Conservation Biology* **18**:698–704.
- Erwin, T. L. 1991. An evolutionary basis for conservation strategies. *Science* **253**:750–752.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**:1–10.
- Fay, J. J., and W. L. Thomas. 1983. Endangered species listing and recovery priority guidelines. *U.S. Federal Register* **48**:43098–43105.
- Feduccia, A. 1995. Explosive evolution in tertiary birds and mammals. *Science* **267**:637–638.
- Gärdenfors, U., C. Hilton-Taylor, G. M. Mace, and J. P. Rodriguez. 2001. The application of IUCN Red List criteria at regional levels. *Conservation Biology* **15**:1206–1212.
- Hey, J. 1992. Using phylogenetic trees to study speciation and extinction. *Evolution* **46**:627–640.
- Hood, G. 2004. Poptools. Pest Animal Control Co-operative Research Centre, Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia. Available from <http://www.cse.csiro.au/poptools/index.htm> (accessed July 2005).
- IUCN (World Conservation Union). 2001. IUCN Red List Categories and Criteria version 3.1. IUCN, Cambridge, United Kingdom.
- Kindvall, O., and U. Gärdenfors. 2003. Temporal extrapolation of PVA results in relation to the IUCN Red List criterion E. *Conservation Biology* **17**:316–321.
- Lepage, D. 2005. Avibase—the world bird database. Bird Studies Canada Ontario. Available from <http://www.bsc-eoc.org/avibase/avibase.jsp> (accessed August 2005).
- Nee, S., and R. M. May. 1997. Extinction and the loss of evolutionary history. *Science* **278**:692–694.
- May, R. M. 1990. Taxonomy as destiny. *Nature* **347**:129–130.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats—toward a re-evaluation of the IUCN threatened species categories. *Conservation Biology* **5**:148–157.
- Meffe, G. K., and C. R. Carroll. 1997. *Principles of conservation biology*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.
- Munroe, B. L., Jr. and C. G. Sibley. 1993. *A world checklist of birds*. Yale University Press, New Haven, Connecticut.
- O'Grady, J. J., M. A. Burgman, D. A. Keith, L. L. Master, S. J. Andelman, B. W. Brook, G. A. Hammerson, T. Regan, and R. Frankham. 2004. Correlations among extinction risks assessed by different systems of threatened species categorization. *Conservation Biology* **18**:1624–1635.
- Pauplin, Y. 2000. Direct calculation of a tree length using a distance matrix. *Journal of Molecular Evolution* **51**:41–47.
- Pavoine, S., S. Ollier, and A. B. Dufour. 2005. Is the originality of a species measurable? *Ecology Letters* **8**:579–586.
- Possingham, H. P., S. J. Andelman, M. A. Burgman, R. A. Medellin, L. L. Master, and D. A. Keith. 2002. Limits to the use of threatened species lists. *Trends in Ecology & Evolution* **17**:503–507.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* **269**:347–350.
- Purvis, A., P. M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Non-random extinction and the loss of evolutionary history. *Science* **288**:328–330.
- Rao, C. P. 1982. Diversity and similarity coefficients: a unified approach. *Theoretical Population Biology* **21**:24–43.
- Semple, C., and M. Steel. 2004. Cyclic permutations and evolutionary trees. *Advances in Applied Mathematics* **32**:669–680.
- Sibley, C. G., and J. E. Ahlquist. 1990. *Phylogeny and classification of birds: A study in molecular evolution*. Yale University Press, New Haven, Connecticut.
- Vanewright, R. I., C. J. Humphries, and P. H. Williams. 1991. What to protect—systematics and the agony of choice. *Biological Conservation* **55**:235–254.
- von Euler, F. 2001. Selective extinction and rapid loss of evolutionary

- history in the bird fauna. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **268**:127-130.
- Weitzman, M. L. 1993. What to preserve - an application of diversity theory to crane conservation. *Quarterly Journal of Economics* **108**:157-183.
- Weitzman, M. L. 1998. The Noah's Ark problem. *Econometrica* **66**:1279.
- Williams, G. R., and D. R. Given. 1981. *The red data book of New Zealand*. Nature Conservation Council and Department of Lands and Survey, Wellington, New Zealand.
- Witting, L., M. A. McCarthy, and V. Loeschcke. 1994. Multi-species risk analysis, species evaluation and biodiversity conservation. Pages 239-249 in V. Loeschcke, J. Tomiuk, and S. K. Jain, editors. *Conservation genetics*. Birkhäuser Verlag, Basel, Switzerland.

