EUROPEAN JOURNAL OF ECOLOGY

EJE 2016, 2(1): 21-34, doi: 10.1515/eje-2016-0003

Global analysis of threat status reveals higher extinction risk in tropical than in temperate bird sister species

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ABSTRACT

Given increasing pressures upon biodiversity, identification of species' traits related to elevated extinction risk is useful for more efficient allocation of limited resources for nature conservation. Despite its need, such a global analysis was lacking in the case of birds. Therefore, we performed this exercise for avian sister species using information about their global extinction risk from IUCN Red List. We focused on 113 pairs of sister species, each containing a threatened and an unthreatened species to factor out the effects of common evolutionary history on the revealed relationship. We collected data on five traits with expected relationships to species' extinction risk based on previous studies performed at regional or national levels: breeding habitat (recognizing forest, grassland, wetland and oceanic species), latitudinal range position (temperate and tropics species), migration strategy (migratory and resident species), diet (carnivorous, insectivorous, herbivorous and omnivorous species) and body mass. We related the extinction risk using IUCN threat level categories to species' traits using generalised linear mixed effects models expecting lower risk for forest, temperate, omnivorous and smaller-bodied species. Our expectation was confirmed only in the case of latitudinal range position, as we revealed higher threat level for tropical than for temperate species. This relationship was robust to different methods of threat level expression and cannot be explained by a simple association of high bird species richness with the tropical zone. Instead, it seems that tropical species are more threatened because of their intrinsic characteristics such as slow life histories, adaptations to stable environments and small geographic ranges. These characteristics are obviously disadvantageous in conditions of current human-induced environmental perturbations. Moreover, given the absence of habitat effects, our study indicates that such perturbations act across different tropical environments. Therefore, disproportionally higher conservation effort in the tropics compared to the temperate zone is urgently needed.

KEYWORDS

Biodiversity, bird, threat, species' traits, sister species, tropics

INTRODUCTION

Explosive growth of human population size and needs over the past decades was accompanied by massive global changes resulting in elevated extinction risk of many taxa (Barnosky et al. 2011). Despite increasing amount of sources allocated to various conservation measures, recent analyses confirmed that the risk of extinction is permanently increasing in vertebrates and other taxa (Butchart et al. 2010; Hoffmann et al. 2010). In this situation, it is crucial to enhance our knowledge about threatened taxa to allocate the conservation effort more efficiently (Pimm et al. 2014).

A comparative analysis of ecological traits of threatened species is particularly useful for this purpose because it reveals general patterns in threat of the focal species groups (Estrada et al. 2015). From this information, we can infer relative importance of particular threatening factors and, based on this assessment, we can set conservation priorities, which is essential for the development of successful strategies to mitigate threatening agents (Cardillo & Meijaard 2012; Dirzo et al. 2014).

In birds, various studies focused on traits correlated with increased extinction risk at the regional scale revealing relationships with habitat use, life histories or climatic niche (e.g. Manne & Pimm 2001; Trivino et al. 2013; Koleček et al. 2014a). However, a global analysis assessing correlates of threat status is still lacking. Only Owens & Bennett (2000) used family-level approach to reveal that taxa more specialised to utilise particular habitats are more threatened due to habitat destruction, whilst taxa with slower life histories are more threatened because of direct human persecution.

To build on these earlier studies, we compiled a global dataset of traits for avian sister species containing a threatened and an unthreatened taxon in each sister species pair. Focusing on sister species is useful for discriminating the traits respon-

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sible for differences in species threat status because it accounts for confounding effects of common evolutionary history of the species within each pair (Webb & Gaston 2003). Therefore, traits that are shared within species pair, that is, those that are evolutionary stable and phylogenetically conserved, do not affect the observed relationships (Pigot & Tobias 2013).

In this study, we focused on following traits in which relationships to species' extinction risk can be expected: habitat use, latitudinal breeding range position, migration strategy, diet and body mass. In respect to species habitat use, we predict (i) higher extinction risk for species breeding in open habitats because of joint effects of agricultural intensification (Doland et al. 2001), expansion of cultivated land at the expense of natural steppe habitats (Foley et al. 2011) and forest encroachment on savannah and abandoned farmland (Sirami & Monadjem 2012). Moreover, we predict (ii) higher extinction risk for oceanic species because of detrimental effects of techniques used in modern fisheries (Croxall et al. 2012). Finally, we predict (iii) higher extinction risk in wetland species because of extensive loss of this habitat (Sterling et al. 2013).

Concerning latitudinal breeding range position, we predict (iv) higher extinction risk of tropical species because of their life style, making them particularly sensitive to environmental changes: small geographic ranges (Orme et al. 2006), adaptation to stable environmental conditions (Janzen 1967; Fjeldså et al. 2012) and slow pace of life (Stutchbury & Morton 2001). Concerning migration strategy, we predict (v) higher extinction risk for long-distance migratory species because of their higher sensitiveness to climate change impacts (Both et al. 2010), hunting pressure during migration and in wintering grounds (Zwarts et al. 2009), habitat loss at stop-over sites and wintering quarters (Vickery et al. 2014). Concerning diet, we predict (vi) higher extinction risk in more specialised species (i.e. carnivores, insectivores, herbivores) than in less specialised species (omnivores) because of lower resilience of specialists to global changes (Jiguet et al. 2007). Concerning body mass, we predict (vii) higher risk of extinction for larger-bodied species because of their lower potential for population recovery after environmental perturbations dictated by their long generation time (Sæther et al. 2005).

The aim of this study is to test these predictions and find the factors explaining elevated extinction risk for bird sister species at the global scale.

1. MATERIALS AND METHODS

1.1. Data

We used a database of bird sister species (n = 568 species pairs) published by Philimore et al. (2008). For each species, we first extracted its threat status from IUCN Red List (www.iucnredlist.org accessed in October 2013). For further analysis, we used only the sister species pairs (n = 113) with one species being unthreatened (threat category 'least concern', LC) and the second species having any of the higher categories indicated elevated extinction risk (i.e. 'near threatened', NT; 'vulnerable', VU; 'endangered', EN; 'critically endangered', CR and 'extinct in the wild', EW; see Mace et al. 2008).

In the next step, we collected information about habitat use and latitudinal range position from Sibley and Monroe (1990). We recognised four broad habitat classes: forest, grassland, desert, wetland and ocean. Habitat class 'forest' (n = 111 species) contains various forest types and woodlands; 'grassland' (n = 62 species) contains various open habitats including steppe, savannah, arable fields, meadows and pastures, semi-desert and scrub formations; 'wetland' (n = 37 species) contains various humid habitats including peatbogs and freshwater; 'ocean' (n = 16 species) contains marine species and species confined to oceanic islands. According to the latitudinal range position, we discriminated tropical (n = 142 species) and temperate (n = 84 species) species using location of their breeding ranges with respect to tropical and temperate zone, respectively. Tropical zone was defined as a latitudinal band between the tropic of Cancer and the tropic of Capricorn, temperate zone outside this band. When a species bred in both tropical and temperate zone, we assigned it to the category overlapping higher proportion of its breeding range. For this purpose, we searched for more information about range location of a given species in del Hoyo et al. (1992–2002, 2003–2011).

To collect information about species' migration strategy, life-history strategy and diet, we used del Hoyo et al. (1992–2002, 2003–2011). However, some species lacked information about one or more of these traits and these variables were thus available only for a subset of species pairs (n = 96). According to migration strategy, we classified species as migrants (n = 41 species) and residents (n = 151 species). As 'migrants', we defined species conducting seasonal movements outside their breeding range. As a surrogate for life-history strategy, we used species' body mass (in grams) assuming that larger bodied species invest more energy to survival and have thus 'slower strategies' being under the so-called 'K-selection', whilst smaller species invest more energy to actual reproduction and have thus 'faster' strategies being under 'r-selection' (Sæther et al. 2005). This gradient was confirmed as the most important life history axis in recent analyses focusing on variability in life history traits across large sets of species (Sol et al. 2012, Koleček et al. 2014b). According to diet, we classified species into four categories defined by prevailing food: carnivores (n = 34 species), insectivores (n = 63 species), herbivores (n = 77 species) and omnivores (n = 18 species). These categories are frequently used in interspecific comparative studies (e.g. Böhning-Gaese et al. 2000, Reif et al. 2010). As the information about diet of the focal species was only available as a qualitative description in the text of del Hoyo et al. (1992–2002; 2003–2011), we identified a given species as a carnivore, insectivore or herbivore, respectively, if some food sources from a given diet category were explicitly described as its main food (e.g. fish for carnivores or seeds for herbivores). If the main food of a given species overlapped all three categories mentioned above, we classified the species as an omnivore.

All species data are provided in Supplementary Table 1.

1.2. Statistical analysis

Species threat status was a response variable in all analyses. For this variable, we used two types of coding: first, recognizing only threatened (1) and unthreatened species (0); and second, expressing increasing risk of extinction by numerical values for particular threat categories in the same way as is widely applying for calculating Red List Index (e.g. Hoffmann et al. 2010): NT = 1, VU = 2, EN = 3, CR = 4, EW = 5. These two coding types mirrored in the error structure used in statistical analyses: binomial error structure has been used for the first type of coding and Poisson error structure for the second type.

We related threat status to species' traits by using generalised linear mixed effects models (GLMMs) with multiple factors and taking identities species pairs into account. In each model, explanatory variables with fixed effects were particular species traits tested together and an identifier of species pairs (each containing a threatened and an unthreatened species, see above) was a factor with a random intercept. As we had two datasets because of lack of data on some explanatory variables for some species, we have performed two sets of analyses: (i) models for analyses with full dataset (n = 113 species pairs) contained only habitat and latitudinal range position and (ii) into models for analyses with reduced dataset (n = 96 species pairs) were added migration strategy, body mass (after log transformation) and diet. For each dataset, we ran a model with binomial and Poisson error structure, respectively, according to the type of coding used for the response variable (see above). These models contained only the main effects of particular explanatory variables and were used for reporting parameter estimates. However, because the effect of habitat can depend on latitudinal range position (e.g. different threat of species breeding in temperate vs. tropical forests), we tested whether including the habitat × latitudinal range position interaction improves the model fit. We do not use these interaction models for reporting the main effects due to dependence of their values on interaction effects. Therefore, we ran eight GLMMs in total (see Table 1 for overview and description of all models).

2. RESULTS

Tropical species had higher threat level than their sisters breeding in the temperate zone according to GLMM taking into account pair-wise comparison between threatened and unthreatened sister species (Table 2). This relationship was consistent irrespective to the type of coding used for the response variable and applied for both full and reduced datasets (Table 2a,b). Irrespective to the type of coding used for the response variable, the relationship between threat level and species' habitat use was insignificant in full dataset (Table 2a). However, focusing on the reduced dataset, we found that the relationship between species' threat level and habitat use became significant when the threat level was coded using categories expressing increasing extinction risk. Specifically, open habitat species were more threatened than their sister species breeding in forest habitats (Table 2b). When using binary coding to discriminate between threatened and unthreatened species, the direction of the relationship remained the same but was much weaker and insignificant (Table 2b).

The interaction between habitat use and latitudinal range position was insignificant irrespective to the type of coding used for the response variable (full dataset–binomial errors: $\chi^2 = 0.36$, P = 0.948, whole model deviance = 305.7, degrees of freedom = 9; full dataset–Poisson errors: $\chi^2 = 1.73$, P = 0.613, whole model deviance = 320.6, degrees of freedom = 9; reduced dataset–binomial errors: $\chi^2 = 2.65$, P = 0.449, whole model deviance = 255.1, degrees of freedom = 14; reduced dataset–Poisson errors: $\chi^2 = 3.20$, P = 0.362, whole model deviance = 265.7, degrees of freedom = 14).

None of the GLMMs showed a significant relationship between species' threat and their migration strategy, body mass and diet, respectively (Table 2).

Table 1: Characteristics of the models used in statistical analysis.

Model	Model terms	Error structure	No. of species pairs	Dataset
1	Habitat + Latitudinal range position	Binomial	113	Full
2	Habitat + Latitudinal range position	Piosson	113	Full
3	Habitat + Latitudinal range position + Habitat × Latitudinal range position	Binomial	113	Full
4	Habitat + Latitudinal range position + Habitat × Latitudinal range position	Piosson	113	Full
5	Habitat + Latitudinal range position + Migration + Body mass + Diet	Binomial	96	Reduced
6	Habitat + Latitudinal range position + Migration + Body mass + Diet	Piosson	96	Reduced
7	Habitat + Latitudinal range position + Habitat × Latitudinal range position + Migration + Body mass + Diet	Binomial	96	Reduced
8	Habitat + Latitudinal range position + Habitat × Latitudinal range position + Migration + Body mass + Diet	Piosson	96	Reduced

Table 2: Relationships between extinction risk (expressed using IUCN categories) and species' traits (habitat: forest, grassland, wetland and ocean; latitudinal range position: temperate and tropical; migration strategy: migratory and residential; body mass; diet: carnivorous, insectivorous, herbivorous and omnivorous) as revealed by generalised linear mixed effects models by pair-wise comparison of avian sister species (each pair contained a threatened and an unthreatened species). Threat level was expressed either as threatened (1) and unthreatened (0) corresponding to the binomial error structure or as increasing extinction risk following IUCN classification: least concern (0), near threatened (1), vulnerable (2), endangered (3), critically endangered (4), extinct in the wild (5), corresponding to Poisson error structure. Full dataset (a) contains all pairs of sister species (n = 113) with data on two trait variables, reduced dataset (b) contains limited number of pairs of sister species (n = 96) with data on five trait variables because of lack of data on some traits for some species (see Materials and methods section for more details). Significant results are in bold.

(a) Full dataset

	Binomial error structure					Poisson error structure			
	(deviance = 306.1, df = 6)					(deviance = 322.3, df = 6)			
	coefficient	SE	z	P		coefficient	SE	z	P
Intercept	−0.69	0.31	−2.18	0.029		−0.57	0.18	−3.20	0.001
Habitat									
Grassland*	0.33	0.33	1.00	0.318		0.20	0.33	0.62	0.532
Wetland*	0.29	0.40	0.71	0.479		0.26	0.16	1.56	0.118
Ocean*	0.59	0.58	1.02	0.310		0.30	0.20	1.48	0.140
Latitudinal range position									
Tropical zone†	**0.80**	**0.31**	**2.58**	**0.010**		**0.49**	**0.17**	**2.89**	**0.004**

df, degrees of freedom
* Difference from the reference level – forest
† Difference from the reference level – temperate zone

(b) Reduced dataset

	Binomial error structure					Poisson error structure			
	(deviance = 257.8, df = 11)					(deviance = 268.9, df = 11)			
	coefficient	SE	z	P		coefficient	SE	z	P
Intercept	−1.66	0.87	−1.92	0.055		−0.98	0.45	−2.19	0.029
Habitat									
Grassland*	0.49	0.36	1.36	0.176		**0.39**	**0.18**	**2.13**	**0.033**
Wetland*	0.27	0.47	0.57	0.567		0.29	0.24	1.21	0.227
Ocean*	0.52	0.80	0.65	0.518		0.08	0.44	0.19	0.851
Latitudinal range position									
Tropical zone†	**0.81**	**0.35**	**2.28**	**0.023**		0.58	0.19	3.02	**0.003**
Migration strategy									
Residents‡	0.32	0.40	0.80	0.427		0.18	0.20	0.88	0.377
Body mass¶	0.13	0.10	1.32	0.186		0.07	0.05	1.41	0.160
Diet									
Insectivores§	0.58	0.58	1.00	0.318		-0.03	0.29	-0.10	0.922
Herbivores§	0.35	0.53	0.66	0.508		0.09	0.26	0.33	0.739
Omnivores§	-0.44	0.64	-0.69	0.487		-0.56	0.36	-1.54	0.123

df, degrees of freedom
* Difference from the reference level – forest
† Difference from the reference level – temperate zone
‡ Difference from the reference level – migrants
¶ Slope
§ Difference from the reference level – carnivorous

3. DISCUSSION

Our analysis of 113 pairs of globally threatened and unthreatened avian sister species showed higher threat for species breeding in the tropics. The result was consistent across different models and robust to manipulations of dataset (i.e. adding more factors to a limited set of species) and types of expression of the response variable: both simple binary coding as threatened versus unthreatened species and numerical transformation of IUCN categories of increasing extinction risk showed tropical breeding ranges of more threatened species. The remaining trait variables, namely, habitat use, migration strategy, body mass and diet, did not show any associations with threat level, albeit one model indicated significantly higher threat in species breeding in open habitats than in forest species.

Higher threat level is for tropical species in accord with the studies recognizing majority of biodiversity hot spots, that is, sites of exceptionally high species richness under extreme human pressures, as being localised in the tropics (e.g. Manne et al. 1999; Orme et al. 2005; Jenkins et al. 2013). One could argue that our result is just an artefact of a strong latitudinal gradient in bird species richness: Because the tropics harbour vast majority of global bird taxonomic diversity (Davies et al. 2007), they should also sample a higher number of threatened species than the temperate zone by chance alone (Hurlbert & Jetz 2007). This is true at the coarse scale of spatial resolution, although there are some mismatches between diversity and threat at the local level (Orme et al. 2005). However, our analysis does not suggest that the higher threat of tropical species results from a sampling artefact. Indeed, tropical species account for almost 80% of total bird diversity (Newton 2003), whereas they represented only 63% of our sample size. Moreover, because of using a sister species approach, our data contained equal numbers of threatened and unthreatened species. This approach thus ensured that a higher threat level observed in tropical species is not caused by a simple fact that most birds are tropical, but that it results from some intrinsic factors elevating avian extinction risk in this part of the world.

Why are the tropical species more threatened that their temperate sisters? First, it is possible that environmental pressures are higher in tropical regions due to higher growth rate of human population and also higher rate of economic development (e.g. Butchart et al. 2010, Janssen & Rutz 2011, Laurance et al. 2014). These pressures are reducing remaining areas of natural habitats forcing their bird species to higher risk of extinction (Gibson et al. 2011, Laurance et al. 2014). Alternatively, even if the pressures were similar in both latitudinal zones, tropical species evolved over long time in stable climatic conditions represented by modest changes in tropical ecosystems during Quaternary contrasting with great climatic oscillations and biome shifts in the temperate zone (Dynesius & Jansson 2000, Sandel et al. 2011). Therefore, temperate species that were unable to adapt to climatically induced disturbance and habitat fragmentation went extinct long before humans arrived. In contrast, their adaptation to stability made tropical species more sensitive to recent human disturbance resulting in their elevated extinction risk. Moreover, conservation legislation may be more developed and especially its enforcement more efficient in countries of “wealth north” (Sodhi et al. 2011, Atkinson et al. 2014) leading to more improved bird protection and reduced extinction risk in the temperate zone compared to the tropics.

In addition, according to the Rapoport’s rule, tropical bird species should have smaller breeding ranges than temperate birds (Stevens 1989). As range size and population size are strongly correlated and small populations go extinct more frequently than large populations (Borregaard & Rahbek 2010), small ranges of tropical birds (Orme et al. 2006) can make their populations more vulnerable to environmental perturbations and thus more threatened. Indeed, recent studies did not find much support for the existence of ecological mechanisms underlying Rapoport’s rule (Šizling et al. 2009) and global variability of birds’ breeding range sizes is predominantly shaped by areas of major land masses (Storch 2000; Orme et al. 2006). On the other hand, threatened birds are concentrated in montane areas in the tropics (Orme et al. 2005) and montane species have generally smaller range sizes (Fjeldså et al. 2012). We thus cannot exclude that small range size of tropical species is the factor making them more vulnerable to threats discussed above resulting in their higher extinction risk.

We did not find a significant interaction between latitudinal position of breeding range and habitat. This indicates that environmental pressures acting in the tropics are not confined to a specific habitat. For example, species breeding in tropical forests are not more threatened than tropical savannah species, despite widely recognised pressures on tropical forests (e.g. Wilcove et al. 2014). Instead, it seems that threatening factors act simultaneously in different environments and we can speculate that despite tropical forests being the key habitat for global biodiversity, other habitats suffer from pressures of similar magnitudes (e.g. Sirami & Monadjem 2012) but less frequently reported. This corresponds to the above mentioned idea about a dominant effect of overall socioeconomic development of human societies in tropical countries.

The main effect of habitat was insignificant in all but one model. This model showed higher threat for open habitat than for forest species. This finding points at significance of various forms of degradation of these habitat including loss of pristine grasslands because of expansion of agriculture (Kamp et al. 2011), agricultural intensification in highly developed regions (Donald et al. 2001) and land abandonment in less productive agricultural regions of North America and Eurasia (Laiolo et al. 2004). Moreover, it seems that climate change and changes in ecosystems functioning drive loss of open grasslands because of forest and shrub encroachment even in the absence of direct human influence, making this habitat particularly vulnerable (Davey et al. 2012; Sirami & Monadjem 2012). On the other hand, despite increasing human pressure on primeval forest habitats in both tropical (Gibson et al. 2011; Wilcove et al. 2014) and temperate zones (Wesolowski 2005; Chyralecki & Selva 2016), global net change in forest area is slightly positive or neutral (Hansen et al. 2013), which can be beneficial for forest birds leading to their lower threat levels.

The model showed a significant effect of habitat contained species' extinction risk as a response variable expressed using several different threat levels (and had thus Poisson error structure). A similar model with the extinction risk expressed by a binary coding discriminating threatened and unthreatened species (and having thus binomial error structure) showed the same direction of the habitat effect, but without the statistical significance. Therefore, we suggest that the discrimination of several levels of threat reflecting an increasing extinction risk is more informative and should be preferably used in analyses testing the contributions of possible threatening factors.

However, the effect of breeding habitat was generally weak in our analyses. Such a weak effect was surprising, given generally high variability in species' habitat use (called beta-niche) at the species level compared to evolutionary stable traits such as beak morphology creating species' alfa-niche (Ackerly & Cornwell 2007, Pearman et al. 2014). However, it seems that this variability is reduced within sister species, indicating the existence of niche conservatism in species' habitat use (Barnagaud et al. 2014). Indeed, the same habitat category for both species was observed in 85% of sister species pairs indicating that our focal sister species did not diverge in their habitat niches, and this limited variability obviously translated into poor ability of this trait to account for variation in threat level. It is, however, possible that the use of a more detailed classification of species' habitat would uncover new patterns. Obtaining more accurate data on habitat use of threatened species should be a priority for avian conservation research.

The remaining three traits (migration strategy, body mass and diet) did not show any relationships to threat level in our focal avian sister species. Body mass and diet are known to be highly conserved in phylogeny (Ricklefs 2007; McGill 2008), and thus it is not surprising that the species within pairs did not differ in these traits resulting in the absence of relationships to threat level. We suggest that their effects would be possible to detect if higher taxa were taken as units for analysis (see Owens & Bennett 2000). Although migration strategies may be very different even amongst closely related species (Bruderer & Salewski 2008), variability in this trait within our focal species pairs was low (82% of pairs showed the same migration strategy for both species). Similar to habitat use, migration strategy is thus not the trait accounting for differences in threat level between avian sister species. However, we note that our data did not discriminate between short- and long-distance migrants. As serious declines were found in long-distance migrants in both North America and Eurasia (Greenberg & Marra 2005), it is possible that a finer classification of migration strategies would reveal a significant pattern.

In summary, our study based on pair-wise comparison of avian sister species showed significantly higher threat for tropical than for temperate taxa irrespective of their habitat use and accounting for several ecological and life-history traits. These results indicate that threatened birds are concentrated in the tropics, and conservation effort should be targeted into these areas not only because of their enormous biological diversity but also because of disproportionally higher threat of tropical compared to temperate species. Given the lower importance of the effect of birds' habitat use, suggesting that species under higher extinction risk are not confined to some specific habitats, we suggest that overall improvement of environmental conditions and legislation in countries located in the tropical zone may be a route to improvement. Lessons from some developing temperate regions, such as Eastern Europe (Koleček et al. 2014b), imply that such a solution is achievable.

Acknowledgements: We wish to thank Lenka Kopsová and two anonymous referees for their comments on earlier versions of this study.

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Supplementary Table 1: *Characteristics of pairs (Pair) of avian sister species (Species) used for the analysis. Species extinction risk was expressed using IUCN categories recognising either threatened (1) and unthreatened (0) species (Threat_1) or levels of increasing threat with least concern (0), near threatened (1), vulnerable (2), endangered (3), critically endangered (4) and extinct in the wild (5) species (Threat_2). Other traits included are habitat: forest, grassland, wetland and ocean; latitudinal range position (Latitude): temperate and tropical; migration strategy (Migration): migratory and residential; body mass (in grams); and diet: carnivorous, insectivorous, herbivorous and omnivorous.*

Pair	Species	Threat_1	Threat_2	Latitude	Habitat	Migration	Body mass (g)	Diet
1	*Aptenodytes patagonicus*	1	1	Temperate	Ocean	Residential	11,000	Carnivorous
1	*Aptenodytes forsteri*	0	0	Temperate	Ocean	Migratory	33,000	Carnivorous
2	*Pygoscelis papua*	1	1	Temperate	Ocean	Migratory	7,000	Carnivorous
2	*Pygoscelis antarctica*	0	0	Temperate	Ocean	Migratory	4,500	Carnivorous
3	*Rollandia rolland*	1	3	Tropical	Wetland	–	–	–
3	*Rollandia microptera*	0	0	Temperate	Wetland	–	–	–
4	*Poliocephalus poliocephalus*	1	2	Temperate	Wetland	Migratory	240	Carnivorous
4	*Poliocephalus rufopectus*	0	0	Temperate	Wetland	Residential	251	Carnivorous
5	*Bulweria bulwerii*	1	1	Tropical	Ocean	–	–	–
5	*Bulweria fallax*	0	0	Temperate	Ocean	–	–	–
6	*Puffinus pacificus*	1	2	Temperate	Ocean	Residential	435	Carnivorous
6	*Puffinus bulleri*	0	0	Tropical	Ocean	Migratory	380	Carnivorous
7	*Puffinus carneipes*	1	2	Temperate	Ocean	–	–	–
7	*Puffinus creatopus*	0	0	Temperate	Ocean	–	–	–
9	*Morus serrator*	1	2	Temperate	Ocean	Residential	2,350	Carnivorous
9	*Morus capensis*	0	0	Temperate	Ocean	Residential	2,600	Carnivorous
10	*Ephippiorhynchus senegalensis*	1	1	Tropical	Wetland	Residential	6,000	Carnivorous
10	*Ephippiorhynchus asiaticus*	0	0	Tropical	Wetland	Residential	4,100	Carnivorous
11	*Chauna torquata*	1	1	Tropical	Wetland	–	–	–
11	*Chauna chavaria*	0	0	Temperate	Wetland	–	–	–
12	*Anas strepera*	1	1	Temperate	Wetland	Migratory	920	Herbivorous
12	*Anas falcata*	0	0	Temperate	Wetland	Migratory	596	Herbivorous
13	*Leptodon cayanensis*	1	4	Tropical	Forest	Residential	510	Carnivorous
13	*Leptodon forbesi*	0	0	Tropical	Forest	Residential	565	Carnivorous
14	*Henicopernis longicauda*	1	2	Tropical	Forest	Residential	594	Carnivorous
14	*Henicopernis infuscatus*	0	0	Tropical	Forest	Residential	595	Carnivorous
15	*Haliaeetus vocifer*	1	4	Tropical	Wetland	Residential	2,821	Carnivorous
15	*Haliaeetus vociferoides*	0	0	Tropical	Wetland	Residential	2,800	Carnivorous
16	*Haliaeetus leucogaster*	1	2	Tropical	Forest	Residential	2,830	Carnivorous
16	*Haliaeetus sanfordi*	0	0	Temperate	Wetland	Migratory	2,497	Carnivorous
17	*Polihierax semitorquatus*	1	1	Tropical	Grassland	Residential	60	Carnivorous
17	*Polihierax insignis*	0	0	Tropical	Grassland	Residential	98	Carnivorous
18	*Aepypodius arfakianus*	1	3	Tropical	Forest	–	–	–
18	*Aepypodius bruijnii*	0	0	Tropical	Forest	–	–	–
19	*Chamaepetes unicolor*	1	1	Tropical	Forest	Residential	675	Herbivorous
19	*Chamaepetes goudotii*	0	0	Tropical	Forest	Residential	1,135	Herbivorous
20	*Crax alector*	1	2	Tropical	Forest	Residential	3,106	Herbivorous
20	*Crax fasciolata*	0	0	Tropical	Forest	Residential	2,600	Herbivorous
21	*Tetrao tetrix*	1	1	Temperate	Forest	Residential	1,050	Herbivorous
21	*Tetrao mlokosiewiczi*	0	0	Temperate	Forest	Residential	840	Herbivorous

22	*Tympanuchus phasianellus*	1	2	Temperate	Grassland	Residential	880	Herbivorous
22	*Tympanuchus cupido*	0	0	Temperate	Grassland	Residential	990	Herbivorous
23	*Cyrtonyx montezumae*	1	1	Tropical	Forest	Residential	186	Herbivorous
23	*Cyrtonyx ocellatus*	0	0	Temperate	Forest	Residential	165	Herbivorous
24	*Tragopan temminckii*	1	2	Temperate	Forest	Residential	1,184	Herbivorous
24	*Tragopan caboti*	0	0	Temperate	Forest	Residential	1,150	Herbivorous
25	*Lophura diardi*	1	1	Tropical	Forest	Residential	1,210	Herbivorous
25	*Lophura ignita*	0	0	Tropical	Forest	Residential	1,817	Herbivorous
26	*Pavo cristatus*	1	3	Tropical	Forest	Residential	4,188	Omnivorous
26	*Pavo muticus*	0	0	Tropical	Forest	Residential	4,425	Herbivorous
27	*Grus rubicunda*	1	2	Tropical	Wetland	Residential	6,003	Omnivorous
27	*Grus antigone*	0	0	Temperate	Wetland	Residential	7,740	Omnivorous
28	*Gymnocrex plumbeiventris*	1	2	Tropical	Forest	Residential	300	Insectivorous
28	*Gymnocrex rosenbergii*	0	0	Tropical	Forest	Residential	310	Insectivorous
29	*Amaurornis bicolor*	1	3	Tropical	Wetland	Residential	55	Herbivorous
29	*Amaurornis olivieri*	0	0	Temperate	Forest	Migratory	59	Herbivorous
30	*Porzana fusca*	1	1	Temperate	Wetland	Migratory	60	Herbivorous
30	*Porzana paykullii*	0	0	Temperate	Wetland	Residential	66	Insectivorous
31	*Ardeotis kori*	1	1	Tropical	Grassland	–	–	–
31	*Ardeotis arabs*	0	0	Tropical	Grassland	–	–	–
32	*Ardeotis australis*	1	4	Temperate	Grassland	–	–	–
32	*Ardeotis nigriceps*	0	0	Temperate	Grassland	–	–	–
33	*Actophilornis africanus*	1	1	Tropical	Wetland	–	–	–
33	*Actophilornis albinucha*	0	0	Temperate	Wetland	–	–	–
34	*Larus belcheri*	1	2	Temperate	Wetland	Residential	929	Carnivorous
34	*Larus atlanticus*	0	0	Tropical	Wetland	Migratory	930	Carnivorous
35	*Larus pipixcan*	1	2	Tropical	Wetland	Residential	280	Carnivorous
35	*Larus fuliginosus*	0	0	Temperate	Wetland	Migratory	285	Carnivorous
36	*Xema sabini*	1	1	Temperate	Ocean	Migratory	190	Omnivorous
36	*Pagophila eburnea*	0	0	Temperate	Ocean	Migratory	610	Omnivorous
37	*Rissa tridactyla*	1	2	Temperate	Ocean	Migratory	408	Carnivorous
37	*Rissa brevirostris*	0	0	Temperate	Ocean	Migratory	385	Carnivorous
38	*Sterna albifrons*	1	2	Temperate	Wetland	Migratory	55	Carnivorous
38	*Sterna nereis*	0	0	Temperate	Wetland	Migratory	57	Carnivorous
39	*Turacoena manadensis*	1	1	Tropical	Forest	Migratory	212	Herbivorous
39	*Turacoena modesta*	0	0	Tropical	Forest	Migratory	214	Herbivorous
40	*Henicophaps albifrons*	1	2	Tropical	Forest	Migratory	247	Herbivorous
40	*Henicophaps foersteri*	0	0	Tropical	Forest	Migratory	251	Herbivorous
41	*Zenaida macroura*	1	5	Tropical	Grassland	Migratory	134	Herbivorous
41	*Zenaida graysoni*	0	0	Temperate	Grassland	Residential	190	Herbivorous
42	*Aprosmictus erythropterus*	1	1	Tropical	Grassland	–	–	–
42	*Aprosmictus jonquillaceus*	0	0	Temperate	Grassland	–	–	–
43	*Nannopsittaca panychlora*	1	1	Temperate	Forest	–	–	–
43	*Nannopsittaca dachilleae*	0	0	Temperate	Forest	–	–	–

44	*Pionites melanocephala*	1	2	Temperate	Forest	–	–	–
44	*Pionites leucogaster*	0	0	Temperate	Forest	–	–	–
45	*Amazona amazonica*	1	2	Tropical	Forest	–	–	–
45	*Amazona guildingii*	0	0	Tropical	Forest	–	–	–
46	*Carpococcyx renauldi*	1	1	Tropical	Forest	–	–	–
46	*Carpococcyx radiceus*	0	0	Tropical	Forest	–	–	–
47	*Hyetornis pluvialis*	1	3	Tropical	Forest	Residential	130	Insectivorous
47	*Hyetornis rufigularis*	0	0	Tropical	Forest	Residential	132	Insectivorous
48	*Phodilus badius*	1	3	Tropical	Forest	Residential	281	Carnivorous
48	*Phodilus prigoginei*	0	0	Tropical	Forest	Residential	195	Carnivorous
49	*Schoutedenapus myoptilus*	1	2	Tropical	Grassland	Residential	22	Insectivorous
49	*Schoutedenapus schoutedeni*	0	0	Tropical	Grassland	Residential	25	Insectivorous
50	*Mearnsia novaeguineae*	1	1	Tropical	Forest	–	–	–
50	*Mearnsia picina*	0	0	Tropical	Forest	–	–	–
51	*Sephanoides sephaniodes*	1	4	Tropical	Grassland	Migratory	5	Herbivorous
51	*Sephanoides fernandensis*	0	0	Tropical	Grassland	Residential	9	Herbivorous
52	*Haplophaedia aureliae*	1	1	Tropical	Forest	Residential	5	Herbivorous
52	*Haplophaedia lugens*	0	0	Tropical	Forest	Residential	5	Herbivorous
53	*Ramphomicron microrhynchum*	1	3	Tropical	Grassland	Residential	4	Herbivorous
53	*Ramphomicron dorsale*	0	0	Tropical	Forest	Residential	4	Herbivorous
54	*Doricha enicura*	1	1	Tropical	Grassland	Residential	2	Herbivorous
54	*Doricha eliza*	0	0	Tropical	Grassland	Residential	3	Herbivorous
55	*Mellisuga minima*	1	1	Tropical	Grassland	Residential	2	Herbivorous
55	*Mellisuga helenae*	0	0	Tropical	Grassland	Residential	2	Herbivorous
56	*Priotelus temnurus*	1	1	Tropical	Forest	Residential	58	Herbivorous
56	*Priotelus roseigaster*	0	0	Tropical	Forest	Migratory	74	Herbivorous
57	*Electron platyrhynchum*	1	2	Tropical	Forest	Residential	61	Carnivorous
57	*Electron carinatum*	0	0	Tropical	Forest	Residential	65	Carnivorous
59	*Atelornis pittoides*	1	1	Temperate	Forest	Residential	92	Insectivorous
59	*Atelornis crossleyi*	0	0	Temperate	Forest	Residential	81	Insectivorous
60	*Anorrhinus galeritus*	1	1	Tropical	Forest	Residential	4,113	Omnivorous
60	*Anorrhinus tickelli*	0	0	Tropical	Forest	Residential	4,000	Omnivorous
61	*Bucorvus abyssinicus*	1	2	Tropical	Grassland	Residential	814	Omnivorous
61	*Bucorvus leadbeateri*	0	0	Tropical	Grassland	Residential	1,190	Omnivorous
62	*Semnornis frantzii*	1	1	Tropical	Forest	Residential	64	Herbivorous
62	*Semnornis ramphastinus*	0	0	Tropical	Forest	Residential	97	Herbivorous
63	*Pteroglossus beauharnaesii*	1	1	Tropical	Forest	Migratory	222	Omnivorous
63	*Pteroglossus bitorquatus*	0	0	Tropical	Forest	Residential	115	Omnivorous
64	*Ramphastos swainsonii*	1	2	Tropical	Forest	Residential	575	Omnivorous
64	*Ramphastos ambiguus*	0	0	Tropical	Forest	Residential	575	Omnivorous
65	*Philepitta castanea*	1	1	Tropical	Forest	–	–	–
65	*Philepitta schlegeli*	0	0	Tropical	Forest	–	–	–
66	*Neodrepanis coruscans*	1	2	Tropical	Forest	–	–	–

66	*Neodrepanis hypoxantha*	0	0	Tropical	Forest	–	–	–
67	*Geositta crassirostris*	1	2	Tropical	Grassland	Residential	52	Insectivorous
67	*Geositta poecilopterus*	0	0	Tropical	Grassland	Residential	18	Insectivorous
68	*Aphrastura spinicauda*	1	4	Temperate	Forest	Residential	11	Insectivorous
68	*Aphrastura masafuerae*	0	0	Temperate	Forest	Residential	14	Insectivorous
69	*Limnornis curvirostris*	1	1	Temperate	Wetland	Residential	28	Insectivorous
69	*Limnornis rectirostris*	0	0	Temperate	Wetland	Residential	18	Insectivorous
70	*Xenerpestes minlosi*	1	1	Tropical	Forest	Residential	11	Insectivorous
70	*Xenerpestes singularis*	0	0	Tropical	Forest	Residential	13	Insectivorous
71	*Premnoplex brunnescens*	1	2	Tropical	Forest	Residential	17	Insectivorous
71	*Premnoplex tatei*	0	0	Tropical	Forest	Residential	23	Insectivorous
72	*Simoxenops striatus*	1	1	Tropical	Forest	Residential	42	Insectivorous
72	*Simoxenops ucayalae*	0	0	Tropical	Forest	Residential	47	Insectivorous
73	*Hylocryptus rectirostris*	1	2	Tropical	Forest	Residential	48	Insectivorous
73	*Hylocryptus erythrocephalus*	0	0	Tropical	Forest	Residential	48	Insectivorous
74	*Deconychura stictolaema*	1	1	Tropical	Forest	Residential	16	Insectivorous
74	*Deconychura longicauda*	0	0	Tropical	Forest	Residential	25	Insectivorous
75	*Pittasoma michleri*	1	1	Tropical	Forest	Residential	110	Insectivorous
75	*Pittasoma rufopileatum*	0	0	Tropical	Forest	Residential	97	Insectivorous
76	*Anairetes parulus*	1	1	Temperate	Grassland	Migratory	4	Insectivorous
76	*Anairetes fernandezianus*	0	0	Temperate	Forest	Residential	6	Insectivorous
77	*Polystictus superciliaris*	1	1	Temperate	Grassland	Residential	6	Insectivorous
77	*Polystictus pectoralis*	0	0	Tropical	Grassland	Migratory	7	Insectivorous
78	*Euscarthmus meloryphus*	1	1	Tropical	Grassland	Residential	7	Insectivorous
78	*Euscarthmus rufomarginatus*	0	0	Temperate	Grassland	Residential	6	Herbivorous
79	*Lathrotriccus euleri*	1	2	Tropical	Grassland	Residential	11	Insectivorous
79	*Lathrotriccus griseipectus*	0	0	Temperate	Forest	Residential	11	Insectivorous
80	*Menura novaehollandiae*	1	1	Temperate	Grassland	Residential	995	Insectivorous
80	*Menura alberti*	0	0	Temperate	Grassland	Residential	930	Insectivorous
81	*Tachycineta thalassina*	1	2	Tropical	Grassland	Migratory	15	Insectivorous
81	*Tachycineta euchrysea*	0	0	Temperate	Grassland	Residential	17	Insectivorous
82	*Anthus lutescens*	1	2	Temperate	Grassland	Residential	15	Herbivorous
82	*Anthus spragueii*	0	0	Temperate	Grassland	Migratory	25	Herbivorous
83	*Anthus correndera*	1	1	Temperate	Grassland	Residential	20	Herbivorous
83	*Anthus antarcticus*	0	0	Temperate	Grassland	Residential	23	Insectivorous
84	*Cinclus leucocephalus*	1	2	Temperate	Wetland	Residential	44	Insectivorous
84	*Cinclus schulzi*	0	0	Tropical	Wetland	Residential	40	Insectivorous
85	*Odontorchilus branickii*	1	1	Tropical	Forest	Residential	10	Insectivorous
85	*Odontorchilus cinereus*	0	0	Tropical	Forest	Residential	11	Insectivorous
86	*Troglodytes aedon*	1	1	Tropical	Forest	Migratory	12	Herbivorous
86	*Thryomanes sissonii*	0	0	Temperate	Grassland	Residential	14	Herbivorous
87	*Toxostoma cinereum*	1	2	Temperate	Grassland	Residential	60	Herbivorous
87	*Toxostoma bendirei*	0	0	Temperate	Grassland	Residential	60	Herbivorous
88	*Turdus nudigenis*	1	1	Tropical	Forest	Residential	62	Herbivorous

88	*Turdus haplochrous*	0	0	Tropical	Grassland	Residential	84	Herbivorous
89	*Turdus pallidus*	1	2	Temperate	Forest	Migratory	77	Herbivorous
89	*Turdus feae*	0	0	Temperate	Forest	Migratory	79	Herbivorous
90	*Turdus jamaicensis*	1	3	Tropical	Forest	Residential	59	Herbivorous
90	*Turdus swalesi*	0	0	Tropical	Forest	Residential	99	Herbivorous
91	*Bathmocercus rufus*	1	1	Tropical	Grassland	Residential	17	Insectivorous
91	*Bathmocercus cerviniventris*	0	0	Tropical	Forest	Residential	16	Insectivorous
92	*Acrocephalus newtoni*	1	2	Tropical	Grassland	Residential	18	Insectivorous
92	*Bebrornis sechellensis*	0	0	Temperate	Wetland	Residential	16	Insectivorous
93	*Schoenicola brevirostris*	1	2	Tropical	Grassland	Residential	15	Insectivorous
93	*Shoenicola platyura*	0	0	Tropical	Grassland	Residential	20	Insectivorous
94	*Sylvia lugens*	1	2	Tropical	Grassland	Residential	15	Herbivorous
94	*Sylvia buryi*	0	0	Tropical	Grassland	Residential	22	Insectivorous
95	*Sylvia deserticola*	1	1	Temperate	Grassland	Migratory	11	Herbivorous
95	*Sylvia undata*	0	0	Temperate	Grassland	Migratory	10	Insectivorous
96	*Ficedula westermanni*	1	1	Tropical	Forest	Residential	8	Insectivorous
96	*Ficedula rufigula*	0	0	Temperate	Forest	Residential	11	Insectivorous
97	*Ficedula buruensis*	1	3	Tropical	Forest	Residential	9	Insectivorous
97	*Ficedula bonthaina*	0	0	Tropical	Forest	Residential	11	Insectivorous
98	*Ficedula albicilla*	1	2	Tropical	Grassland	Migratory	11	Insectivorous
98	*Ficedula subrubra*	0	0	Temperate	Forest	Migratory	11	Insectivorous
99	*Ficedula tricolor*	1	1	Tropical	Forest	Migratory	8	Insectivorous
99	*Ficedula nigrorufa*	0	0	Temperate	Forest	Residential	9	Insectivorous
100	*Ficedula harterti*	1	1	Tropical	Grassland	Residential	8	Insectivorous
100	*Ficedula timorensis*	0	0	Tropical	Forest	Residential	9	Insectivorous
101	*Rhyacornis fuliginosus*	1	2	Tropical	Wetland	Residential	18	Insectivorous
101	*Rhyacornis bicolor*	0	0	Tropical	Wetland	Residential	19	Insectivorous
102	*Parus elegans*	1	1	Tropical	Forest	Residential	13	Herbivorous
102	*Parus amabilis*	0	0	Tropical	Forest	Residential	15	Herbivorous
103	*Heleia crassirostris*	1	1	Tropical	Forest	–	–	–
103	*Heleia muelleri*	0	0	Tropical	Forest	–	–	–
104	*Woodfordia superciliosa*	1	1	Tropical	Grassland	Residential	30	Herbivorous
104	*Woodfordia lacertosa*	0	0	Tropical	Grassland	Residential	33	Herbivorous
105	*Sphecotheres viridis*	1	1	Tropical	Forest	Residential	77	Herbivorous
105	*Sphecotheres hypoleucus*	0	0	Tropical	Forest	Residential	77	Herbivorous
106	*Ergaticus ruber*	1	2	Tropical	Forest	Residential	8	Herbivorous
106	*Ergaticus versicolor*	0	0	Tropical	Forest	Residential	10	Herbivorous
107	*Conothraupis speculigera*	1	4	Tropical	Grassland	Migratory	26	Herbivorous
107	*Conothraupis mesoleuca*	0	0	Tropical	Grassland	Migratory	15	Herbivorous
108	*Nemosia pileata*	1	4	Tropical	Forest	Residential	14	Herbivorous
108	*Nemosia rourei*	0	0	Tropical	Wetland	Migratory	22	Herbivorous
109	*Tangara seledon*	1	2	Tropical	Forest	Residential	18	Herbivorous
109	*Tangara fastuosa*	0	0	Temperate	Forest	Residential	22	Herbivorous
110	*Pselliophorus tibialis*	1	2	Temperate	Forest	Residential	31	Herbivorous

110	*Pselliophorus luteoviridis*	0	0	Temperate	Forest	Residential	35	Herbivorous
111	*Agelaius humeralis*	1	3	Tropical	Wetland	Residential	36	Omnivorous
111	*Agelaius xanthomus*	0	0	Tropical	Grassland	Residential	38	Herbivorous
112	*Agelaius phoeniceus*	1	3	Temperate	Wetland	Residential	53	Herbivorous
112	*Agelaius tricolor*	0	0	Temperate	Wetland	Residential	56	Herbivorous
113	*Euphagus cyanocephalus*	1	2	Temperate	Grassland	Residential	63	Omnivorous
113	*Euphagus carolinus*	0	0	Temperate	Grassland	Residential	63	Omnivorous
114	*Curaeus curaeus*	1	3	Tropical	Grassland	Residential	83	Omnivorous
114	*Curaeus forbesi*	0	0	Temperate	Grassland	Residential	87	Herbivorous
115	*Macroagelaius imthurni*	1	3	Tropical	Forest	Residential	77	Omnivorous
115	*Macroagelaius subalaris*	0	0	Tropical	Forest	Residential	79	Herbivorous