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Global wildlife trade across the tree of life

Brett R. Scheffers[1]*, Brunno F. Oliveira[1,2], Ieuan Lamb[3], David P. Edwards[3]*

(Shared first authorship)

[1]Department of Wildlife Ecology & Conservation, Newins-Ziegler Hall, University of Florida/IFAS, Gainesville, FL 32611, USA.

[2]Department of Biology and Environmental Sciences, Auburn University at Montgomery, Montgomery, AL 36124, USA.

[3]Department of Animal and Plant Sciences, University of Sheffield, S10 2TN, UK.

*corresponding authors
brett.scheffers@ufl.edu
david.edwards@sheffield.ac.uk

Abstract

Wildlife trade is a multi-billion dollar industry that is driving species towards extinction. Eighteen percent of >31,500 terrestrial bird, mammal, amphibian and squamate reptiles species (N = 5,579) are traded globally. Trade is strongly phylogenetically conserved and the hotspots of this trade are concentrated in the biologically diverse tropics. Using different assessment approaches, we predict future trade to impact up to 3,196 additional species based on their phylogenetic replacement and trait similarity to currently traded species—all together totaling 8,775 species at risk of extinction from trade. Our assessment underscores the need for a strategic plan to combat trade with policies that are proactive rather than reactive, which is especially important since species can quickly transition from being safe to endangered as humans continue to harvest and trade across the tree of life.

INTRODUCTION

The tree of life is being pruned by human activities at an unprecedented rate (1). Yet, while we understand the global footprint of land degradation and deforestation and how that manifests in species loss (2), we have limited understanding of the global extent and patterns of the wildlife trade. So substantial is the trade of wildlife for pets, luxury foods, and medicinal parts that it now represents the most prominent driver of vertebrate extinction risk globally, joint with land-use change (3). Each year, billions of wild plants and animals are traded to meet a rapidly expanding global demand (4, 5), and so insatiable is this demand that globally US$8-21 billion is reaped annually from the illegal trade, making it one of the world's largest illegitimate businesses (5, 6).

The high demand for wildlife products and pets has driven dramatic losses in enigmatic species like tigers, elephants, rhinos, and poison dart frogs (7). Some subspecies are already extinct (e.g. the last individual of the Javan rhino Rhinoceros sondaicus annamiticus was shot for its horn in 2010 in Vietnam (8)) or on the cusp of extinction in the wild (e.g., Bali myna, Leucopsar rothschildi)—all due to trade. There is an insidious aspect of this market force in that these emblematic species only represent a tiny, yet well publicized, fraction of animal species traded. Importantly, if cultural preferences change, wildlife trade can rapidly drive a species towards extinction. For instance, the emergence of widespread demand in East Asia for pangolin scales and meat has triggered major declines in some species (e.g. Sunda pangolin (Manis javanica)) in just two decades (9), while growing demand for the ivory-like casque of helmeted hornbill (Rhinoplax vigil) resulted in tens of thousands of individuals traded annually since around 2012 (10). Both species are now Critically Endangered (11). Moreover, wildlife trade indirectly places significant pressure on biodiversity through the introduction of pathogens, including the globally lethal amphibian fungus Batrachochytrium dendrobatidis (12), and invasive species, such as Burmese python (Python bivittatus) in Florida, USA (13).

The enormous trade in wildlife begs the question whether we can better protect species from human demand, which is a question at the forefront of the wildlife trade crisis. Combating wildlife trade first requires the identification of what species are being traded and second the identification of where traded species occur. Here, we searched the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the International Union for Conservation of Nature Red list of Threatened Species (IUCN Red List) databases to identify traded terrestrial vertebrate species (birds, mammals, amphibians, and squamate reptiles). Using our list, we provide an evaluation of the global extent of wildlife trade across the tree of life to determine if trade targets unique evolutionary branches. We then used species range maps to identify global hotspots of wildlife exploitation, and how those hotspots vary between trade for pets or products (i.e. medicine, luxury foods, skins). While emerging gene- and web-based techniques can help to identify the precise sources of traded individuals, our approach allows us to identify the likely global epicenters of diversity in traded animals.

What species are traded?

Trade in wildlife affects approximately 18% of all extant terrestrial vertebrate species on Earth. Specifically, our assessment shows that 5,579 of the 31,745 vertebrate species have been reported as traded, with a higher percentage of all birds (23% of 10,278 species) and mammals (27% of 5,420 species) globally traded than reptiles (12% of 9,563 species) and amphibians (9% of 6,484 species) (Fig. 1, Table S1). Our assessment across both CITES and IUCN yields a total that is 40-60% higher than prior recorded estimates (e.g., (3, 14, 15)). Importantly, traded species are in higher categories of threat compared to non-traded species (especially among mammals and birds; Fig.1, Table S2), confirming wildlife trade as a driver of extinction risk.

We found trade occurs in 65% of all terrestrial vertebrate families (312 of 482 families; Table S1). This pattern is evident across all terrestrial vertebrate groups considered, with mammals and reptiles showing the highest percentage of families traded (mammals=81%, N= 110; reptiles=73%, N=53), followed by amphibians (55%, N= 41) and birds (55%, N=108). Despite this broad exploitation, humans are targeting specific components of the tree of life (Fig. 2 and S1), as indicated by a significant phylogenetic signal in wildlife trade for all taxa (Fig. S2). Mammals and birds showed a signal as strong as expected under a Brownian motion model of evolution (Fig. S2), indicating higher levels of phylogenetic clustering relative to reptiles and amphibians (16). Highly traded families—those with more than 50% of their species traded—comprise more than one quarter (27%; 128 of 482 families) of the total families, which breaks down to 51% of mammal (N=69), 32% of reptile (N=23), 16% of bird (N=32), and 5% of amphibian (N=4) families (Tables S1 and S3).

Non-randomness in trade across the tree of life implies high susceptibility for select clades likely based on similar traits (such as voice quality, folklore, ivory, etc). In exploring this, we found that large-bodied species are more traded than small-bodied species, a pattern that holds regardless of IUCN threat category (Fig. S3 and Table S4), and that the probability of being traded is positively related to body size (Fig. S4). Over millennia, primitive human societies impacted large-bodied species through hunting for subsistence, which changed contemporary biogeographical patterns of animal body size (17, 18). Our analysis shows that this pattern continues in modern humans through the wildlife trade.

Trade also targets species that are unique and/or distinctive in traits. In our assessment of evolutionary distinctiveness (a measure of phylogenetic isolation) (19), which may yield species with unique traits (19, 20), our results suggest that, for birds, traded species are more evolutionary distinctive than non-traded species (Fig. S5), but not for mammals, amphibians or reptiles. Furthermore, mean family-wide evolutionary distinctiveness predicts the proportion of traded birds (Fig. S6; linear model: standardized coefficient = 0.18, P-value = 0.01), but again not for mammals, amphibians or reptiles. Humans have long admired birds' aesthetic attributes, including song and plumage complexity, and perhaps a consequence of this long-standing admiration is reflected in the bird trade.

Because we show that trade non-randomly targets species within specific clades and with specific traits, we were able to predict the species not yet (or not yet known to be) traded but at high risk of future trade as congeneric species become rare or go extinct, or as their ranges become accessible to hunters. Based on identified correlates of current trade, we provide meaningful estimates of future trade based on >95% and >90% probabilities (Fig. 3, Table S5). First, based on species in highly traded families, we predict between 5 to 48 species (i.e., 95 and 90% probability, respectively) that are not yet traded but of high risk of being traded in the future. Second, for all non-traded species with available phylogenetic information (N=29,132), we identified between 303 to 3,152 species at risk of future trade based on their high phylogenetic similarity with conspecifics known to be traded. Third, we used a phylogenetic logistic regression framework to identify which species are at high risk of future trade based solely on their body size. Here, we found between 11 to 35 species (all mammals) at risk of future trade. Our fourth approach used evolutionary distinctiveness, which did not predict any species at risk of future trade.

In total, based on those species with a probability >95% and >90% in any one of the four assessment schemes described above, we predict future trade to impact between 317 to 3,196 additional species (Fig. 3, Table S5) amounting to between 101 and 826 bird, 121 and 241 mammal, 9 and 268 amphibian, and 86 and 1,861 reptile species with a >95% and >90% probability of future trade, respectively. As a precaution, we recommend conservation attention to not just be given to currently traded species, but also those species with the highest probabilities of being targeted by trade in the future (see Table S5 for the complete list of species and their probability of future trade).

Where are the hotspots of traded species?

Although the footprint of trade spans all of Earth's habitable continents, we uncovered a pan-tropical dominance in the trade for vertebrates (Fig. 4 and S7). Importantly, biogeographical patterns in trade richness closely match patterns in species richness (Fig. 4, Table S6). South America, central to southeast Africa, Himalayas, Southeast Asia and Australia are the main epicenters of the wildlife trade, containing areas with the highest numbers of traded species (i.e., top 5 and 25% richest cells in trade; Fig. 4 andS7).

Regional differences exist across taxa (Fig. 4 andS7 and Table S7). For example, in South America, the Andes, Atlantic forest and eastern Amazon contain a high diversity of traded birds, whereas the western and central Amazon contains a high diversity of traded amphibians. Although many mammals are traded in South America (as revealed by a large area containing the top 25% of trade richness), the main hotspots for mammal trade are in Africa and Southeast Asia (Fig. 4). The African tropical savanna-woodland belt consists of hotspots for all taxonomic groups (Fig. S7). In Asia, Indonesia and Malaysia, as well as the Himalayas, are hotspots for trade (Fig. S7), especially amphibians and mammals. Australia and Madagascar stand out as the main trade hotspots for reptiles. Perhaps surprisingly, Indonesia, which is considered an epicenter of bird trade (21), was not identified as a hotspot. Although Indonesia contains a lower diversity of traded bird species relative to some other areas (e.g., the Andes and Atlantic coast of South America), birds in Indonesia are traded in very high abundance (21). Thus, across vertebrates, some species may only be collected for trade in small pockets of their entire distribution range, with higher trade volumes within certain countries, outside protected areas, or closer to human settlements (21–23). However, absent of such fine-scale data for the majority of species and regions, our global maps reveal the spatial idiosyncrasies in hotspots of trade diversity among taxa.

Focusing on specific kinds of trade reveals that amphibians and reptiles are most commonly traded as pets (including species traded as household pets, for expositions, circus, or zoological gardens), birds are traded both as pets and products (those used for commercial meat, trophy hunting, clothing, medicine, or religion proposes), whereas mammals are predominately traded as products (Fig. 5, Table S8). The pet trade occurs across the tropics, whereas species traded as products are concentrated in tropical Africa and Southeast Asia, including the Himalayas. Although birds and mammals show a strong association between the richness of species traded as pets and as products, there are important geographical differences in these trade types for all vertebrate groups (Fig. 5). For instance, the pet trade of reptiles occurs mostly in Australia and Madagascar, whereas most amphibians are collected from the Amazon for pets and collected from Africa and Southeast Asia for products.

Tackling global wildlife trade

Species possessing rare phenotypes, such as conspicuous plumage color, body shape and size, behavior, and/or (perceived) medicinal application tend to bring high market price. Trade follows a rarity-value feedback model, whereby increasing rarity drives both higher demand and prices of a species (22, 24), with this positive feedback loop shown in both legal and illegal wildlife trade. For example, in Europe, CITES-listed pets command a higher price than non-CITES-listed species (24). Trade also quickly shifts to conspecifics as the availability of a targeted species declines, which likely explains why we uncovered a strong phylogenetic signal in the trade of all vertebrate groups (Fig. S2). For instance, as Asian pangolin species decline, they are increasingly replaced by African pangolins in trade, with strength of demand for African pangolin meat and scales in Asia now high despite a relative price increase of 211%, versus 4.6% baseline inflation (25). Based on identified morphological and phylogenetic correlates of trade, we predict an increase between 5% and 57% (probabilities >95% and >90%, respectively) in the total number of traded vertebrate species (Fig. 3, Table S5), which amounts to as many as 8,775 species at risk of current and future trade.

That trade tracks cultural (e.g. the Harry Potter-inspired trade of owls in Asia; (26)) and economic vogue suggests that abundant species may not be safe. Often, species are flagged for conservation only after a severe decline is documented (e.g., pangolins, (25)). Our study offers two possible rectifications of this issue.

Firstly, with the strong predictive strength of phylogeny revealed in our analysis, we can circumvent cryptic, yet-to-come declines by flagging species that are currently of little concern but have a high likelihood of being traded in the future based on their evolutionary proximity to traded species (Fig. 3, Table S5). For instances, some highly colorful bird groups with high risk of future trade include Tangara tanagers (n=46), Serinus finches (n=35), and Ploceus weavers (n=37), while Rhinella beaked toads (n=55) and Rhinolophus horseshoe bats (n=55) were the highest risk amphibian and mammal genera, respectively. Reptiles yielded the largest number of species at risk of future trade. Here, Liolaemus iguanian lizards (n=229), Atractus (n=135) and Tantilla (n=61) colubrid ground snakes, Bothrops (n=43) pitvipers, and Lycodon wolf snakes (n=48) are all genera at high risk of future trade. We caution, however, that our identification of a species as potentially traded in the future does not reveal the potential trade volume of this species.

Secondly, the IUCN Red list, the largest assessor of species threat for conservation, needs to ensure that any evidence of trade is recorded in species threat accounts, regardless of current IUCN status. For example, we found that IUCN indicates 1,641 traded species omitted by CITES, while CITES indicates an additional 2,029 traded species omitted by IUCN (Fig. S8). In turn, future IUCN assessments would benefit from new analytical approaches that incorporate extinction risk from trade (e.g. (21, 27)), as well as increased communication among all conservation groups that document and monitor trade (27).

More broadly, our global assessment of wildlife trade underscores the need for a strategic plan to combat trade. That trade is predictable by evolutionary history suggests that policies may be proactive rather than reactive in approach. First, online black markets and mainstream online stores, such as eBay or Facebook (28), facilitate a large volume of transactions with few regulations to stifle trade activity. Novel machine-learning computer systems can be used by vendors to monitor and stem this activity (29, 30). Stricter penalties to merchants of trade, as well as consumer pressure for more sustainable and cheaper alternatives (e.g., humanely harvested horn from the least rare rhino species (31)), may hasten the adoption of these techniques. Importantly, our comprehensive list of traded and at risk species can inform these computerized search systems.

Our global maps of trade hotspots are an important first step in prioritization. In identifying many tropical regions as epicenters of traded species diversity, combating the surge of illegal wildlife trade will likely require action at the local community level (32), combined with targeting key countries that import and export wildlife (33), especially those countries within hotspot areas that share continuous borders (34). In many areas, hunting for wildlife trade occurs out of sheer necessity—occurring in impoverished areas where harvesting wildlife to sell to middlemen represents the only source of cash income (32). Borrowing from other programs to halt criminal trading of humans, arms, and drugs, wildlife trade policies would gain strength if they were linked to transnational agreements such as the United Nations Programme on Reducing Emissions from Deforestation and Degradation (REDD). This may also offer economic incentives for protection rather than exploitation within local communities. For instance, carbon-trading schemes could increase the value of carbon in areas that are combating wildlife trade – with the ecological co-benefit of areas that maintain large-bodied vertebrates yielding higher carbon stocks over the long-term (35).

METHODS

We compiled information on traded birds, mammals, amphibians, and squamate reptiles using the CITES list and IUCN Red list. We identified species traded through the IUCN API platform and classified each species as being traded as pets and/or products (see SM for details). We superimposed range maps of all species in a 110 x 110 km global grid and recorded species presence/absence within each cell. We determined total, pet and product trade richness as the number of traded species within each cell. We defined hotpots as the upper 25% and upper 5% richest cells for traded species and assessed the correlation between spatial patterns in total, traded, and threatened species richness.

We used updated time-calibrated species-level phylogenetic trees for each vertebrate group from which we obtained one maximum clade credibility tree, and used these trees in downstream analyses. We tested whether closely related species are traded more than random using the D-statistic. We used phylogenetic ANOVA to test whether traded and non-traded species differ in body size and evolutionary distinctiveness, and phylogenetic logistic regression to test whether these traits influence the probability of a species being traded. We determined risk of future trade by 1) identifying for each non-traded species the proportion of all species traded in their respective family and 2) for each non-traded species, averaging its phylogenetic distance with the ten closest related species that are traded.

Figure Legends

Fig. 1. Wildlife trade in terrestrial vertebrates (birds, mammals, amphibians and reptiles) impacts 18% of species globally. Numbers in brackets are the total number of traded species. IUCN threat codes: DD=Data Deficient; LC=Least Concern; NT=Near Threatened; VU=Vulnerable; EN=Endangered; CR=Critically Endangered.

Fig. 2. Wildlife trade occurs across the tree of life, but some clades are more heavily targeted than others. Phylogeny branches for birds (a), mammals (b), amphibians (c) and reptiles (d) are colored to represent the impact of wildlife trade up-to each node (i.e., clade). Warmer colors (red) represent heavily traded branches (i.e., high percent of traded species). The 20 highest traded families are labelled (high richness, bold or both high richness and proportion of total, not bold). The first outer band indicates threatened (VU, EN, and CR; orange) and non-threatened species (LC and NT; yellow). The second outer band indicates traded (red) and non-traded (pink) species. Gray concentric circles scale a 20 million year period.

Fig. 3. Predicted future traded species. Probability of a species being traded in the future based on body size (a), phylogenetic relatedness (b), and the proportion of species traded in respective families (c). Upper panels show the probability of trade across all currently non-traded species, lower panels reflect the probability distribution of trade around the 0.9 and 0.95 confidence intervals.

Fig. 4. The geography of wildlife trade in terrestrial vertebrates. Wildlife trade richness increases with the number of species in a cell for birds (a), mammals (b), amphibians (c) and reptiles (d). Wildlife trade richness and hotspots of wildlife trade (b,d,f,h) are concentrated in tropical regions. Top 5% and 25% indicate areas with the largest number of traded species per cell globally. Color ramp in hexagon scatter plots (a,c,e,g) represent the number of observations per grid-cell, with warmer colors indicating more observations and colder colors less observations. Black line in hexagon scatter plots indicates a LOESS fit.

Fig. 5. Geographical patterns in wildlife trade type across birds, mammals, amphibians and reptiles. Pet trade includes species traded as household pets, for expositions, circus, or zoological gardens. Species traded for products include those used for bush meat, trophy hunting, clothing, medicine, or religion proposes. Points are color coded by the geographic realm. Points occurring above the 1:1 equivalency line indicate higher levels of trade as products than pets.

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