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Ecological correlates of extinction risk in Chinese birds

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Abstract. China is one of the countries with the richest bird biodiversity in the world. Among the 1372 Chinese birds, 146 species are considered threatened and three species are regionally extinct according to the officially released China Biodiversity Red List in 2015. Here, we conducted the first extensive analysis to systematically investigate the patterns and processes of extinction and threat in Chinese birds. We addressed the following four questions. First, is extinction risk randomly distributed among avian families in Chinese birds? Second, which families contain more threatened species than would be expected by chance? Third, which species traits are important in determining the extinction risk in Chinese birds using a multivariate phylogenetic comparative approach? Finally, is the form of the relationship between traits additive or nonadditive (synergistic)? We found that the extinction risk of Chinese birds was not randomly distributed among taxonomic families. The families that contained significantly more threatened species than expected were the hornbills, cranes, pittas, pheasants and hawks and eagles. We obtained eleven species traits that are commonly hypothesized to influence extinction risk from the literature: body size, clutch size, trophic level, mobility, habitat specificity, geographical range size, nest type, nest site, flocking tendency, migrant status and hunting vulnerability. After phylogenetic correction, model selection based on Akaike's information criterion identified the synergistic interaction between body size and hunting vulnerability as the single best correlate of extinction risk in Chinese birds. Our results suggest that, in order to be effective, priority management efforts should be given both to certain extinction-prone families, particularly the hornbills, pelicans, cranes, pittas, pheasants and hawks and eagles, and to bird species with large body size and high hunting vulnerability.

Introduction

Extinction rates are increasing rapidly and recent extinction rates are estimated to be 100–1000 times those of pre-human times (Pimm et al. 1995). Accumulating evidence indicates that extinction risk is not randomly distributed among taxa (Bennett and Owens 1997, Russell et al. 1998, Purvis et al. 2000a). Typically, extinction risk is clustered within closely related species that share some common traits predisposing them to extinction (Jones et al. 2003, Kotiaho et al. 2005). Identifying traits associated with increased extinction risk is an important prerequisite for the development of effective conservation strategies to minimize future biodiversity losses (Laurance 1991, Jones et al. 2003). Accordingly, conservation biologists and ecologists have invested considerable effort identifying the ecological and life-history traits that render species vulnerable to extinction (McKinney 1997, Purvis et al. 2000b, Brashares 2003).

Theory predicts that species with particular traits may be at greater risk of extinction than others (McKinney 1997, Purvis et al. 2000b). First, rarity in the form of small geographic range and high habitat specificity has been widely recognized as good predictors of extinction risk (Rabinowitz et al. 1986, Kattan 1992, Gaston 1994). Second, large body size, high trophic level, low fecundity and low mobility are commonly hypothesized to increase a species' vulnerability to extinction (Bennett and Owens 1997, Purvis et al. 2000b, Henle et al. 2004). In addition, flocking birds, migratory species and hunted species are often predisposed to extinction (Terborgh 1974, Van Houtan et al. 2006, Price and Gittleman 2007). Finally, species with exposed nests or ground nesting are also predicted to be more vulnerable to extinction because of higher nest predation rates (Terborgh 1974, Wilcove 1985).

Both theory and empirical evidence have long suggested that some species are extremely vulnerable to extinction because they have combinations of traits that promote extinction (Lawton 1994, McKinney 1997, Henle et al. 2004). So far, however, ecologists have rarely considered whether the form of the relationship between traits is additive or nonadditive (synergistic) (Davies et al. 2004). The synergistic effect indicates that the traits involved act nonadditively, rendering species more vulnerable to extinction than the additive effect predicted by those single traits (Davies et al. 2004, Wang et al. 2015). It is important to make the distinction between the interactive forms among species traits, because this can dramatically affect the probability of extinction and conservation efforts (Davies et al. 2004).

Birds are an ideal study group for analyses of extinction risk for several reasons. First, birds are one of the few taxa whose species are described well enough (Del Hoyo et al. 1992-2013, Zheng 2011). Second, the species-level phylogeny of birds has been widely investigated (Sibley and Ahlquist 1990, Jetz et al. 2012, Rubolini et al. 2015). Additionally, their ecological and life-history traits are better known than other taxonomic groups (Collar et al. 1994, Bennett and Owens 2002). Lastly, the extinction risk of almost all bird species has been evaluated either at global (IUCN 2015) or regional scales (e.g. Gombobaatar and Monks 2011, BirdLife International 2015, Taylor et al. 2015).

China is one of the countries with the richest bird biodiversity in the world. There are currently 1372 bird species recorded in China (Zheng 2011). Among all the Chinese birds, 146 (10.6%) species are classified as threatened (Vulnerable, Endangered and Critically Endangered) and three species (0.2%) are regionally extinct, according to the officially

released China Biodiversity Red List in 2015 (MEP and CAS 2015). However, other bird species seem secure. Why are some bird species at risk while others appear safe? Do threatened species share some unfortunate ecological characteristics that render them more at risk? Finding solutions to these puzzles would help predict the threat of extinction and facilitate the protection of Chinese birds. However, to date, no study has explicitly examined the patterns and processes of extinction and threat in Chinese birds.

In this study, we conducted the first extensive analysis to systematically investigate the patterns and processes of extinction and threat in Chinese birds. The following four questions were addressed. First, is extinction risk randomly distributed among avian families in Chinese birds? Second, which families contain more threatened species than would be expected by chance? Third, which species traits are important in determining the extinction risk in Chinese birds? Finally, is the form of the relationship between traits additive or nonadditive (synergistic)? We hypothesized that we would find nonadditive relationships between at least some of the eleven traits considered, given the prevalence of the idea of synergistic interactions in the literature (Lawton 1994, Davies et al. 2004). Understanding the relationships between species traits and extinct risk of Chinese birds has important implications for proactive conservation and can be used to help direct management efforts.

Materials and methods

Data collection

All measures of extinction risk were derived from the recently released China Biodiversity Red List (MEP and CAS 2015) and the International Union for Conservation of Nature (IUCN) Red List (IUCN 2015). The China Biodiversity Red List evaluates the risk of extinction for Chinese species mainly using the IUCN Red List Categories and Criteria (Version 3.1) (IUCN 2012a) and Guidelines for Application of IUCN Red List Criteria at Regional and National Levels (Version 4.0) (IUCN 2012b). It comprehensively evaluated the status of all the 1372 bird species in China for the first time (Zhang et al. 2016). We used both China Biodiversity Red List and the IUCN Red List (IUCN 2015) to determine whether the patterns and processes of extinction and threat in Chinese birds were consistent between these two threat assessment criteria. Extinction risk was recorded (following Purvis et al. (2000b)) as Least Concern (LC) = 0, Near Threatened (NT) = 1, Vulnerable (VU) = 2, Endangered (EN) = 3, Critically Endangered (CR) = 4, and Extinct (EX) or Regionally Extinct (RE) = 5. Regionally Extinct, which is applicable only to regional levels, is one of the main differences in threat categories between the IUCN and regional Red Lists (IUCN 2012b).

We omitted some species from our analyses of the correlates of extinction risk in Chinese birds. First, 157 data deficient (DD) species were excluded from the analyses (Purvis et al. 2000b, Jones et al. 2003). Second, we omitted several newly discovered species (e.g. Phylloscopus calciatilis, Locustella chengi, Zoothera salimalii) and some species that were viewed as subspecies (e.g. Montifringilla henrici, Strix davidi, Riparia diluta, Parus bokharensis) by the IUCN Red List (IUCN 2015) because their threat status were not assessed. Moreover, some species are listed as threatened because of their small geographical range size, so any relationship between extinction risk and geographical range size could be circular (Cooper et al. 2008). To avoid this problem, we omitted 46 species listed as threatened due to

their small geographical range size (IUCN Red List criteria B and/or D) (Baillie et al. 2004, Cooper et al. 2008). Finally, species classified under IUCN Red List criteria E should also be excluded because for most species available data are not sufficient for building quantitative models (e.g. Population Viability Analyses) that can be used to estimate the probability of extinction (Akçakaya et al. 2016). In our study, no species was classified under IUCN Red List criteria E. Accordingly, a total of 1151 species were retained in the extinction risk correlate analyses (Supplementary material Appendix 1). We then built a phylogenetic tree for these 1151 bird species (Fig. 1) following the method of Jetz et al. (2012). To obtain the phylogenetic tree, we pruned the global phylogenetic tree of birds from BirdTree (http://birdtree.org) under the option of "Hackett All Species: a set of 10000 trees with 9993 OTUs each" to include these 1151 Chinese birds (Jetz et al. 2012). We sampled 5000 pseudo-posterior distributions and constructed the Maximum Clade Credibility tree using mean node heights by the software TreeAnnotator version 1.8.2 of the BEAST package (Drummond and Rambaut 2007, Ricklefs and Jønsson 2014).

We collected data on eleven ecological and life-history traits that are commonly linked to extinction risk for each species using the published literature (Supplementary material Appendix 1). We used body length (mm) to represent body size (Wang et al. 2015). Clutch size was defined as the median number of eggs per nest (Morrow and Pitcher 2003). Trophic guilds were quantified as omnivores (1), granivores (2), frugivore (3), nectarivores (4), insectivores (5), piscivores (6) and carnivores (7) (Sekercioglu et al. 2002). We used the IUCN Habitats Classification Scheme to classify habitats as: forest, savannah, shrubland, grassland, inland wetlands, rocky areas, caves, desert, marine neritic, marine oceanic, marine coastal, marine intertidal, artificial terrestrial/aquatic and exotic vegetation (http://www.iucnredlist.org/technical-documents/classification-schemes/habitats-classificatio n-scheme-ver3) (Newbold et al. 2013). Habitat specificity was then calculated as the number of Chinese habitats a species has been recorded in (Feeley et al. 2007; Sodhi et al. 2010). Following Jones et al. (2003), the recent geographic range size (km^2) within China was obtained from published species range maps by digitizing the area into a Geographic Information System (ArcView 10.2). Zheng (2011) provided the most recent distribution range maps for all 1372 Chinese birds. To obtain an index of a species' mobility, we calculated a dispersal ratio (dp) for each species by dividing its mean wing length (mm) by the cube root of its mean mass (g) (Woinarski 1989, Wang et al. 2015). Nest type was classified as exposed (no nest, platform, saucer, scrape) (1) or not (0) (Sodhi et al. 2010). Nest substrate was classified as cavity (1), tree (2), shrub (3), water (4), and ground (5) (Barbaro and van Halder 2009, Wang et al. 2015). Flocking tendencies were classified as strictly solitary (0), occasionally social (1), and strictly social (2) (Beauchamp 2004). Migrant status was classified as resident (0), partial migrant (1), and full migrant (2) (Van Turnhout et al. 2010). Following Thornton et al. (2011), hunting vulnerability was quantified as rarely/never hunted or killed (0), occasionally hunted or killed (1), and often hunted or killed (2). We searched all potential Chinese literature to determine hunting vulnerability. Bird species were quantified as high hunting vulnerability (2) if they were listed as preferred game species (Galliformes) (Zheng 2015), common trade species (e.g. Leucodioptron canorus, Falco cherrug) (ESIEMOPRC 2002, Li and Jiang 2014), common cage species (e.g. Acridotheres cristatellus, Leiothrix lutea) (Wang 2013), or actively persecuted species (e.g. Emberiza aureola, Thalasseus bernsteini) (Chen et al. 2015, Kamp

2015). Bird species were classified as medium hunting vulnerability (1) if they were not preferred game species or actively persecuted species, but were reported to be occasionally hunted or killed in related literature (Li and Li 1998, Wang et al. 2001, Xu et al. 2002, Zhou and Jiang 2004, Bi and He 2005, Zhang et al. 2008, Liang et al. 2013, Dai and Zhang 2015). The other Chinese bird species that were rarely/never hunted or killed were then quantified as low hunting vulnerability (0) (Supplementary material Appendix 1).

These eleven ecological and life-history traits were selected mainly for two reasons. First, they are commonly hypothesized to influence vulnerability to extinction in birds based on empirical and theoretical evidence (Terborgh 1974, Wilcove 1985, Rabinowitz et al. 1986, Bennett and Owens 1997, Van Houtan et al. 2006, Price and Gittleman 2007). In addition, they were available for almost all Chinese birds except for body length (39 species) and clutch size (86 species) (Supplementary material Appendix 1). For these unavailable species-specific values of body length and clutch size, we used the estimates based on mean values for congeners (Newbold et al. 2013). To ensure these species traits are appropriate to the scale of the China Species Red List, all the above data were obtained from China literatures such as Zhuge (1990), Zhao (2001), Zheng (2011, 2015) and Liang et al. (2013). For each of the species traits, if a range instead of the mean was given, we used the arithmetic mean of the limits (Wang et al. 2009, Gaston and Blackburn 1995).

Statistical analyses

Following Bennett and Owens (1997), we performed a simulation to determine whether variation in extinction risk among Chinese birds is randomly distributed among families. Because 146 of all bird species were classified as threatened (Vulnerable, Endangered and Critically Endangered), we randomly picked 146 species from the complete list of 1372 bird species. We noted which families these species were from (using the classification of Zheng (2011)), and then calculated the proportion of species in each family that had been randomly picked. We repeated this simulation 10000 times, after which there was no significant change in proportions, and drew a frequency histogram of the mean number of families in each proportion class across all 10000 simulations (Bennett and Owens 1997). The frequency histogram was divided into ten mean bins, each with a magnitude of 0.1. This frequency histogram represented the predicted distribution of extinction risk (Bennett and Owens 1997). If extinction risk is randomly distributed among families, the observed pattern would not differ significantly from this predicted distribution. The null hypothesis that the observed and predicted distributions did not differ was tested using the chi-square (χ^2) test (Sokal and Rohlf 1995). The χ^2 test is particularly suitable to compare binned data (e.g. a histogram) with another set of binned data or the predictions of a model binned in the same way (Sokal and Rohlf 1995, Zar 2010). For the χ^2 test, we combined six threatened groups (0.3-0.9) into one category because these threatened groups had very small or zero frequencies (Bennett and Owens 1997).

We used the binomial distribution to determine which families contained an unexpectedly large or small number of threatened species (Bennett and Owens 1997, Bielby et al. 2006). Under the null hypothesis that the species in each family are threatened randomly, the probability that a family of N species contains K threatened species follows the binomial distribution (Bennett and Owens 1997), where the probability of a species being threatened is 0.106 (146 threatened species out of a total of 1372 species). Because this question was tested

independently for each of the 101 avian families in Chinese birds, adjusted critical values were calculated using the Dunn–Sidak method (Sokal and Rohlf 1995). For 101 independent tests, the critical values corresponding to conventional significance levels of 5% and 1% are $p < 5.08 \times 10^{-4}$ and $p < 9.95 \times 10^{-5}$, respectively.

We employed phylogenetic generalized least squares (PGLS) models and an information-theoretic approach to determine which species traits were important in determining the extinction risk of Chinese birds. To control for phylogenetic non-independence between species, we fitted PGLS models to the data using the pgls function of the caper package in R (Orme et al. 2012). Pagel's λ, a branch length transformation indicating the strength of the phylogenetic signal (Pagel 1999), was optimized in each model by the maximum likelihood method (Orme et al. 2012). The other two branch length transformations, κ and σ, were set as constant (1) which assumed a Brownian motion model of evolution (Orme et al. 2012). To test our hypotheses, we built a set of relevant PGLS models. We began our analysis by examining the significance of each of the eleven ecological predictors of extinction risk separately. We then tested the importance of the combinations of species traits and their synergistic interactions as predictors of extinction risk. To avoid potentially spurious or statistically intractable problems common in large-scale correlative studies, we limited our models to plausible a priori co-varying ecological traits (Supplementary material Appendix 2) (Sodhi et al. 2008, Wang et al. 2015). These specific models were chosen because of logical relationships and suspected interactions between ecological traits (Swihart et al. 2003). This strategy also avoided the problem of data dredging that conducts exploratory analyses with all combinations of the eleven ecological traits (Burnham and Anderson 2002).

We calculated Akaike's information criterion (AIC) for each fitted model. The difference in AIC values (Δ_i) between models can be used to calculate Akaike weights (ω_i), which is the probability that the model is the best in the set of candidate models, given the data (Burnham and Anderson 2002). Only models with $\Delta_i \leq 2$ are considered to have substantial support (Burnham and Anderson 2002).

Prior to analyses, logarithmic transformations were performed on body length and geographic range size to achieve normality. We assessed correlations between species traits to determine the potential effect of collinearity on the results of the multivariate analyses (Neter et al. 1996). Since none of species traits were highly correlated (Spearman $\rho < 0.45$) in our study (Supplementary material Appendix 3), we retained all the variables for further analyses. All the above analyses were conducted for the China Species Red List and the IUCN Red List separately.

Results

Extinction risk of Chinese birds

According to the recently released China Species Red List in 2015, 876 (63.8%) species of Chinese birds were currently not threatened, 190 (13.8%) were near-threatened, 80 (5.8%) were vulnerable, 15 (1.1%) were endangered, 51 (3.7%) were critically endangered, 3 (0.2%) were regionally extinct, while 157 (11.4%) species were data deficient (Fig. 2). The IUCN threat assessments of Chinese birds were significantly correlated with that of the China Species

Red List (Spearman $\rho = 0.652$, P < 0.001). However, there were large differences in extinction risk between the IUCN Red List and the China Species Red List (Fig. 2). Among Chinese birds, 225 species were more endangered in China than globally (Supplementary material Appendix 1). For example, Ciconia ciconia, Falcipennis falcipennis and Grus antigone were classified as Least Concern or Near Threatened by the IUCN Red List, but were listed as Regionally Extinct by the China Species Red List (Supplementary material Appendix 1).

The extinction risk of Chinese birds was not randomly distributed among families. The observed and predicted frequency distributions of extinction risk were significantly different using either the criteria of the China Species Red List (chi-square test, $\chi^2 = 11.20$, df = 4, P < 0.05) (Fig. 3a) or the IUCN Red List ($\chi^2 = 29.23$, df = 4, P < 0.001) (Fig. 3b).

We identified a number of families that contained significantly more threatened species than would be predicted by chance (Table 1). Overall, sixteen families contained a remarkably large number of threatened species (twice or more as high as expected, i.e. 20% or more) (Table 1). The families that contained significantly more threatened species than expected were the hornbills (Bucerotidae), cranes (Gruidae), pittas (Pittidae), pheasants (Phasianidae) and hawks and eagles (Accipitridae) (Table 1).

Ecological correlates of extinction risk

Model selection based on AIC identified the synergistic interaction between body size and hunting vulnerability as the single best correlate of extinction risk in Chinese birds using either the criteria of the China Species Red List (ΔAIC = 0, ω_i = 0.8445) (Table 2, Fig. 4a) or the IUCN Red List (ΔAIC = 0, ω_i = 0.9592) (Table 3, Fig. 4b). The synergistic model explained a large amount of variance for the criteria of the China Species Red List (F = 117.2, P < 2.2 × 10^{-16}, adjusted R^2 = 0.39) or the IUCN Red List (F = 129.3, P < 2.0 × 10^{-16}, adjusted R^2 = 0.36). In contrast, an additive model with both body size and hunting vulnerability as main effects, but no interaction accounted for 21.8% of the variance for the criteria of the China Species Red List (F = 58.5, P < 2.2 × 10^{-16}) or 18.9% of the variance for the IUCN Red List (F = 84.5, P < 2.0 × 10^{-16}). Thus, including the interaction improved the amount of variance explained by more than one-half over the additive model. The synergistic model indicated that species with large body size and high hunting vulnerability were extremely vulnerable to extinction (Fig. 4). However, any single traits or additive effects among traits did not receive strong support as predictors of extinction risk using the criteria of the China Species Red List (all ΔAIC > 3.39) or the IUCN Red List (all ΔAIC > 6.49) (Tables 2-3).

Discussion

In this study we conducted the first extensive analysis to systematically investigate the patterns and processes of extinction and threat in Chinese birds. We found that the extinction risk of Chinese birds was not distributed randomly across families. Certain families contained an unusually large proportion of threatened species. The synergistic interaction between body size and hunting vulnerability was the single best correlate of extinction risk in Chinese birds.

Extinction risk of Chinese birds

There were large differences in extinction risk between the China Species Red List and the IUCN Red List. Mismatches between the two Red Lists are most likely to be caused by

scale-dependent changes in listing and access to different data (Milner-Gulland et al. 2006). It is expected that the smaller the area of assessment, the higher the threat status, because a smaller area often implies a smaller population size and a higher chance of meeting red listing criteria (Milner-Gulland et al. 2006). This is generally the case in our study, in which 225 bird species were more endangered in China than globally (Supplementary material Appendix 1). To take an extreme example, Ciconia ciconia, Falcipennis falcipennis and Grus antigone are highly endangered (Regionally Extinct) in China, but are much less endangered (Least Concern or Near Threatened) at the global scale (Supplementary material Appendix 1). In addition, data quality and availability for bird species at the national scale are often better than that of global scale (Zhang et al. 2016). This makes the national assessment more accurate and more practical for species conservation in China.

We found that the extinction risk of Chinese birds was not distributed randomly across families. This result supports the hypothesis that the risk of extinction is not randomly distributed among taxa (Bennett and Owens 1997, Russell et al. 1998, Purvis et al. 2000a, Bielby et al. 2006). One of the main explanations for the phylogenetic nonrandom extinction is that members of lineages share endangering traits predisposing them to extinction (Bennett and Owens 1997, Purvis et al. 2000b, Jones et al. 2003).

We observed that certain families of Chinese birds contained a remarkably large proportion of threatened species. Five families had significantly more threatened species than would be expected by chance. These extinction-prone families were the hornbills, cranes, pittas, pheasants and hawks and eagles. However, it should be noted that the binomial test has relatively low statistical power when the family is small (Sokal and Rohlf 1995, Bennett and Owens 1997). This may largely explain why a number of small families, such as the pelicans, bustards, storks, ibises and grouses, contain surprisingly large proportions of threatened species but these proportions are not significant in statistical terms. However, as Bennett and Owens (1997) argued, these small families may represent a large fraction of avian life history diversity. Consequently, species loss from these small families would lead to a disproportionately large loss of avian diversity (Jetz et al. 2014, Nunes et al. 2015).

Habitat loss and degradation, hunting and trade, and human activities such as dam-construction and tourism are listed as three main extrinsic factors that threaten Chinese birds (Li and Wilcove 2005, Zhang et al. 2016). For the five families that had significantly more threatened species than expected, hornbills, pittas and pheasants are particularly associated with primary forests, while cranes are exclusively dependent on wetlands (Zhao 2001, Wang and Xie 2009). Thus, the loss of primary forests was identified as the exclusive factor that threatened pittas (Wang and Xie 2009). Apart from habitat loss and degradation of forests and wetlands, hunting and trade was another main extrinsic factor that threatened the other four extinction-prone families (hornbills, cranes, pheasants, and hawks and eagles) (Wang and Xie 2009, IUCN 2015, Zhang et al. 2016).

Ecological correlates of extinction risk

Consistent with our hypothesis, we found synergistic interaction between body size and hunting vulnerability in Chinese birds. These two traits act synergistically so that bird species with large body size and high hunting vulnerability are especially vulnerable to extinction (Fig. 4). In Chinese birds, larger-bodied species are more likely to be hunted (Supplementary material Appendix 3), which in turn was more vulnerable to extinction. Pheasants, hornbills,

pelicans and hawks are such typical kinds of Chinese birds with large body size and high hunting vulnerability. From a conservation perspective, an important implication of our findings is that it may be risky to make predictions about extinction risk from a single trait, such as body size or hunting vulnerability, because traits may act synergistically rendering species more vulnerable than predicted by that single trait.

There is plenty of empirical evidence that body size and hunting vulnerability are traits that place species at risk. For example, hunters have been shown to prefer to hunt larger-bodied species (Jerozolimski and Peres 2003, Price and Gittleman 2007). In addition, large body size has been found to correlate with threat status in exploited birds (Owens and Bennett 2000, Keane et al. 2005) and hunted primates (Isaac and Cowlishaw 2004). However, these studies have not explicitly examined synergistic interactions between body size and hunting vulnerability. Our study provides the first evidence that the synergistic interaction between body size and hunting vulnerability can put species at greater risk of extinction than the additive effect predicted by these single traits.

Our results highlight the importance of combined effects of species traits in determining species vulnerability to extinction. We found that any single ecological trait was not sufficient to predict species vulnerability to extinction. Had we not analyzed the combined effects of species traits on extinction risk, we would have incorrectly concluded that hunting vulnerability was the single best predictor of extinction risk in Chinese birds (Tables 2–3). Our results support the idea that single traits alone usually have limited predictive powers for species vulnerability to extinction (Henle et al. 2004, Wang et al. 2015). We thus suggest that future studies, if possible, should analyze the combined effects of species traits on extinction risk.

To date, there are only a few global studies examining the relationships between ecological traits and extinction risk of birds (Gaston and Blackburn 1995, Bennett and Owens 1997, Morrow and Pitcher 2003, Lee and Jetz 2011, White and Bennett 2015). However, in these studies, only one or two ecological traits, usually body size and/or clutch size, are analyzed to determine their relationships with extinction risk. Accordingly, the relative importance of extinction-prone traits often cannot be compared because only one or two ecological traits are analyzed (Bennett and Owens 1997). In addition, the data on ecological traits are only available for a small proportion of all bird species in these studies (e.g. Bennett and Owens 1997, Morrow and Pitcher 2003). Using a broader range of life history and ecological traits for nearly all Chinese birds, our study can overcome these limitations and distinguish the relative importance of these extinction-prone traits using current information on extinction risk.

Our findings indicate that the synergistic interaction between body size and hunting vulnerability explains a large amount of variance of the extinction risk in Chinese birds. Other ecological traits such as population fluctuation, annual survival rates, home range size, sexual selection, edge or disturbance sensitivity, have also been proposed as potential predictors of extinction risk in other systems (Pimm et al. 1988, Purvis et al. 2000b, Morrow and Pitcher 2003). The role of these species traits in determining extinction risk in Chinese birds cannot be excluded from present study. These traits alone or in combination may account for some of the remaining variation in species vulnerability to extinction. As we currently have no data on these traits in Chinese birds, however, the idea warrants further study.

Management implications

Our results highlight the phylogenetic nonrandom extinction and the synergistic effects of species traits in determining the extinction risk of Chinese birds. These findings have several general and specific implications with regard to management practices. First, we should prioritize conservation efforts to certain extinction-prone families, especially the hornbills, pelicans, cranes, pittas, pheasants and hawks and eagles, because they contain a remarkably large proportion of threatened species. Second, we should consider the synergistic effect between species traits for the effective conservation of Chinese birds. In contrast, as single traits alone are poor predictors of extinction risk, it would be inefficient to allocate conservation resources based on any single ecological trait (Henle et al. 2004, Davies et al. 2004, Wang et al. 2015). Specifically, our results show that the synergistic interaction between body size and hunting vulnerability is the single best correlate of extinction risk in Chinese birds. Chinese birds with large body size and high hunting vulnerability, such as pheasants, hornbills, cranes, pelicans and hawks and eagles, are extremely vulnerable to extinction. Therefore, conservation efforts giving priority to species with large body size and high hunting vulnerability may prove effective for the preservation of Chinese birds.

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Supplementary material (Appendix ECOG-03158 at <www. ecography.org/appendix/ecog-03158>). Appendix 1–3.

Table 1. Unusually highly threatened families of Chinese birds.

Family name	Common name	# species in family[a]	# species threatened[b]	Proportion threatened	Binomial probability[c]
Bucerotidae	Hornbills	5	5	1.00	1.51×10^{-5}**
Pelecanidae	Pelicans	3	3	1.00	0.0012
Otididae	Bustards	3	2	0.67	0.0315
Gruidae	Cranes	9	6	0.67	9.76×10^{-5}**
Pittidae	Pittas	9	6	0.67	9.76×10^{-5}**
Tetraonidae	Grouses	8	4	0.50	0.0056
Ciconiidae	Storks	6	3	0.50	0.0170
Threskiornithidae	Ibises	6	3	0.50	0.0170
Sittidae	Nuthatches	9	4	0.44	0.0091
Psittacidae	Parrots	9	3	0.33	0.0540
Diomedeidae	Albatrosses	3	1	0.33	0.2589
Phasianidae	Pheasants	55	18	0.33	9.04×10^{-6}**
Accipitridae	Hawks and eagles	50	14	0.28	4.75×10^{-4}*
Rallidae	Rails	19	5	0.26	0.0351
Falconidae	Falcons	13	3	0.23	0.1160
Certhiidae	Treecreepers	5	1	0.20	0.3428

[a] 1372 species, data from Zheng (2011).

[b] 146 threatened species (Vulnerable, Endangered and Critical Endangered), data from China Biodiversity Red List (2015).

[c] Probability (R) calculated from the binomial distribution ($R = \binom{N}{k} p^k (1 - p)^{N-k}$), where N = Number of species in family, k = Number of threatened species in family, and p = 0.106 (overall proportion of species threatened across all families).

* Adjusted significant at the 5% level allowing for the fact that multiple comparisons have been made.

** Adjusted significant at the 1% level allowing for the fact that multiple comparisons have been made.

Table 2. Performance of PGLS models relating the extinction risk of Chinese birds based on the China Species Red List to plausible combinations of eleven ecological traits.

Model description	K	AIC	ΔAIC	ω_i
Single-process models				
Hunting vulnerability	3	2336.35	19.30	5.43E-05
Geographic range size	3	2381.03	63.98	1.08E-14
Habitat specificity	3	2401.61	84.56	3.66E-19
Body size	3	2402.00	84.95	3.02E-19
Clutch size	3	2408.17	91.12	1.38E-20
Flocking tendency	3	2422.42	105.37	1.11E-23
Nest type	3	2426.41	109.36	1.51E-24
Trophic level	3	2426.97	109.92	1.14E-24
Nest site	3	2427.17	110.12	1.03E-24
Dispersal ratio	3	2427.21	110.16	1.01E-24
Migrant status	3	2427.23	110.18	1.00E-24
Additive models				
Body size + Hunting vulnerability	4	2320.44	3.39	0.1551
Flocking + Hunting vulnerability	4	2332.66	15.61	0.0003
Body size + Geographic range size	4	2357.62	40.57	1.31E-09
Clutch size + Geographic range size	4	2373.63	56.58	4.37E-13
Habitat specificity + Geographic range size	4	2375.14	58.09	2.06E-13
Body size + Habitat specificity	4	2379.86	62.81	1.94E-14
Geographic range size + Migrant status	4	2381.00	63.95	1.10E-14
Trophic level + Geographic range size	4	2382.83	65.78	4.38E-15
Dispersal ratio + Geographic range size	4	2383.03	65.98	3.97E-15
Body size + Clutch size	4	2390.76	73.71	8.34E-17
Body size + Flocking tendency	4	2397.75	80.70	2.53E-18
Body size + Dispersal ratio	4	2402.19	85.14	2.74E-19

Trophic level + Habitat specificity	4	2403.32	86.27	1.56E-19
Body size + Trophic level	4	2403.90	86.85	1.16E-19
Clutch size + Nest type	4	2409.57	92.52	6.84E-21
Clutch size + Dispersal ratio	4	2409.82	92.77	6.05E-21
Clutch size + Nest site	4	2410.10	93.05	5.26E-21
Dispersal ratio + Migrant status	4	2429.19	112.14	3.77E-25
Interactive models				
Body size × Hunting vulnerability	3	2317.05	0.00	0.8445
Clutch size × Geographic range size	3	2376.15	59.10	1.24E-13
Habitat specificity × Geographic range size	3	2392.00	74.95	4.47E-17
Body size × Geographic range size	3	2394.87	77.82	1.07E-17
Dispersal ratio × Geographic range size	3	2395.76	78.71	6.82E-18
Body size × Habitat specificity	3	2405.25	88.20	5.95E-20
Flocking × Hunting vulnerability	3	2406.31	89.26	3.49E-20
Clutch size × Dispersal ratio	3	2408.53	91.48	1.15E-20
Trophic level × Habitat specificity	3	2413.24	96.19	1.09E-21
Body size × Clutch size	3	2414.18	97.13	6.83E-22
Clutch size × Nest site	3	2416.62	99.57	2.02E-22
Trophic level × Geographic range size	3	2417.10	100.05	1.59E-22
Clutch size × Nest type	3	2417.38	100.33	1.38E-22
Body size × Flocking tendency	3	2423.67	106.62	5.94E-24
Geographic range size × Migrant status	3	2424.44	107.39	4.05E-24
Body size × Dispersal ratio	3	2424.69	107.64	3.58E-24
Dispersal ratio × Migrant status	3	2427.18	110.13	1.03E-24
Body size × Trophic level	3	2427.24	110.19	9.99E-25

Table 3. Performance of PGLS models relating the extinction risk of Chinese birds based on the IUCN Red List to plausible combinations of eleven ecological traits.

Model description	K	AIC	ΔAIC	ω_i
Single-process models				
Hunting vulnerability	3	1862.04	13.85	0.0009
Geographic range size	3	1940.84	92.65	7.31E-21
Body size	3	1942.33	94.14	3.46E-21
Clutch size	3	1956.85	108.66	2.43E-24
Habitat specificity	3	1963.80	115.61	7.54E-26
Migrant status	3	1963.97	115.78	6.94E-26
Nest type	3	1964.44	116.25	5.48E-26
Nest site	3	1968.37	120.18	7.68E-27
Dispersal ratio	3	1968.38	120.19	7.62E-27
Trophic level	3	1968.56	120.37	6.99E-27
Flocking tendency	3	2422.42	574.23	1.95E-125
Additive models				
Body size + Hunting vulnerability	4	1854.68	6.49	0.0373
Flocking + Hunting vulnerability	4	1860.10	11.91	0.0025
Body size + Geographic range size	4	1916.33	68.14	1.54E-15
Geographic range size + Migrant status	4	1929.22	81.03	2.43E-18
Body size + Dispersal ratio	4	1935.53	87.34	1.04E-19
Clutch size + Geographic range size	4	1937.37	89.18	4.13E-20
Body size + Clutch size	4	1937.41	89.22	4.06E-20
Body size + Flocking tendency	4	1937.74	89.55	3.44E-20
Body size + Habitat specificity	4	1938.00	89.81	3.02E-20
Trophic level + Geographic range size	4	1942.77	94.58	2.78E-21
Habitat specificity + Geographic range size	4	1942.78	94.59	2.77E-21
Dispersal ratio + Geographic range size	4	1942.83	94.64	2.69E-21

Body size + Trophic level	4	1943.97	95.78	1.53E-21
Clutch size + Nest type	4	1956.08	107.89	3.58E-24
Clutch size + Dispersal ratio	4	1957.85	109.66	1.47E-24
Clutch size + Nest site	4	1958.59	110.40	1.02E-24
Dispersal ratio + Migrant status	4	1965.34	117.15	3.48E-26
Trophic level + Habitat specificity	4	1965.80	117.61	2.77E-26
Interactive models				
Body size × Hunting vulnerability	3	1848.19	0.00	0.9592
Clutch size × Geographic range size	3	1942.59	94.40	3.04E-21
Flocking × Hunting vulnerability	3	1947.69	99.50	2.38E-22
Dispersal ratio × Geographic range size	3	1951.30	103.11	3.90E-23
Clutch size × Dispersal ratio	3	1954.97	106.78	6.24E-24
Body size × Geographic range size	3	1955.52	107.33	4.74E-24
Habitat specificity × Geographic range size	3	1960.22	112.03	4.52E-25
Body size × Clutch size	3	1961.28	113.09	2.65E-25
Clutch size × Nest site	3	1963.80	115.61	7.53E-26
Trophic level × Geographic range size	3	1964.59	116.40	5.07E-26
Dispersal ratio × Migrant status	3	1965.30	117.11	3.56E-26
Body size × Dispersal ratio	3	1965.97	117.78	2.54E-26
Clutch size × Nest type	3	1966.21	118.02	2.26E-26
Trophic level × Habitat specificity	3	1966.70	118.51	1.77E-26
Body size × Flocking tendency	3	1967.43	119.24	1.23E-26
Geographic range size × Migrant status	3	1967.83	119.64	1.01E-26
Body size × Trophic level	3	1967.98	119.79	9.34E-27
Body size × Habitat specificity	3	2405.25	557.06	1.04E-121

Figure legends

Figure 1. Phylogenetic tree of the 1151 bird species used in the comparative analysis. The phylogeny is built following the tree construction method of Jetz et al. (2012). The extinction risk of each species is based on the China Species Red List (inner color circle) and the IUCN Red List (outer color circle).
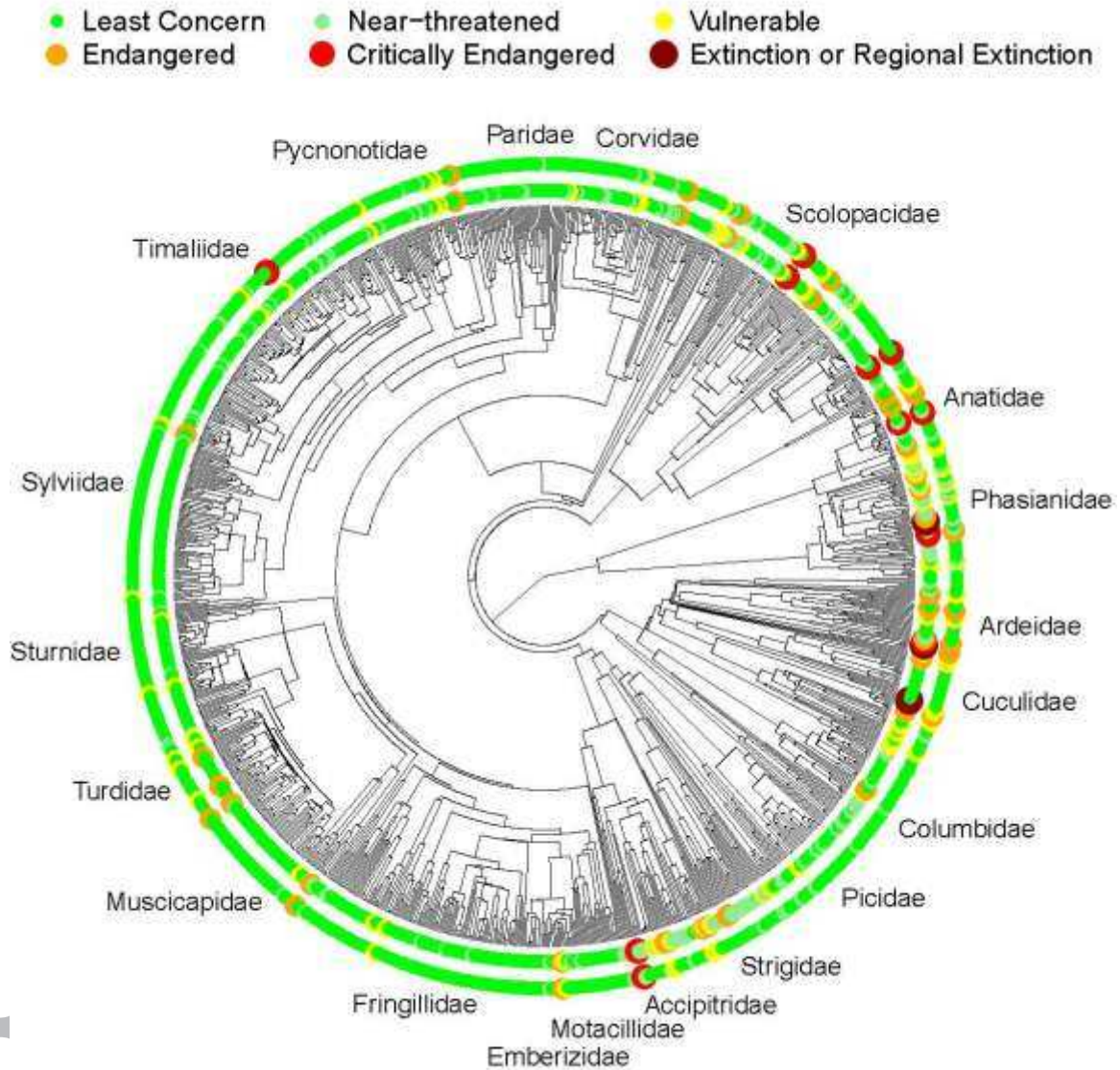
Figure 2. Extinction risk categories of Chinese birds based on the China Species Red List (black bars) and the IUCN Red List (white bars). LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, and EX = Extinction or regional extinction.
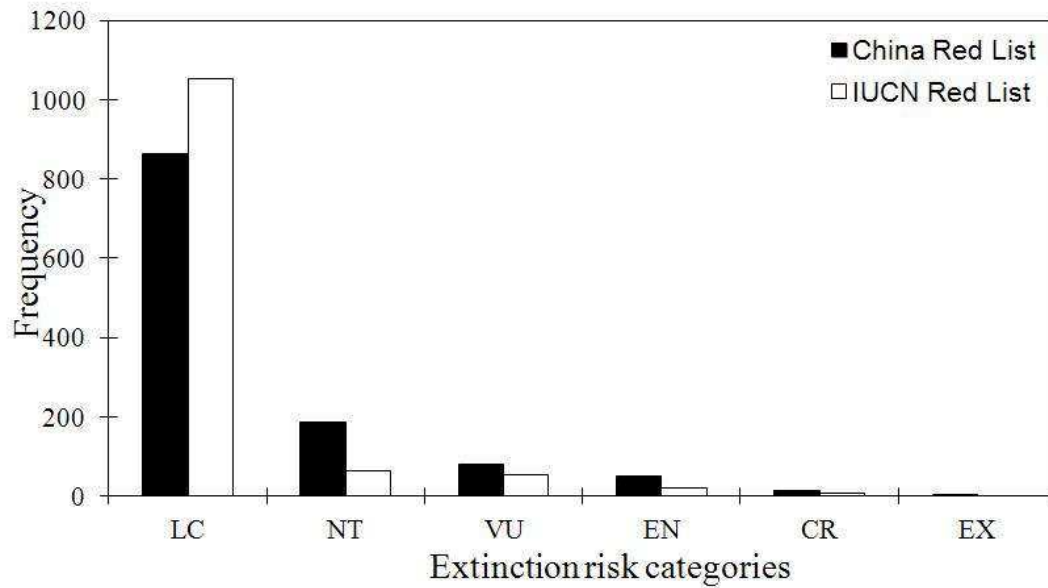
Figure 3. Frequency histogram across families of the proportion of species in a family that are classified as being threatened by extinction (N = 101 families). Predicted frequency distribution is based on simulations. Extinction risk criteria are based on (a) the China Species Red List or (b) the IUCN Red List.
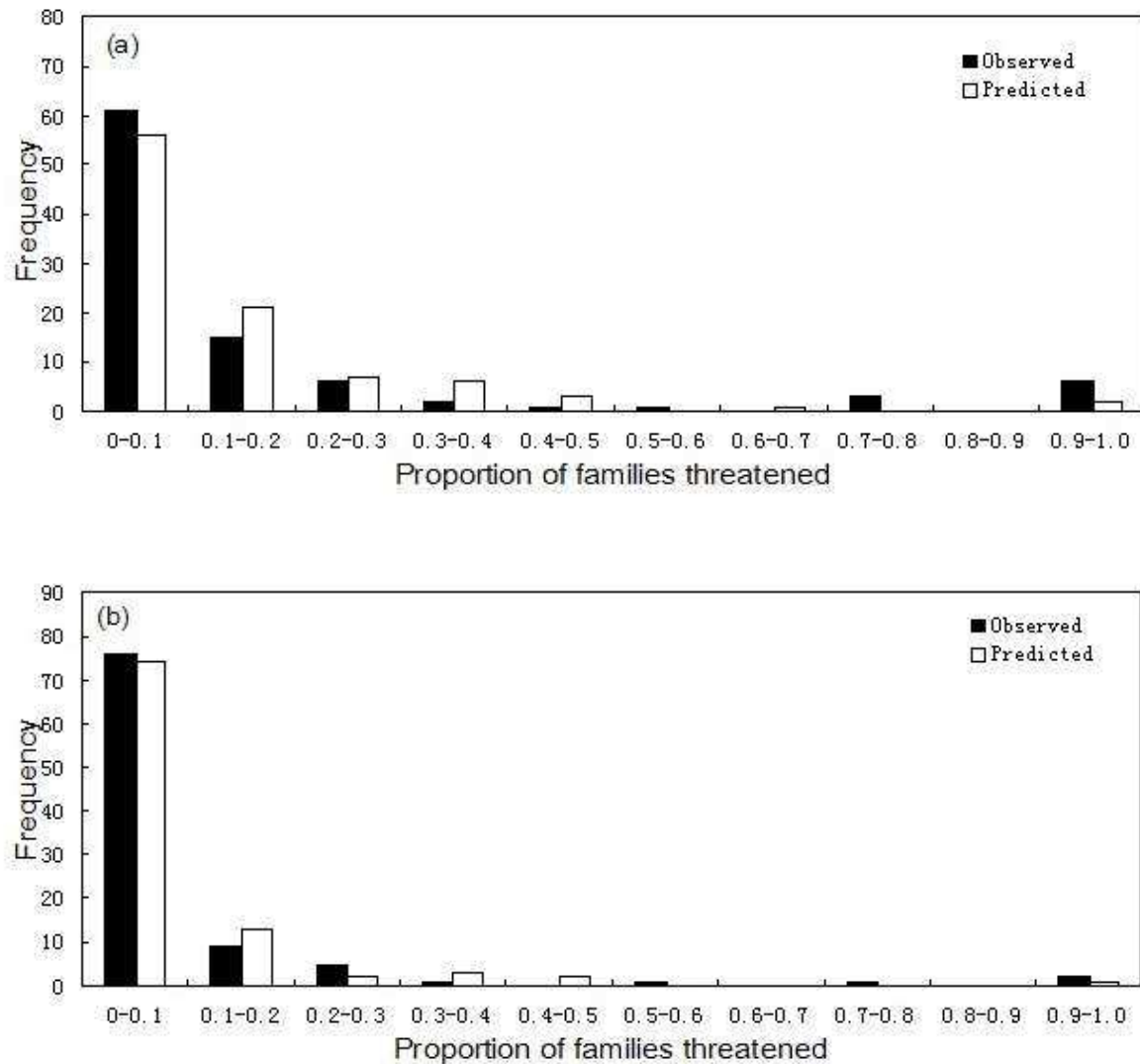
Figure 4. Interactive models of the extinction risk of Chinese birds based on their body size and hunting vulnerability. The solid and broken lines represent predictions from the regression models for bird species with high and low hunting vulnerability, respectively. Triangles represent bird species that are rarely/occasionally hunted or killed, and circles are bird species that are often hunted or killed. Extinction risk criteria are based on (a) the China Species Red List or (b) the IUCN Red List.