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Understanding the species-level impacts and patterns of wildlife trade

O. Morton

A thesis submitted in partial fulfilment of the requirements for the degree of

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General summary

The global wildlife trade involves thousands of species and is relied upon by millions of people for nutrition and income. Reconciling the demand for species with their conservation is crucial, resulting in a need for a greater understanding of the volumes in which species are traded and whether this is likely to harm their populations. Most previous work has focused on the trade patterns of specific species (e.g., pangolin *spp.*) or cumulative trade totals across entire taxonomic groups. The former assumes we are already aware of species that need action or study, while the latter risks obscuring species-specific deviations from the wider trend. This thesis broadly addresses the need for large-scale, species-level studies of the impacts and management of the wildlife trade. In Chapter 2, I conducted a meta-analysis of 31 studies examining the impacts of wildlife trade on terrestrial vertebrate species abundance. I found evidence of mean declines in species abundance of 62% where trade occurred relative to untraded locations, but also a swathe of systematic geographic and taxonomic biases, underpinned by great inter-specific variation in severity of impact from minimal to local extirpation. Chapters 3 and 4 focus on unpicking species-level nuance in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) trade database, which comprehensively captures the legal international trade in CITES-listed species. In Chapter 3, I developed hierarchical Bayesian hurdle models to unpick the species-level occurrence and volumes of 1025 wild-sourced birds, mammals, amphibians, and reptiles in commercial trade. Across species and threat status (as assessed by the International Union for Conservation of Nature, IUCN), the wild-sourced trade is largely declining to absence. However, traded volumes were largely unconnected to changes in a species' threat status, often because trade had disappeared prior to the change, but in some cases, because trade continued unchanged despite increasing extinction risk. In Chapter 4, I applied modified hierarchical Bayesian hurdle models to contrast the captive- and wild-sourced international trade in 779 commercially traded CITES-listed bird species and their relative associations with key reproductive traits. This revealed a pervasive species-level shift from wild- to captive-sourced trade, with adult survival, age at first reproduction and longevity reproductive traits associated with captive trade volumes. In combination, the results across the thesis highlight the critical importance of species-specific data to generate informed conclusions on trade, with impacts, volumes, and trends varying by orders of magnitude for both closely related and demographically similar species. Integrating transparent assessments of sustainability into CITES processes is key to both protecting species and ensuring a future for sustainable use and trade.

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The work presented in this thesis is my own and has not been submitted for any other award at this or any other institution. This work also owes considerable thanks to the intellectual contributions of my supervisors (D.P.E, B.R.S and T.H).

Chapter II has been published as:

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The published manuscript is reproduced in full here with only minor alterations. Author contributions are as follows, O.M., B.R.S. and D.P.E. conceived the study. O.M. led the literature search, data extraction and analysis. B.R.S., T.H. and D.P.E. assisted with methodological development and the evaluation of the results. O.M. wrote the first draft of the manuscript. B.R.S., T.H. and D.P.E. contributed to the revisions.

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Chapter 1:

General Introduction

1.1 The biodiversity crisis

There have been five mass extinction events that drastically reshaped global biodiversity. In each, up to 95% of all biodiversity was lost (Benton and Twitchett, 2003). Each separate extinction event was caused by geophysical or atmospheric processes, including marine anoxia, warming, acidification, acid rain and ozone damage (Bond and Grasby, 2017). Scientists now believe we are in the sixth mass extinction event, a human- driven occurrence, where regional ecosystem collapse is already a reality (Ceballos et al., 2020). The loss of ecosystem functioning will have profound implications on a range of ecosystem functions which we as a species rely on, including food security, the water cycle and carbon sequestration (Mace et al., 2012). The haunting reality of the current extinction crisis is not that we are awaiting the arrival some uncontrollable phenomenon, but that we sleep walked and subsequently leapt headfirst into a crisis of our own making. Even with increasing awareness, attempts to halt the crisis are failing, in both 2010 and 2020 we failed to meet any self-imposed targets to slow biodiversity loss (Butchart et al., 2010; Secretariat of the Convention on Biological Diversity, 2020).

Five factors are considered the key drivers of extinction and biodiversity collapse: land-use change, exploitation, climate change, pollution and invasive species (IPBES, 2019). The severity and relevance of each threat varies by taxa and ecosystem specific factors, for example the greatest threats facing insular species are invasive species, exploitation, and land use change for cultivation (Leclerc et al., 2018). Conversely, primates are principally threatened by land use change for agriculture, ranching or logging, and exploitation (Estrada et al., 2017). Where multiple threats co-occur, species-level extinction risk intensifies leading to both population declines (Symes et al., 2018) and a loss of population resilience (Capdevila et al., 2022).

As our population expands and land use change intensifies throughout the century (Maxwell et al., 2016; Sala et al., 2000) we will place ever greater strain on the planets natural resources. Exploitation through hunting for either commercial or subsistence purposes is a fundamental practice for millions across the global south (Nielsen et al., 2018), and also drives average population declines 58% in mammals and 83% in birds (Benítez-López et al., 2017). Balancing the needs of those reliant on exploitation and species persistence remains an unresolved challenge for many communities and species. A crucial facet of exploitation is the global commercialization of wildlife. The trade in wildlife is not restricted to the common and flawed perception of small markets predominantly outside the global North (Margulies et al., 2019). The reality is instead millions of plants and animals shipped around the globe each year contributing income to both marginalised communities and global corporations.

1.2 What is wildlife trade?

Wildlife trade as a term covers a vast range of practices, generally here I define it as the extraction and commercialization of a plant or animal or its derivatives. This definition includes the often overlooked trade in plants, the lucrative trade in timber often discussed separately as logging, and the trade in aquatics and commercial fishing. Trade occurs at a diverse array of scales. At the local scale, wild meat trade offers both subsistence and additional income for up to 154 million households across the global South (Nielsen et al., 2018). In contrast the international legal trade alone moves 100 million individuals around the world annually (Harfoot et al., 2018a). The legal trade is a burgeoning commercial enterprise with its values estimated at €249 billion with timber and fisheries making up 90% of this figure (Engler and Parry-Jones, 2007). In comparison estimates for the illegal trade range from $7.8 – 10 billion, however quantifying illicit networks remains challenging so these estimates are likely conservative (Haken, 2011). A further important distinction between forms of trade is between the legal and illegal, and the sustainable and unsustainable trade. These are two separate distinctions that should not be conflated e.g. legal does not equate to sustainable and illegal does not equate to unsustainable (’t Sas-Rolfes et al., 2019).

Across these types and scales of wildlife trade, the reality of traded species and products manifests itself in astounding diversity. Many species are traded as food products both within local communities (Rao et al., 2011a) and further afield as a luxury product (e.g. caviar) (van Uhm and Siegel, 2016). Species are further traded in a catalogue of derived products including souvenirs (e.g. shells (Nijman, 2019) or carvings (Sims et al., 2011) etc.) and medicinal products (e.g. for traditional Chinese medicine (Hinsley et al., 2020)). A large pet trade also thrives across a diversity of taxa including birds, mammals, reptiles, amphibians, and arachnids, with some species becoming rapidly exploited immediately after being described (Bush et al., 2014; Hughes et al., 2021; B. M. Marshall et al., 2020; Marshall et al., 2022). Species are also traded for a further variety of culturally specific purposes including merit or prayer release across Southeast Asia. In Phnom Penh alone over 600,000 birds were sold for this purpose in a 13 month period (Gilbert et al., 2012).

It is estimated that 24% of terrestrial vertebrates are traded globally, including 4576 bird, 1238 mammal, 542 amphibian and 1282 reptile species (Scheffers et al., 2019). Hotspots for traded species are found across South America, Central and Southwest Africa, Southeast Asia and Australia. Traded birds were mainly found in Southeast Asia with the majority traded for the burgeoning pet trade (Scheffers et al., 2019; Shepherd and Cassey, 2017). This trade has given rise to the concerning songbird crisis in the region (Shepherd and Cassey, 2017). Based on phylogenetic relatedness a further four thousand additional species are also at risk of entering the wildlife trade in the future (Scheffers et al., 2019). Trade also effects non-vertebrate species, where a litany of taxa are traded for a diversity of purposes: molluscs for food, medicine or souvenirs (shells), corals for building materials, local lime production, or souvenirs, crustaceans for food, and insects and arachnids for the pet trade (Fukushima et al., 2020). It is estimated that up to 23% of vascular plants, 10% of Basidiomycota fungi, 14% of molluscs, 4% of arthropods, 20% of echinoderms and 70% of cnidarians assessed by the IUCN (Fukushima et al., 2020) are also traded in some form.

Forty percent of all species assessed by the IUCN are recorded as being intentionally used, for 11% of species this is contributing to elevated extinction risk (Marsh et al., 2021). As one of the key drivers of the current biodiversity crisis (IPBES, 2019), reconciling current wildlife demand with the conservation of species has never been more urgent. The potential threats of the wildlife trade are numerous and interwoven (Smith et al., 2009). The direct removal of individuals can contribute to population declines and extinction risk (Benítez-López et al., 2017; Symes et al., 2018). Trade further provides an avenue for invasive species to enter and establish, potentially to the detriment of native species (García-Díaz et al., 2017). The large scale trade in species further provides paths for disease transmission including past outbreaks of severe acute respiratory syndrome (SARS) and Ebola outbreaks in humans linked to the trade in primates and small carnivores respectively (Karesh et al., 2005), and H5N1 influenza outbreak in poultry which was linked to the illegal import of Mountain hawk eagles (*Nisaetus nipalensis*) (Van Borm et al., 2005). The devastating current coronavirus pandemic itself is believed to have originated from live animal markets in Wuhan, China. Establishing effective regulatory and legal frameworks to manage the vast wildlife trade must be a conservation priority to enhance global biosecurity, protect species and safeguard livelihoods.

1.3 Trading to save species or saving traded species

Overexploitation and trade are key threats to species and drivers of the extinction crisis, and this is widely acknowledged. However, the best solutions for tackling this are a topic of great debate. On one side many advocate the development of sustainable use and a wider shift in what we view as conservation (Roe et al., 2020). While others instead view the end of global trade as the only strategy able to halt current precipitous wildlife declines (D’cruze et al., 2020). These polarised views present a clashing dichotomy in both research and policy (Dickman et al., 2019).

1.3.1 Sustainable trade and conservation

Sustainable use of wildlife is at the forefront of current global conservation efforts to combat the biodiversity crisis (Convention on Biological Diversity, 2020). Fundamental to this is the fact that nearly all of humanity uses wildlife in some form and will continue to do so, as for many it is a necessity rather than a choice (Hutton and Leader-Williams, 2003). Therefore, any changes to the use and trade of wildlife must consider not only conservation outcomes, but also the socio-economic, financial, and cultural outcomes of change (Cooney et al., 2021).

Sustainable use when carefully implemented has the potential for a diversity of benefits (Abensperg-Traun et al., 2011). The Urial (*Ovis vignei*) and Suleiman Markhor (*Capra falconeri jerdoni*) were experiencing precipitous declines in Pakistan due to widespread poaching prior to the 1980’s. A community led initiative proposed a ban on their hunting by local tribes people, and established a limited trophy hunting program where the income derived from paying hunters was used to fund guards and various community infrastructure projects including transport, healthcare and agricultural expansion thus reducing livestock dependence (Frisina and Tareen, 2008). Since implementation populations of both species have been increasing steadily (Frisina and Tareen, 2008). The success of such programs stems in part from the community engagement and leadership, the imposition of a hunting ban from national authorities would have likely have failed, due to the established rights and traditions of local people.

Similarly, in the United States of America (USA) the American alligator (*Alligator mississippiensis*) has historically been exploited since the 1800's for the leather goods industry (Thorbjarnarson, 1999). Largely indiscriminate exploitation decimated populations before moving on to a new area. Contemporary estimates posit more than 3 million alligator skins passed through just six Louisianan towns in a 53-year period (1880 – 1933) (McIlhenny, 1935). However, strong law enforcement and subsequent sustainable use programs have facilitated the recovery of the species across nearly all its historical range. Alligator aquaculture now generates millions in yearly revenue, with both the skins and meat being sold. In the USA alligator farming currently has limited wider community benefits beyond the owners and workers of the farm or ranch, except potentially tourism or wildlife education opportunities. Outside of the USA however, there is evidence of wider community benefits with communities deriving income by harvesting the wild eggs or neonates for ranching (J. Nickum et al., 2018).

Key to sustainable trade regardless of the scale are the livelihood and income benefits it can provide for those reliant on wildlife. Often these are as simple as providing the predominant yearly household income or being a supplementary income source in conjunction with other variable income sources e.g. agriculture (Cooney et al., 2015). Extraction and trade is attractive to many economically poorer households and communities globally because of the often low entry skills and year round availability of many products. In rural communities in Madagascar the trapping and trade of amphibians, reptiles and invertebrates is highly profitable compared to other livelihood options and contributed a quarter of households yearly incomes (Robinson et al., 2018). However, the practice was still viewed as an unreliable income source by trappers especially relative to jobs further up the supply chain e.g. exporters. Trappers are estimated to receive less than 2% of the final sale price, and because collection permits are held by exporters rather than collectors there are few opportunities to move up the supply chain or increase their income (Robinson et al., 2018). Thus in many cases trade can provide income, but not actually alleviate poverty or drastically improve livelihoods.

A key issue at both the individual and wider landscape level remains that the benefits of sustainable use often can be outweighed by the immediate, often status quo, benefits of continued unstainable use. In the Peruvian Amazon, shifting hunting practices away from vulnerable species and to a more sustainable model was estimated to drive a 36.4% decrease in annual economic benefit, therefore national development projects would be needed to offset this significant loss in income (Bodmer and Lozano, 2001). Similarly, surveys of ungulate species in Pakistan highlight that while community led measures have protected populations of trophy hunted species, other species not regarded as important trophies have suffered further declines (Khan et al., 2014).

1.3.2 Unsustainable trade

Conceptual economic theory posits that species extinction is unlikely to be caused solely by economic exploitation. As individuals become scarcer the resources expended on locating them will increase ultimately to the point where the costs exceed the benefits and exploitation ceases to be viable (Courchamp et al., 2006). However, where the commercial value of species negatively correlates with its abundance, and this rarity fuels demand, exploitation can remain viable inducing a positive feedback loop driving species to extinction (Courchamp et al., 2006). Theory is now reality as pangolin species suffer extreme population declines from rampant collection and trade, with all species assessed as Threatened and declining (as per the IUCN Red List). The continued exploitation of these species despite numerous national and international efforts to protect them (Heinrich et al., 2016), has been attributed to demand for both meat as a luxury food and their scales for traditional medicine (Ingram et al., 2018; Nash et al., 2016).

Across Southeast Asia the trade in passerine songbirds for pets and competitions has emerged as a key threat for hundreds of species, prompting an international conservation response (Shepherd and Cassey, 2017). Even species receiving international attention and national legislation are commonly found in markets across the region, with critically endangered species present in markets including species while less than 250 individuals remain in the wild (Nijman et al., 2017). Even historically abundant species such as the Sunda laughingthrush (*Garrulax palliatus*) - one of the most abundant species in Indonesian markets – are now declining with soaring prices and declining numbers of individuals offered for sale suggesting the species' increased rarity (Leupen et al., 2020; Shepherd et al., 2016). In Sumatra less than half of the remaining forests are more than 5km from road access and trapping has already depleted high value bird populations along this distance (Harris et al., 2017). As wild populations for desirable species plummet (e.g. Straw-headed bulbul, *Pycnonotus zeylanicus* (Bergin et al., 2018), Javan pied starling, *Gracupica jalla* (Nijman et al., 2021), and Black-winged myna, *Acridotheres melanopterus* (Nijman et al., 2017)) individuals of nearly extinct species are increasingly drawn from captive-bred sources. As yet this has not translated to benefits for wild populations (Nijman et al., 2021).

Population declines are not limited to charismatic species and international markets but often stem from local practices and markets. In Nepal, the sought after caterpillar fungus (*Ophiocordyceps sinensis*) used predominantly in medicinal practices is rapidly declining in the face of increasing demand and the increasing number of harvesters exploiting the high prices and potential additional income (Shrestha and Bawa, 2013). Similarly, across the global south the hunting and trade in meat (or bushmeat) is a key protein and income source for participants (Nielsen et al., 2018). Across Sub-Saharan Africa we are seeing the extirpation of larger mammals across hunted areas as these vulnerable, slower reproducing species are unable to persist against market demand (Bachmann et al., 2020). A common end result around established bushmeat markets is the loss of such species and a switch to smaller, faster reproducing species (e.g. rodents) that can meet market demand without declines (Cowlishaw et al., 2005). Where it occurs unsustainable extraction and trade undoubtedly has the potential to decimate species populations across a range of taxa.

1.4 CITES and trade regulation

The potential threats posed by the trade in wildlife has been historically recognized by international conservation bodies as early as the Second IUCN General Assembly in 1950, where songbirds bought from local traders were displayed on a table as a protest against this commercialisation. It wasn’t until Seventh General Assembly in 1960 that the IUCN urged all countries to restrict imports of “*rare animals in harmony with the export laws of the country of origin*”. The subsequent 1963 Assembly went further and called for an international convention to draft legislation regarding to the import, export and transit of threatened species. In Washington, 10years later, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) opened for signatures and was ratified by the 10th signature on the 1st July 1975. That original text clearly outlines CITES aims and the Parties original commitment to prevent unsustainable trade:

> Recognizing *that wild fauna and flora in their many beautiful and varied forms are an irreplaceable part of the natural systems of the earth which must be protected for this and the*

> *generations to come;*
>
> **Conscious** *of the ever-growing value of wild fauna and flora from aesthetic, scientific, cultural, recreational and economic points of view;*
>
> **Recognizing** *that peoples and States are and should be the best protectors of their own wild fauna and flora;*
>
> **Recognizing***, in addition, that international co-operation is essential for the protection of certain species of wild fauna and flora against over-exploitation through international trade;*
>
> **Convinced** *of the urgency of taking appropriate measures to this end…*

There are currently 184 Parties to the Convention (although a smaller number have accepted subsequent amendments to the Text of the Convention). Parties are required to designate at least one Management and Scientific Authority to implement the Convention. The Management Authorities primary duty is communicating with the CITES Secretariat, issuing permits, determining exemptions and liaising with the Scientific Authority. The Scientific Authority primarily determines whether import or exports of species is not detrimental to their survival, track permits and actual exports to ensure compliance conducive to species survival and a litany of national tasks including but not limited to: interpreting nomenclature, advising on confiscated specimens, assess status of traded species. Crucially, the Management Authority must consult with the Scientific Authority when issuing permits.

The primary mechanisms outlined in the Convention are the three Appendices, these are lists of selected species, subspecies and broader taxonomic groups, each subject to differing trade restrictions. Appendix I is the most stringent and as per the Convention text covers "*all species threatened with extinction which are or may be affected by trade*". All commercial trade in these species is prohibited, but trade for other purposes e.g. scientific research, is permitted when both import and export permits have been granted. Currently there are over 1000 species of plant and animal listed in Appendix I. Appendix II includes all species "*which although not necessarily now threatened with extinction may become so unless trade in specimens of such species is subject to strict regulation".* There are currently more than 37,000 species listed in Appendix II, however orchid species comprise the vast majority of these species (Hinsley et al., 2018). All orchid species (bar a small number listed in Appendix I) are listed under Appendix II due to the precautionary look-alike principle as the taxa is often subject to misidentification. Crucial to trading either Appendix I or II species is evidencing that the export of a species will not be detrimental to the survival of the species in the form of a Non Detriment Finding (NDF). An NDF should be based on the best evidence available and include data on population sizes and trends, species role in ecosystems, monitoring approaches, species ecology and historical trade patterns. The NDF's conclusion should be whether the proposed export will be detrimental or what offtake can be taken without threatening the species survival. Finally, Appendix III can include any species requested by a Party, that the Party already regulates the trade of but requires international cooperation to prevent detrimental or illegal trade

The effectiveness of CITES in the modern day arena has been called into question on numerous fronts. The CITES Appendices do not cover every species (nor are they designed to) but in some cases it has been slow to recognize and respond to species that are threatened by trade with up to 28% of species threatened by international use not listed on the Appendix and a further 35% of species threatened by international trade only protected after the IUCN already recognized the threat (Frank and Wilcove, 2019). When CITES does act strongly by listing or up listing species to Appendix I (a near ban on international trade), this can compound risk and stimulate trade, as in the case of Kleinmanns tortoise (*Testudo kleinmanni*) when traded volumes peaked during the transition period (Rivalan et al., 2007). Similarly, while inclusion in Appendix I is often falsely regarded as a conservation success, the implication of such trade bans are often poorly considered. Often such bans have adverse consequences for those reliant on trade and can even contribute to emerging illegal markets and further risk to threatened species (Challender et al., 2019c). Regardless of these shortcomings, as the world's largest binding international conservation agreement, CITES will play a pivotal role in tackling overexploitation. Whether that is in its current form or an amended version better able to guarantee conservation and societal goals remains to be seen.

1.5 Thesis overview

Reconciling the commercial and socioeconomic importance of trade with its combined potential for great benefit and great harm to biodiversity is pivotal to stem the ongoing biodiversity crisis. The largest gaps in our understanding of trade revolve around two principles, both key to averting biodiversity loss and enabling equitable and effective sustainable use. Firstly, the impacts of trade on species are often poorly known and rarely evidenced. And secondly, are the measures we enact to combat unsustainable trade effective? These are both utterly fundamental concepts that need quantifying for trade management to move forward. The key difficulty in quantifying either issue stems from the scale of trade. The overall aim of this thesis was to determine the species-level impacts of the wildlife trade and assess whether international trade patterns were likely to benefit or damage species populations.

Firstly, I conducted a global meta-analysis to compare species abundances between sites where species were extracted for commercialisation and where they were not. Ranges of ecological and geographic variables were extracted from the literature to examine the patterns of trade impacts. Next, I used the CITES trade database and hierarchical hurdle models to examine species presence and volume in the wildlife trade, explicitly to compare whether species becoming more or less threatened moderated their presence in the wildlife trade. Finally, using the processed CITES data and modified hierarchical Bayesian hurdle models I examined the variation in life history traits between the captive and wild trade to assess the prevalence of `faster` and `slower` species in trade and whether we are witnessing a species level switch from wild- to captive-sourced trade.

Chapter 2: Impacts of wildlife trade on terrestrial diversity

Research has quantified the impacts of many key threats to biodiversity including deforestation, land use change and climate change. However, the impacts of commercial extraction on species remains largely unknown. Despite this, the literature is rife with contradictory claims of trade both decimating species abundances and benefiting species. The objective here was to formally investigate species abundance changes where trade occurs in species by conducting a meta-analysis. Specifically I investigated (1) the general impact of trade across species, (2) how the impact of trade varied with access to markets and finally, (3) whether protected areas effectively reduced any impact of trade on species.

Chapter 3: Mixed protection of threatened species traded under CITES

The international wildlife trade is known to encompass thousands of species. A fundamental basis for trading a CITES listed species internationally is that the extraction and trade will not further harm or endanger wild populations. Therefore, species presence and volume in this trade should largely reflect how threatened individual species are. More threatened species are unlikely to be able to sustain the same levels of offtake as comparatively less threatened and more abundant species. Using the CITES yearly traded volumes for over a thousand bird, mammal, amphibian, and reptile species I developed Bayesian hurdle models to contrast species presence and volume in trade through time and across individual species threat assessments. The objectives of this chapter were to (1) assess whether threatened and non-threatened species were differentially traded, (2) did CITES own Appendix I and II listings differ in trade patterns through time, and (3) when a species became rarer did traded volumes change.

Chapter 4: Contrasting life-history traits in captive and wild-sourced trade over time

There is currently a broad shift in the international bird trade away from wild sourced individuals. As the captive trade grows, understanding whether it in fact trades a distinct plethora of species or a subset of those that were previously traded from wild sources is crucial. Ecological theory indicates species will fall along a spectrum of slow to faster life history traits,with faster traits including lower adult survival and lower body mass, and slower traits being longer lived and higher ages at first reproduction. We used phylogenetic logistic regressions and modified hierarchical Bayesian hurdle models to examine the effect of four life history traits on the captive and wild bird trade through time. The objectives of this chapter were to (1) examine whether demographic traits correlated with the probability of a species being CITES listed or trade, (2) assess whether trade volumes varied with species life-history traits and whether these patterns remains consistent in both captive and wild sourced trade, and finally (3) whether species-level captive and wild-sourced volumes have varied through time.

Chapter 2:

Impacts of wildlife trade on terrestrial biodiversity

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2.1 Abstract

Wildlife trade is worth billions of dollars annually and affects most major taxonomic groups. Despite this, a global understanding of the trade's impacts on species populations is lacking. We performed a quantitative meta-analysis of wildlife trade that synthesised 506 species-level effect sizes from 31 studies, estimating trade-driven declines in mammals (452 effect sizes), birds (36) and reptiles (18). Overall, species declined in abundance by 62% (20 to 82%) where trade occurs. Reductions were greatest involving national or international trade, driving declines of 76% (36 to 91%) and 66% (12 – 87%), respectively. The impacts of trade were pervasive, requiring over 102 hours of travel time from settlements for trade to have no mean effect. Current protective measures fail species, with significant declines even where the harvesting for trade occurs in protected areas. Population declines tracked species threat status, indicating heightened extirpation and extinction risk in traded species. Critically, for such a severe global threat to wildlife, our analysis unearthed a limited number of studies using treatment versus control comparisons, and no studies on amphibians, invertebrates, cacti or orchids. Improved management, tackling both unsustainable demand and trade reporting, must be a conservation priority to prevent rampant trade-induced declines.

2.2 Introduction

The wildlife trade is a burgeoning global industry worth US$4 - 20 billion per year(Haken, 2011). This encompasses both regulated, legal trade, and poorly regulated, illegal trade, co-occurring at local to international levels (Bager Olsen et al., 2019; Patel et al., 2015; Tittensor et al., 2020). At least 100 million plants and animals are internationally trafficked each year(Harfoot et al., 2018b), involving a hyper-diversity of species (Scheffers et al., 2019). For instance, 24% (N = 7638) of terrestrial vertebrate species, spanning 75% of terrestrial vertebrate families, have recently been or are currently traded (Scheffers et al., 2019). Understanding the drivers and impacts of wildlife trade is therefore one of the key challenges for modern conservation (Maxwell et al., 2016).

Local-scale trade for both food and income security supports an estimated 150 million rural households involved with the extraction or commercialisation of bushmeat (Nielsen et al., 2018). Conversely, the national to international trade in pets, medicines and luxury meats often involves a small number of highly specialised parties extracting and trafficking species of high commercial value. At all scales, trade has the potential to support livelihoods and even protect species from extinction ('t Sas-Rolfes et al., 2019; Cooney et al., 2017), with sustainable trade potentially as lucrative as unsustainable methods (Bodmer and Lozano, 2001). But at its worst, intensive extraction and trade is a prominent driver of extinction risk and a global threat to species (McClenachan et al., 2016). This is demonstrated by the ivory-fueled declines of African elephants (Wittemyer et al., 2014), the killing of the last Javan rhinoceros of the subspecies *annamiticus* for its horn in Vietnam in 2010 (Brook et al., 2011), and the rapid demise of pangolin species across Asia and Africa (Heinrich et al., 2016).

A quantitative global assessment of trade impact on individual species, and the prevalence and strength of positive and negative effects is sorely lacking. Studies inferring positive outcomes of trade have synthesised evidence from secondary literature and market trends to assess sustainability, but generally have not directly examined trade impacts on species abundances in the wild ('t Sas-Rolfes et al., 2019; Cowlishaw et al., 2005; Hutton and Webb, 2003). Potentially positive results include the sustainable extraction and trade of more tolerant species, although at the cost of less tolerant species (Cowlishaw et al., 2005). Those inferring negative outcomes of trade synthesized evidence from multi-species market surveys, combining expert opinion with market share trends, to infer population changes (Harris et al., 2015). Such studies suggest that current volumes of animals traded are unsustainable and likely contribute to species declines. However, they can be confounded by pre-existing market trends (Milner-Gulland and Clayton, 2002) and concurrent threats driving species losses, including deforestation, subsistence hunting, and climate change (Benítez-López et al., 2017; Gibson et al., 2011; Thuiller et al., 2006).

Our study quantifies the impact of wildlife trade on species abundances via a meta-analysis comparing traded sites with unexploited, control sites. We answer three key questions: (1) what is the impact of wildlife trade on species abundance; (2) how does the impact of trade vary with spatial scale and access to markets; and (3) how effective are current measures designed to protect species? Without precise quantification of the effects of trade, future policies managing trade fail to be evidence-based and thus cannot claim to safeguard species.

2.3 Results and Discussion

Trade-induced impacts on species' abundance

We performed a systematic search of the primary and secondary literature for studies comparing the impact of wildlife trade between traded (treatment) and untraded (control) sites on vertebrate, invertebrate, orchid and cacti species abundance. We incorporated all forms of wildlife trade, ranging from local, to national and international scales, and spanning both legal and illegal trade. From suitable studies (see Supplementary Information), we extracted the location, reported purpose, scale of trade, species abundance, and associated variance. We calculated effect sizes as the log response ratio (RR) of the abundances in traded and untraded sites; for clarity in interpretation, in the main text we present RR as percentage change in abundance (Supplementary Methods). Our systematic search obtained 506 effect sizes (452 mammals, 36 birds, and 18 reptiles, no suitable studies were found for other taxa) from 31 studies comparing the impact of wildlife trade between traded (treatment) and untraded (control) sites (all using space-for-time substitution, none using before-after comparisons; Figure 1; Supplementary Table 1).

We uncovered several alarming patterns in geographic coverage and taxonomic representation of studies using robust methods to characterize abundance responses to trade. First, there was a predominance of studies in the South American and African tropics, whereas there were only four studies from Asia—a known hotspot of trade diversity (Scheffers et al., 2019)—one from North America, and none in Europe (Figure 1; Supplementary Table 11). Second, we document asynchrony between taxa represented in research and those listed by CITES as warranting attention. For example, there is a dominance of mammalian studies (Figure 1B) even though mammals account for only 47.5% (318/689 species) of CITES Appendix I and just 10.4% (513/2171 species) of Appendix II listed animals (CITES, 2020a). Our findings also highlight the absence of paired studies on the impacts of trade for several highly traded taxonomic groups, including amphibians, lepidopterans, arachnids, orchids and cacti (Figure 1). Orchids represent >70% of all CITES-listed species and market-based studies suggest overharvesting and population declines (Phelps and Webb, 2015).

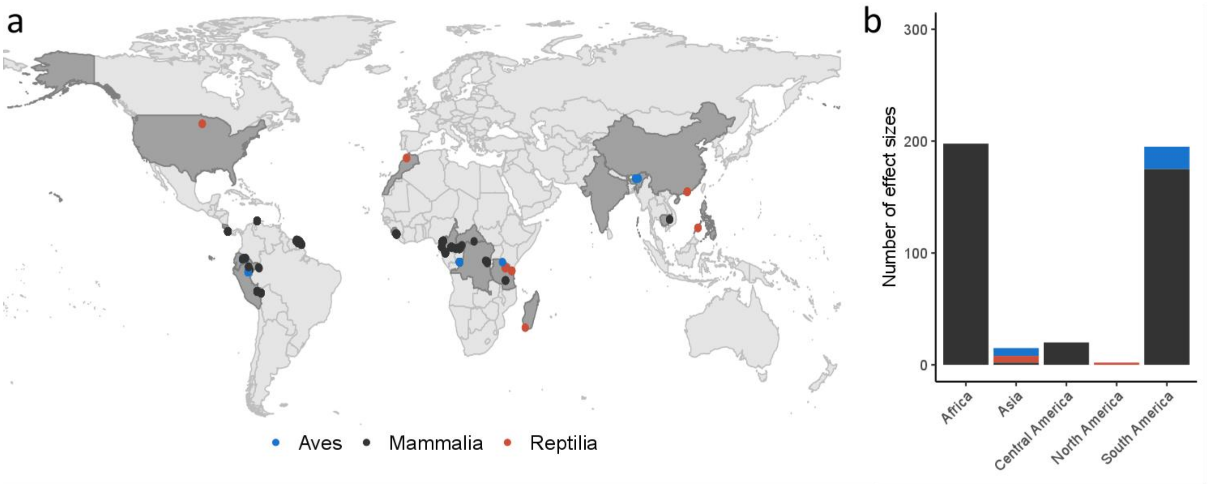


Figure 1. Distribution of A) the 31 data sources and B) the 506 extracted effect sizes for birds, mammals and reptiles included in the meta-analysis. Shaded countries contain at least one study and points denote locations of individual study sites. Antarctica was removed from this graphic as no studies were present.

Overall, wildlife trade associated a 61.6% decline in species abundance (Figure 2A), with local species extirpations observed in 16.4% of the cases (83 out of 506 reported effect sizes). Although mammals made up the majority of species (76% of 145 species) included in our meta-analysis, mean declines were comparable across taxa and on par with our overall estimates (Figure 2B and S5).

Only 15.8% of effect sizes (n=80) were positive. We closely reviewed the original data sources for this positive subset, revealing three author-reported causal links (Supplementary Table 11). First, relatively low demand within trade, especially when a species is less palatable and only traded as by-catch (Davies et al., 2008). Second, the extirpation of intensively traded large-bodied species facilitated the proliferation of less-frequently traded small-bodied squirrel and bird species via competitive release (Linder and Oates, 2011). Third, inaccessible habitats served as sources for nearby traded areas (sinks) (Gilroy and Edwards, 2017). These three points underscore how maintaining low off-take and retaining no-hunting and wilderness areas (Watson et al., 2016) can be effective. Without more species-level understanding of offtake limits it remains a research frontier to robustly quantify sustainability for most species.

Extraction for bushmeat trade (subsistence studies were not included) correlated with significant declines of 59.7% (95% CI: 12.4 – 81.5%), while pet trade precipitated extreme declines of 73.0% (95% CI: 32.1 – 89.2%) (Figure 2C). Of five trade purposes recorded, 88.1% of effect sizes were for bushmeat trade. Despite the enormous scale of pet trade globally—up to 84 million songbirds are kept in Java alone (H. Marshall et al., 2020a)—just 5.1% of effect sizes focused on the pet trade. This may reflect the difficulty of finding suitable control sites not already impacted by trade (Harris et al., 2017). Our study highlights an important deficit in the field of conservation biology—that although the scale of the wildlife trade is immense (Scheffers et al., 2019) and our evidence-based analyses shows striking declines in abundances, our understanding of species-level impacts lags behind our knowledge of other key threats to biodiversity, including deforestation, forest degradation (Gibson et al., 2011) and over-hunting (Benítez-López et al., 2017). This underlines an urgent need for a diversification of trade studies across taxa, biogeographic realms, and purposes.

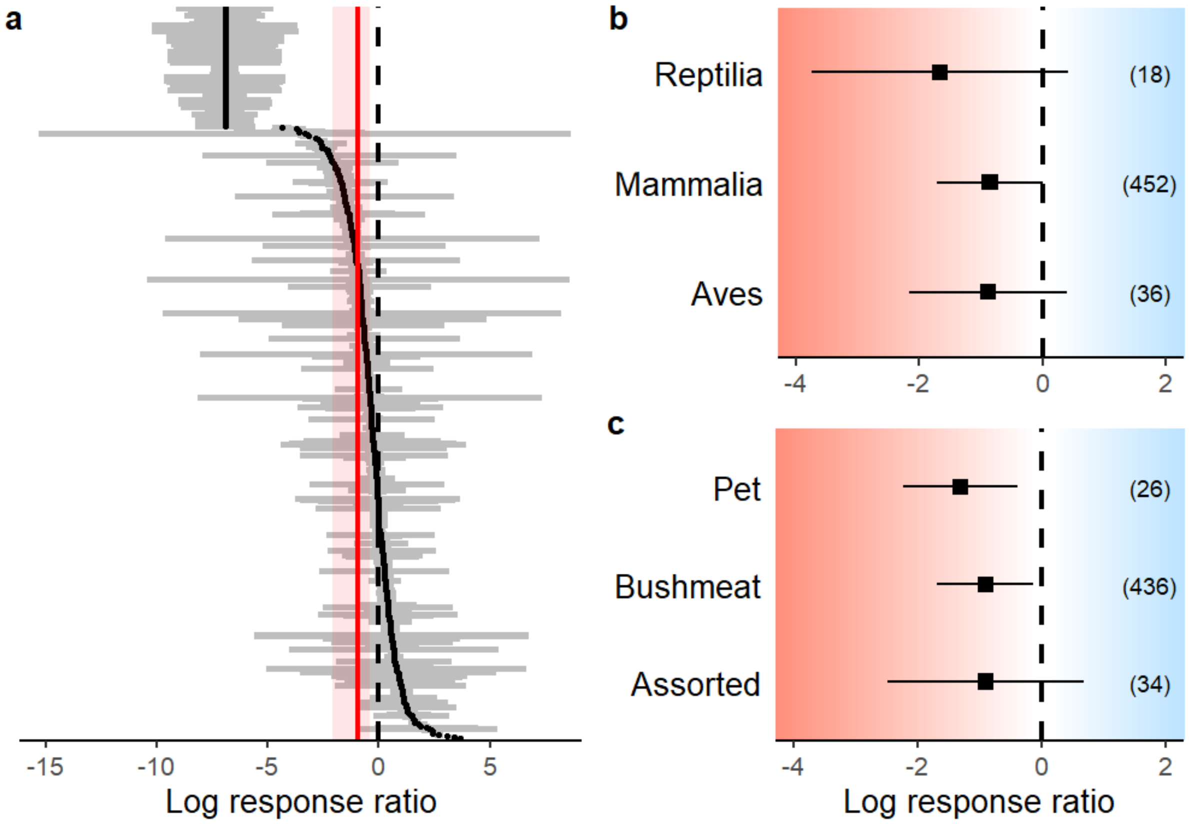


Figure 2. Individual, class, and purpose effect size estimates. A) 506 taxa-wide effect size estimates showing the 95% confidence interval. Weighted mean population declines of 61.6% (95% CI: 20.0 – 81.6%) are shown by the red line and the dashed black line denotes no impact of trade. Extremely negative results indicate local extirpations (population declines of 100%). B) Taxa-specific effect size estimates. C) Stated trade-purpose estimates of effect size. Assorted includes ivory, traditional medicine and laboratory use. Points show weighted means and lines 95% confidence intervals. Estimates obtained through single mixed meta-regressions.

Trade impacts across spatial scales

National and international trade significantly reduced species abundance by 76.3% (95% CI: 35.8 – 91.2%) and 65.8% (95% CI: 11.7 – 86.7%), respectively, (Figure 3A and Supplementary Table 4), whereas local trade had limited impacts. This finding demonstrates how distant demand pressures cause disproportionate losses to target species (Carrasco et al., 2017) and highlights the need for more effective and transparent documentation of trade volumes (Blundell and Mascia, 2005).

We used a spatial travel time layer accounting for road quality, most likely transportation mode, slope, and surface type to derive estimates of travel times (Nelson et al., 2019). Trade-induced declines were greatest when travel time to human settlements of >5000 inhabitants (Nelson et al., 2019) is shortest (Figure 3B). A travel time of 102.7 hours from settlements was required for no mean effect of trade on species abundance ($Q_M = 2868.56$, df = 1, $p < 0.0001$)—an estimate that is considerably longer than previously published estimates for hunting-induced (~33-42 hours) population declines (Benítez-López et al., 2017). Greater expenditures on travel are likely due to higher monetary rewards of trade than personal consumption (Rao et al., 2011b). For example, in Indonesia, Harris and colleagues(Harris et al., 2017) found that bird trapping had depleted target populations across an entire remoteness gradient.

Local trade negatively affected species abundance at all observed travel times to settlements (Figure 3C; $Q_M = 2426.73$, df = 1, $p < 0.0001$). Similarly, for national-scale trade, the species-level impact declined to no effect only after 8 hours of travel away from settlements (Figure 3D; $Q_M = 651.37$, df = 1, $p < 0.0001$). Such distances indicate that where people are present, few locations can be deemed beyond the reach of the wildlife trade (Symes et al., 2018).

Impacts of international-scale trade decline more rapidly with distance, to reach no net effect 5 hours away from settlements (Figure 3E; $Q_M = 60.53$, df = 1, $p < 0.0001$). While local and national trade have tangible links to nearby settlements, international trade is likely decoupled from proximate settlements, with supply affected by distant sources of demand. This is particularly worrying given plans to synergise the traditional Chinese medicine trade into China’s Belt and Road Initiative, creating trade links with 62% of the world population (Hinsley et al., 2020). This expansion is recognized as a key threat to biodiversity (Lechner et al., 2018), increasing both access and potential demand for medicinally prized species, including brown bear (*Ursus actos*) and snow leopard (*Panthera uncia*) (Farhadinia et al., 2019; Hinsley et al., 2020). Scaling up trade networks without a robust understanding of current impacts could be disastrous to species conservation, accelerating population losses and species extinctions.

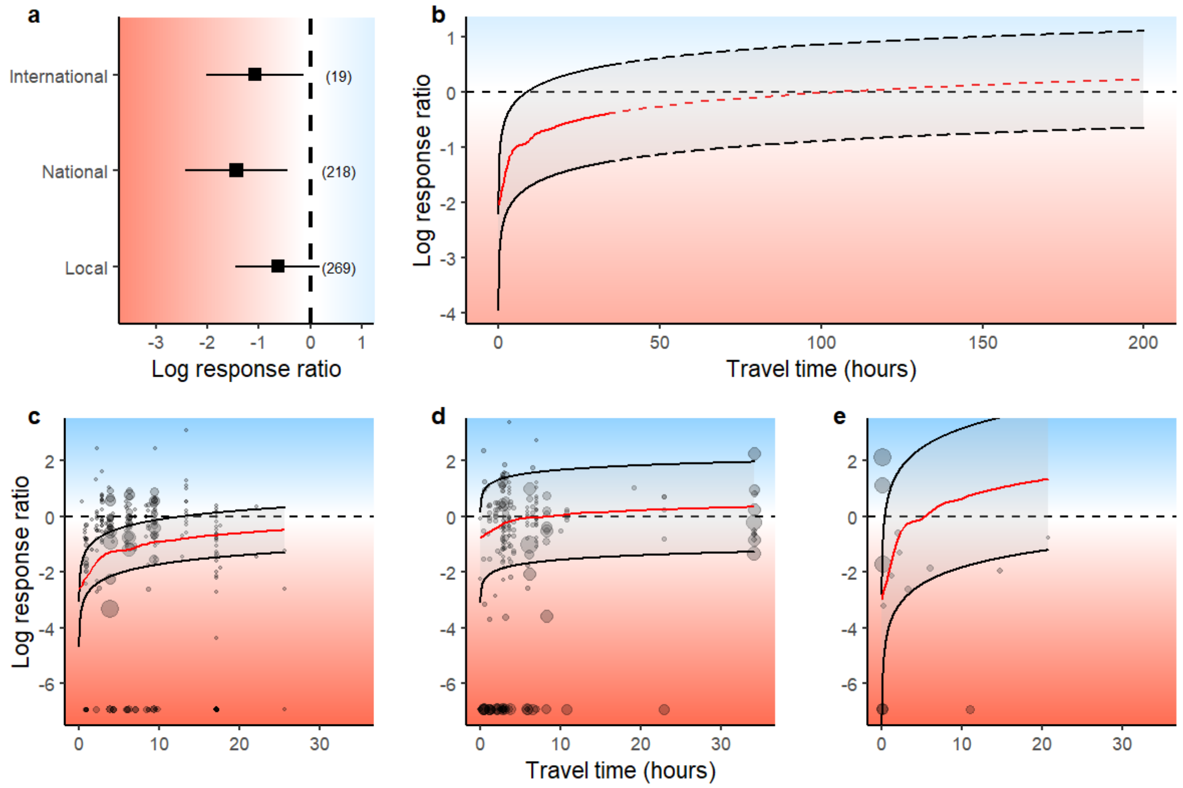


Figure 3. Effect of trade on species abundance with travel time to settlements (with a population greater than 5000). A) Effect size estimates across levels of trade. Error bars correspond the estimates 95% confidence interval. B) The effect of travel time on species across all trade levels, from local to international. Effect sizes of travel time for C) local, D) national and E) international trade. Extremely negative results indicate local extirpations (population declines of 100%). Points denote the raw effect sizes, solid red line is the mean predicted effect size, dotted red line is the model extrapolation, and black lines denote the 95% confidence intervals. Point size corresponds to each effect's sampling variance.

Effectiveness of conservation measures

Species declines increased with threat status (Figure 4A), indicating a substantial risk of trade-compounded extinctions. Species classified as least concern or near threatened do not suffer significant declines, whereas endangered species suffer significant trade-induced declines of 81.2% (95% CI: 35.1 – 94.6%) (Supplementary Table 4). Endangered species at particular risk of decline include spider monkey species, *Ateles belzebuth* (99.9%, 95% CI: 95.7 – 99.9%) and *Ateles chamek* (99.9%, 95% CI: 77.7 – 99.9%), and Baird's Tapir, *Tapirus bairdii*, (99.9%, 95% CI: 78.6 – 99.9%) (Supplementary Figure 5). The correlation between threatened species, which typically have smaller populations, and greater declines highlight the risk of trade-driven extinctions and the need for proactive management of species most at risk (Courchamp et al., 2006). Data deficient species display mixed responses to trade, highlighting the need for more research, especially given that many such species will likely be of conservation concern (Jetz and Freckleton, 2015).

Where the extraction for trade occurred in globally recognised protected areas the impact of trade was significantly lower compared to in unprotected areas ($Q_M = 789.06$, df = 2, $p < 0.0001$ and Tukey HSD, $p < 0.001$). However, trade still drove declines of 56.0% (95% CI: 2.5 – 80.2%) in protected areas compared to 70.9% (95% CI: 35.4 – 86.9%) in unprotected areas. Locally protected areas (Figure 4C), where guards enforce trade bans (see Supplementary Methods), also significantly reduced trade-induced declines in abundance ($Q_M = 25.07$, df = 2, $p < 0.0001$ and Tukey HSD, $p < 0.001$). Where there is no local protection we find declines of 64.6% (95% CI:, 26.4 – 83.0%) compared to 38.9% (95% CI:, -31.3 - 71.5%) in areas with protection. That protected area status offers an imperfect outlook for preventing trade-induced declines is of particular concern given that urbanisation and transport routes are predicted to expand throughout the century (Dulac, 2013), increasing the catchment for trade, and necessitating the existence of truly protected areas (Figure 4B).

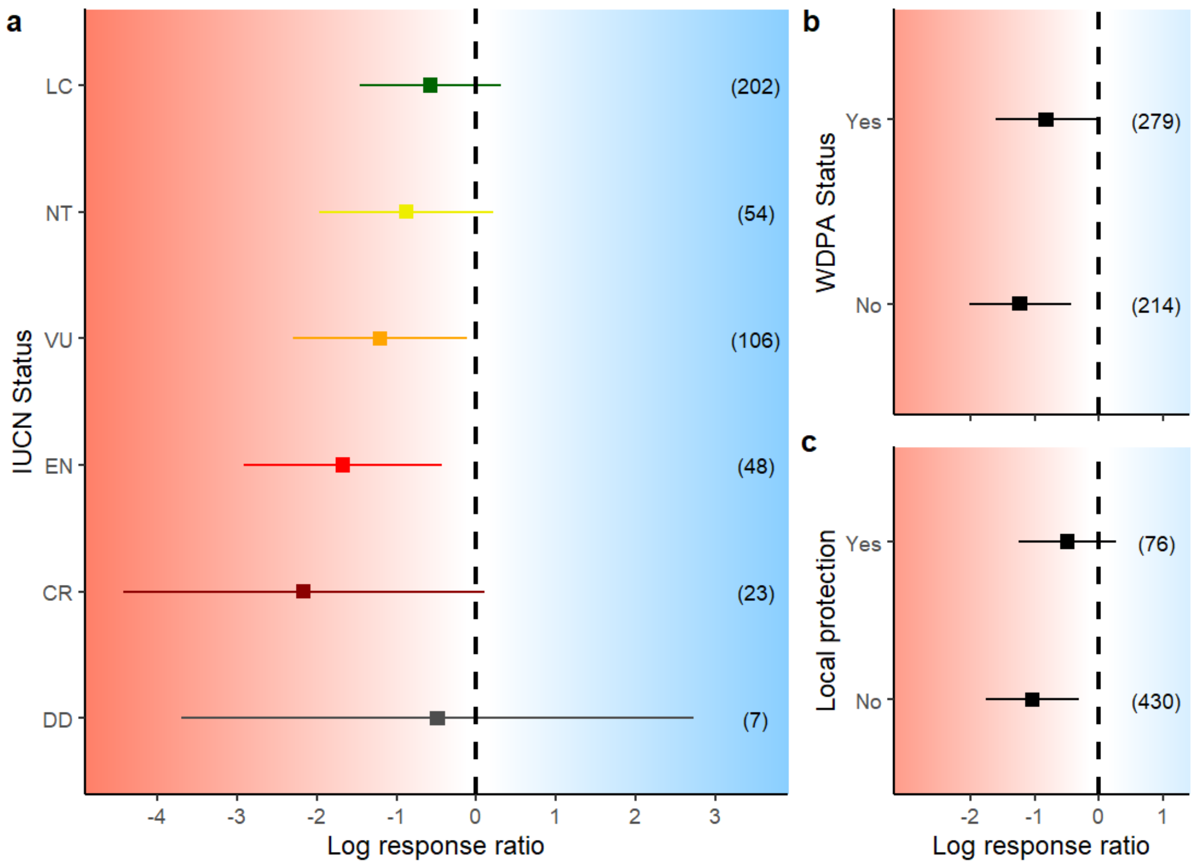


Figure 4. Impact of trade on species conservation and protected area status. A) Trade-induced population declines by IUCN threat status. Aggregated species effect sizes excluded. B) Effect of internationally listed protected areas. C) Effect of local protection, see Supplementary Methods for details on classification. Points denote the mean weighted effect size, lines the corresponding 95% confidence interval and the dashed black line no impact of trade. Estimates obtained through single mixed meta-regressions, Tukey HSD post hoc tests used to assess differences within panels B) and C).

Key predictors of trade and conservation action

The most important predictors of changes in species abundance highlighted in an optimum multiple meta-regression were travel time to the nearest settlements, protected status and the interactions between travel time and both levels of protected status (Supplementary Table 6 and S7). The model was highly significant according to Wald-type omnibus tests (Q_M = 5191.1, $P < 0.0001$, McFadden's pseudo-$R^2 = 0.297$, McFadden's pseudo adjusted-R^2 = 0.296). This further emphasises that successful conservation of many traded species is intertwined with improved integrity of protected areas and maintenance of true wilderness

(Gilroy and Edwards, 2017; Watson et al., 2016). Where unavoidable, infrastructural expansion into such areas must be designed to minimize negative externalities (Vilela et al., 2020). Significant residual heterogeneity remained in the model, likely attributable to the dynamic nature of the wildlife trade and its complex links to distant demand pressures, local food security issues, transnational trends, and evolving regulations (Challender et al., 2015a).

There are two possible biases in the underlying data used in our study, which could inflate the declines we have found. Firstly, some species at exploited sites could exhibit more cryptic behaviour to avoid detection, reducing apparent species abundances relative to control sites (Papworth et al., 2013). Secondly, although we carried out numerous supplementary analyses and tests to detect bias in the literature some of the original studies might have deliberately focused on sites for which there was *a priori* knowledge of extreme exploitation-induced declines relative to other exploited locations, but did not report this in their methods. As such, there is a possibility that some of our effect sizes present ‘worst-case’ declines from exploitation for wildlife trade.

In presenting multisource evidence that extraction for the wildlife trade drives large population declines there are crucial considerations for conservation management and policy. We examined 1807 peer-reviewed articles and >200 TRAFFIC reports, yet found no support for a quantified, existing sustainable trade (but see (Toledo-Aceves et al., 2014)), wider environmental benefits, nor evidence of an infrastructure for population monitoring and data acquisition to create sustainable trade. We urgently need quantitative studies in support of sustainable wildlife trade and the potential for well-managed trade to reduce the negative impacts of other conservation issues (Challender et al., 2019b). Assessing the sustainability of trade and its long-term impact on the myriad of traded populations is critical knowledge that takes significant time and funds to generate. Our study neither evidences unsustainability nor sustainability, as a global understanding of carrying capacity and offtake levels is missing. Rather, we reveal where the exploitation for trade causes populations to decline significantly in abundance. Future work should exploit population records through time to truly assess sustainability. Analyses using the Living Planet Index, highlight temporal population trends for “used” species are highly variable and must be interpreted with care (Leung et al., 2020; Tierney et al., 2014).

We must better protect traded species in the wild, via enhanced enforcement or improved local awareness of trade and hunting laws (Jachmann, 2008). However, these approaches can unfairly punish the economically marginalized, such as smallholders reliant on bushmeat for income and supplementary protein (Cooney et al., 2017), and so they must be combined with programs for up-skilling or income guarantees for local peoples (Cooney et al., 2017). Finally, international wildlife trade requires a globally coordinated and funded response to generate and synthesize data, plus enact focused trade bans (Cardador et al., 2019) and appropriate policing. We need to combine this with enhanced global education and awareness to reduce global demand before local extirpations become global extinctions.

2.4 Methods

Search Methodology

Suitable studies for inclusion were identified through a systematic literature search. Searches were conducted via ISI Web of Science, SCOPUS, Google Scholar and the White Rose thesis repository. Within Web of Science the following accessible databases were searched: the Core Collection, Data Citation Index, SciELO Citation Index, KCI – Korean Journal Database, BIOSIS Index, MEDLINE and Zoological Record. The search was completed over December 2019 and January 2020, with the final study list extracted on the 21st January 2020. A naïve Boolean search string of “Wildlife trade impact* population* AND (threat)” was used initially, resulting in 247 results. The citation record and abstracts of all 247 results were then exported for keyword co-occurrence network analysis using “Litsearchr” (Grames et al., 2019) in R 3.6.1 (R Core Team, 2019). This was used to create a comprehensive Boolean search string written as “("bushmeat* trade*" OR "illeg* trade*" OR "pet trade*" OR "wildlif* trade*") AND (popul* OR specie*) AND ("appendix* ii" OR "biodivers* loss*" OR "*sustainab*" OR "conserv* status*" OR "continu* declin*" OR "extinct* risk*" OR "iucn* red list*" OR "main* threat*" OR "major* threat*" OR "negat* impact*" OR "relat* abund*" OR "sever* impact*" OR "signific* impact*" OR "signific* threat*" OR "spec* rich*" OR "spec* surviv*" OR impac* OR "*sustainable*")”. This final search string was used to search the ISI Web of Science databases, and modified search strings were used for the other databases.

As search term length in SCOPUS is limited, a shortened string of “("bushmeat* trade*" OR "pet trade*" OR "wildlif* trade*") AND (popul* OR specie*) AND ("biodivers* loss*" OR "conserv* status*" OR "continu* declin*" OR "extinct* risk*" OR "relat* abund*" OR "impact*" OR "spec* rich*" OR "spec* surviv*")” was used. Google scholar is able to handle longer Boolean search strings but does not recognize wildcard components (*) so the search string used was “("bushmeat trade" OR "illegal trade" OR "pet trade" OR "wildlife trade") AND (population OR species) AND ("appendix ii" OR "biodiversity loss" OR "sustainable" OR "conservation status" OR "continuing decline" OR "extinction risk" OR "iucn red list" OR "main threat" OR "major threat" OR "negative impact" OR "relative abundance" OR "severe impact" OR "significant impact" OR "significant threat" OR "species richness" OR "species survival" OR impact)”. The White Rose eTheses repository does not handle Boolean search strings so two simple searches were used and the results pooled for screening, “Wildlife trade population impacts” and “Bushmeat trade population impacts”.

In addition, publications by TRAFFIC (The Wildlife Trade Monitoring Network) were reviewed for suitability. An exploratory review was conducted whereby all TRAFFIC Reports and Publications for birds (n = 24) and all TRAFFIC Bulletins for the years 2017 to 2019 were read in full. However, we found that despite performing detailed and comprehensive studies of wildlife trade market dynamics, conditions, and trends, TRAFFIC did not perform studies investigating the direct impacts of the trade in the control and treatment experimental design we required for this meta-analysis.

Finally, we reviewed the bibliography of a recent hunting meta-analysis and read the full text of all referenced studies to review them for inclusion (Benítez-López et al., 2017).

Inclusion and Exclusion Criteria

Studies were screened by title and abstract, before finally being selected based upon whether they met the following criteria. 1) Evaluates the impact of the wildlife trade on wild populations. 2) Contains data to the species or genus level. 3) Reports changes in abundance in areas hunted for trade and a control area. However,no studies were removed for the sole reason they presented only presence-absence data. 4) Assesses only areas without internal confounding factors, unless such factors were consistent across both the treatment site and the control site. An example of this would be the presence of agriculture or logging. Such studies are included if both the control and treatment site are subject to the same degree of agriculture or logging. Studies will be included if they are assessing the impacts of hunting on wild populations and the stated purpose of the hunt is for trade.

Furthermore, this analysis focuses specifically on the impacts of the commercial trade of species rather than their subsistence consumption. Therefore, where studies reported control and treatment data for numerous species but explicitly stated that only certain named species were predominantly traded, only traded species from that study were included. For example, in Espinosa-Andrade (2012) only 13 of the 25 reported species are included in our analysis.

Data Extraction

The data were structured into a source, study, species (effect-size) hierarchy. A source was taken as any single thesis, publication or peer-reviewed article. Within each source there could be more than one study. Numerous studies per data source were typically found if the effect of trade was assessed in treatment and control sites where groups of paired sites are either temporally or spatially separated. For example, if the same pair of sites were assessed in 2005 and then again in 2015, both years would represent a distinct study within a data source and the value would not be directly comparable across years. Additionally, each study should follow identical methodological protocols; for example, if the effect of trade was assessed in two treatment and two control sites, where one pair of sites was assessed using daylight transect surveys and the second pair assessed using nocturnal transect surveys, these pairs of sites would each represent a distinct study. This facilitates the calculation effect sizes by comparing observations within a single study. Each study typically contained data for at least one species where the density was recorded in both control and treatment plots/sites/transects.

For each species within each study, we extracted the following information: the mean abundance, the standard deviation, the standard error, the variance, the confidences interval, the sample size, the transect length (where reported), any reported distances to local markets, the reported scale of trade (local, national, international) and the reported purpose of trade (i.e. bushmeat, pet, laboratory, ivory, etc.). This information was extracted for both the treatment and control plots/sites/transects. We further recorded details of the methods and units of abundance (i.e. Individuals/km^2, groups/km^2 or encounters/km). Where the data required was not reported in the main body of the text, tables, supplementary information and after the authors had been contacted regarding data sharing, figures containing the required data were digitized using GetGraph Digitizer (Version 2.26) software.

Where possible we also extracted the coordinates of both treatment and control sites from the study. Where this was not possible or not reported, we georeferenced the study site maps using QGIS 3.12.0. For a small number of studies the exact coordinates either given or marked in figures were not given, in most cases this was due to the authors choosing not to publish the exact coordinates so not to increase the risk of extraction for their isolated control populations (Schoppe et al., 2010). Where this was the case we attempted to contact the authors for the locations. The extracted data was further supplemented with IUCN (International Union for Conservation of Nature) data, which included threat status, population trends, whether biological resource use is a known *Threat*, the details of the species recorded levels of *Use and Trade.* We used EltonTraits 1.0 (Wilman et al., 2014) to include the body mass and feeding guild of each mammal and bird species. The feeding guild of a species was deduced from the relative proportions of each dietary component and were as follows, carnivore (>50% of the diet is vertebrate species), insectivore (>50% of the diet is invertebrate species), herbivore (>50% of the diet is from plants), frugivore (>50% of the diet is fruit and seeds) or an omnivore (where no previous categorisation applies).

In certain cases, aggregated species data were presented. This was common for certain inconspicuous taxa, such as duikers (of the genus *Philantomb*a and *Cephalophus*). In such cases, we deduced mean body masses from EltonTraits by taking the averages of all species within that genus known to occur in the area, the same process was applied to feeding guild. For reptiles, the same approach was applied to body mass using the Slavenko et al (2016) dataset.

In total, our database included 506 species level effect sizes from 31 studies (mammals – 21, birds – 6 and reptiles 7; noting the total does not sum to 31 because 3 studies considered both birds and mammals) (Aquino et al., 2016; Aquino and Calle, 2003; Carrillo et al., 2000; Cronin, 2013; Dasgupta and Hilaluddin, 2012; Davies et al., 2008; De Thoisy et al., 2005; Espinosa-Andrade, 2012; Fay, 1991; Gamble and Simons, 2004; Gonzalez, 2003; Gray and Phan, 2011; Hall et al., 1997; Klemens and Moll, 1995; Kümpel et al., 2008; Linder and Oates, 2011; Magige et al., 2009; Maldonado et al., 2009; Maldonado and Peck, 2014; Muchaal and Ngandjui, 1999; Nuñez-iturril and Howe, 2007; O'Brien et al., 2003; Patrick et al., 2011; Poulsen et al., 2011; Remis and Kpanou, 2010; Rist et al., 2009; Rovero et al., 2012; Schoppe et al., 2010; Segura and Acevedo, 2019; Sung et al., 2013; Topp-Jorgensen et al., 2009; Yasuoka, 2006). The 506 effect sizes are comprised of 452 for mammals, 36 for birds and 18 for reptile. This included 82 treatment sites (mammals – 62, birds – 11 and reptiles - 14) and 44 control sites (mammals – 30, birds – 7 and reptiles - 10). Note - the totals again do not sum to the overall site count as 3 studies considered both mammals and birds at the same sites. The dataset includes 144 species (or groups of similar species that authors were unable to distinguish in the field), comprising 110 mammals, 25 birds and 10 reptiles. By trade purpose, 115 species were involved in the bushmeat trade, 16 species in the pet trade and 24 species in an assortment of trade purposes (note, these do not sum to 144 total species, because some species appear in multiple studies in which the purpose differed).

Spatial Variables

For each study we extracted the locations of both the treatment and control sites (Fig. S1). All travel and spatial metrics were calculated from control and treatment sites. This was to ensure our analysis accounted for the variable ‘quality’ of controls used in studies. For example, in a hypothetical example, (Fig. S1) it is possible that in Study 1 the control, C_1, is much closer to the settlement that the control used in Study 2, C_2 and therefore may have reduced species densities solely due to this closer proximity to the treatment site and the settlement itself. For this reason, both the control site distance and the treatment site distance were recorded and included in regression analyses.

From the available georeferenced coordinates of each control and treatment site we extracted further information (despite efforts, for 45 effect sizes, locations and therefore travels times could not be extracted from maps, methods or authors). Using the travel time raster layers formulated in Nelson et al, (2019), we calculated the travel in time in minutes from each control and treatment sites to urban centres with a population >5000, (mean, maximum : minimum time, Control [502.889, 7 : 2145], Treatment[414.543, 0 : 2047]). The raster layers calculate travel time based on the existing topography, terrain, infrastructural network along the route, and use the most common mode of transport used in the pixel (e.g. walking, car, boat etc.). We further assessed the protected area status of each site using two methods. Firstly, we cross-referenced each location with the World Database of Protected Areas (UNEP-WCMC and IUCN, 2020). Secondly, we recorded the level of protection each site was described as having in the original data source. For example, this was scored as yes if the traded area was recorded in the study as having guard patrols or active enforcement of quotas etc. All spatial analysis and extraction were completed using QGIS 3.12.0 (QGIS

Development Team, 2020) and R 3.6.1 (R Core Team, 2019). All spatial operations were completed using a Mollweide equal-area projection (UNEP-WCMC, 2019).

Effect Size Calculations

We used log response ratios (RR) to calculate effect sizes (Eq. 1), as is common in ecological and environmental meta-analyses when comparing two groups (treatment and control) where the expectation for zero values is low (Hedges et al., 1999).

$$RR = \ln\left(\frac{\bar{X}_{TS}}{\bar{X}_{CS}}\right) \qquad \text{(Equation 1)}$$

Effect sizes were calculated for individual species from sites within each study. Each effect size is calculated from a treatment ($\bar{X}_T$) and control ($\bar{X}_C$) mean abundance per study (S). The control sites were those where the extraction of species for trade was not thought to occur or was stated to occur to at very minor levels, and was not confounded by the extraction of species for subsistence consumption. Where the RR for any species is negative (RR < 0) this represents a decrease in species abundance where the extraction for trade occurs; similarly, a positive RR (RR >0) indicates that species abundances are greater where trade occurs. A RR equal to 0 would indicate there is no impact of trade on species.

At certain treatment sites the extraction for trade has driven species abundance to zero, representing localised extirpations. This results in a division of zero values by the control mean ($\bar{X}_C$) giving an unlogged effect size of zero, and a mathematically undefined logged value. Therefore, we performed a transformation (Eq. 2) on zero abundance values using a modified version of the approach proposed by Smithson and Verkuilen (2006), as used in similar meta-analyses, where:

$$\bar{X}_{TS} = 0, \text{ let } R = \frac{\bar{X}_{TS}}{\bar{X}_{CS}}$$

$$R' = \frac{R(N-1)+\frac{1}{2}}{N} \qquad \text{(Equation 2)}$$

Here, R’ can be used to calculate the RR. Such a transformation displaces the range of unlogged values to now minutely favour higher values (all unlogged effect sizes before transformation (median, minimum : maximum) [0.58391, 0 : 38], and after [0.58487, 0.00096 : 38.00096]. For mammals before transformation [0.58824, 0 : 38], and after [0.58919, 0.00096 : 38.00096]. For birds before transformation [0.69190, 0 : 21.66667], and after

[0.692861, 0.00096 : 21.66762]. For reptiles before transformation [0.2400000, 0 : 8.34426], and after [0.24096, 0.00096 : 8.34522].

Our observed effect sizes (RR) were not weighted using the inverse sampling variance, as weighting in such a manner negates the complex random effects structure used in these analyses. Instead, we used the inverse marginal variance-covariance matrix which weights across the entire matrix as calculated using *rma.mv*. As a small number of studies did not report the standard deviation, standard error or confidence intervals we imputed the missing values using Brackens 1992 approach (Lajeunesse, 2013). We also calculated the missing values by assuming the data followed a Poisson distribution and therefore $\bar{x} = \sigma^2$, and also using the HotDeck_NN approach (Rubin and Schenker, 1991). Due to the presence of zero densities at a number of treatment sites necessitated a continuity correction factor (*k* = ½) (Sweeting et al., 2004). As all results were highly similar (Supplementary Table 10) the Bracken imputations were used, thus avoiding potential shortcoming of the correction factor approach for the SD values (Sweeting et al., 2004).

Modelling

All meta-regressions were undertaken using *metafor* 2.4-0 (Viechtbauer, 2010), the *rma.mv* function was used to fit multilevel mixed-effects meta-regressions. This approach was taken to account for the nested structure and non-independence of having multiple effect sizes from a single data source. The subsequent modelling was separated into three distinct stages, a random-effects mixed-effects regression, single mixed-effects regressions and multiple mixed-effects regression models. In all cases, models were assessed using the Bayesian Information Criterion (BIC). This criterion was selected over the first and second-order Akaike Information Criterion (AIC, AICc) for two reasons 1) it is known to perform better where there is large heterogeneity in the data and 2) the BIC penalises additional parameters to a greater degree than the AICc. However, we report the AIC, AICc and BIC values for reference (Supplementary Table 3, S5).

The random-effects only model was used to assess the overall impact of trade on species abundance, the final BIC selected model structure was ~ 1 | Study + 1 | Order/Species. This structure was then carried forward to be used as the optimal random structure for both the single and multiple meta-regressions. We applied the same process to deduce optimal random effects structures for the local, national and international subset (Supplementary Table 4).

Single mixed-effects models were used to estimate how the impact of trade varied depending on certain continuous and categorical moderators (Supplementary Table 4). However, as trade is a multifaceted and complex threat we used multiple mixed-effects meta-regressions to control for interactions and multiple effects. We staggered our complex multiple regressions into three distinct facets; spatial, species-specific and human-induced variables. This was then used to inform a global multiple regression to assess the complex predictors of the wildlife trade, additional interactions across categories were also tested (i.e. WDPAstatus*TradeLevel, as protected status may be more effective at curtailing local level trade than international trade). We used Tukey's Honestly Significant Difference to assess the impact of trade level and protected status using the "*multcomp*" package (Hothorn et al., 2016), and all p values presented are adjusted to account for multiple comparisons.

The most supported model was assessed for its approximate residual heterogeneity using Cochran's Q (Q_E) (Cochran, 1954; Hoaglin, 2016). An Omnibus test of parameters was used to assess the heterogeneity explained by the given combination of moderator variables (Q_M). We used profile likelihood plots of variance to assess whether the models were over parametrized (Supplementary Figure 7). Finally, we assessed the quality of fit of the meta-regressions using two methods, initially using McFadden's pseudo R^2 (Eq. 6) and finally with McFadden's pseudo adjusted R^2 (Eq. 7) which penalises models for over-complexity (McFadden, 1977).

$$R^2 = 1 - \frac{\ln \hat{L}(M_{full})}{\ln \hat{L}(M_{null})} \qquad \text{(Equation 5)}$$

$$R_a^2 = 1 - \frac{\ln \hat{L}(M_{full}) - (K_{full-null})}{\ln \hat{L}(M_{null})} \qquad \text{(Equation 6)}$$

The model estimates are presented in the text as percentages for clarity. The following formula was used to convert log response ratios to percentage declines (Equation 7).

$$\%\, declines = (1 - e^{RR}) * 100 \qquad \text{(Equation 7)}$$

Publication Bias and Diagnostic Tests

In our meta-analysis, we only used studies published in international journals (we did not find a single suitable report from TRAFFIC): thus each was subject to rigorous peer review.

Furthermore, interrogation of each study revealed that traded sites were selected randomly (i.e. without prior knowledge of the intensity of exploitation), having initially stratified site selection by undisturbed controls versus impacted locations or across a disturbance gradient. These approaches follow standard scientific practice in research on the impacts of anthropogenic disturbances on biodiversity, including deforestation and logging (Gibson et al., 2011) or hunting (Benítez-López et al., 2017).

We performed two broad classes of diagnostic test to assess publication bias. First, we assessed publication bias visually through funnel plots of the inverse variance and effect size residuals (Fig. S3). There was little potential for bias across the whole dataset. Second, we used two analyses to assess the validity of the calculated effect sizes (RR). We used the original methods proposed by Geary (1930), whereby effect sizes are viewed as valid when the standardised mean of either group is greater than 3 (Eq. 4). We then further tested our effect sizes using a small sample size corrected version as proposed by Lajeunesse (2015), which was modelled to assess validity with greater accuracy where small sample sizes are present, as is the case here (Eq. 5).

$$\frac{\bar{X}_i}{SD_i}\sqrt{N_i} \geq 3 \qquad \text{(Equation 3)}$$

$$\frac{\bar{X}_i}{SD_i}\left(\frac{4(N_i)^{\frac{3}{2}}}{1+4(N_i)}\right) \geq 3 \qquad \text{(Equation 4)}$$

Effect sizes were either a “Pass” or “Fail” for each diagnostic analysis. An overall “Fail” was assumed where either the treatment or control variable for a given effect size failed either diagnostic assessment. We then compared our results after excluding those results that failed the diagnostic tests and found the results highly similar (Supplementary Table 9).

We also ran two single mixed-effects meta-regressions to further examine the potential for publication bias. Firstly, we assessed whether estimates from studies that directly quantified the intensity of trapping at the sites (trap density, hunter counts etc.) differed significantly to those that simply stated that hunting for trade occurred. Secondly, we assessed whether studies that compared a single trapped site with a single untrapped versus those that compared an untrapped site with multiple sites on a gradient of trapping pressure (distance, accessibility etc.).We found effect size estimates were not significantly different whether trapping level was assessed or not (Tukey HSD, z-value = 0.543, *p* = 0.587) or whether the study design was paired or across a gradient of trapping pressure (Tukey HSD, z-value = -0.554, *p* = 0.580). In combination, these three broad categories of evidence strongly support that there is no cryptic bias in the literature in terms of seeking sites that are known to be particularly heavily traded.

Fail-safe Numbers and Precautionary Reanalysis

We confirmed the confidence of our findings by calculating fail-safe numbers as proposed by Rosenthal (1979) and Rosenberg (2005), which describes the number of additional null studies that would be needed to increase the p-value to greater than 0.05. A low number suggests that the results are unlikely to robust and could easily be influenced by missing or new studies not included in the analysis. Both Rosenberg’s and Rosenthal’s fail-safe numbers are high enough for us to confident in our robust effect sizes for the whole dataset and the trade-level subsets (Supplementary Table 8).

Many ecological studies suffer from small, true, sample sizes, as when comparing the impacts of trade, certain studies used only a single site where the extraction of species for trade occurs and a single site where it does not (mean sample size = 5.004). This is expected, as the logistics involved finding, reaching and sampling such sites is complex. However, at each site many km of transects are walked, which can be viewed as another metric of sample or study size. Therefore, we recalculated our effect sizes and sampling variances using the total transect length and found that our original estimates using the true sample size were robust to a more general measure of study size (Supplementary Figure 3), and the total decline in abundance was found to highly similar. Results were 64.2% with a 95% CI: 23.1 – 83.3% using total transect length compared to 61.6% with a 95% CI: 20.0 – 81.6% using the true sample size. Therefore, the results we present are calculated using the true sample size.

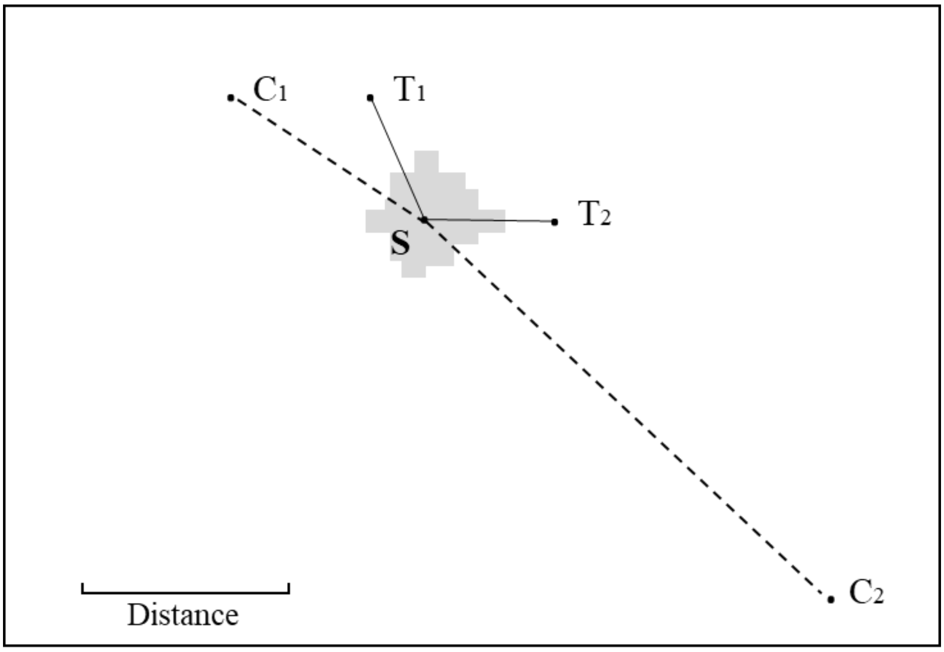
2.5 Author contributions

OM, BRS and DPE conceived the study. OM led the literature search, data extraction and analysis, with BRS, TH and DPE assisting with methodological development and evaluation of results. OM wrote the first draft of the manuscript with BRS, TH and DPE contributing to the revisions.

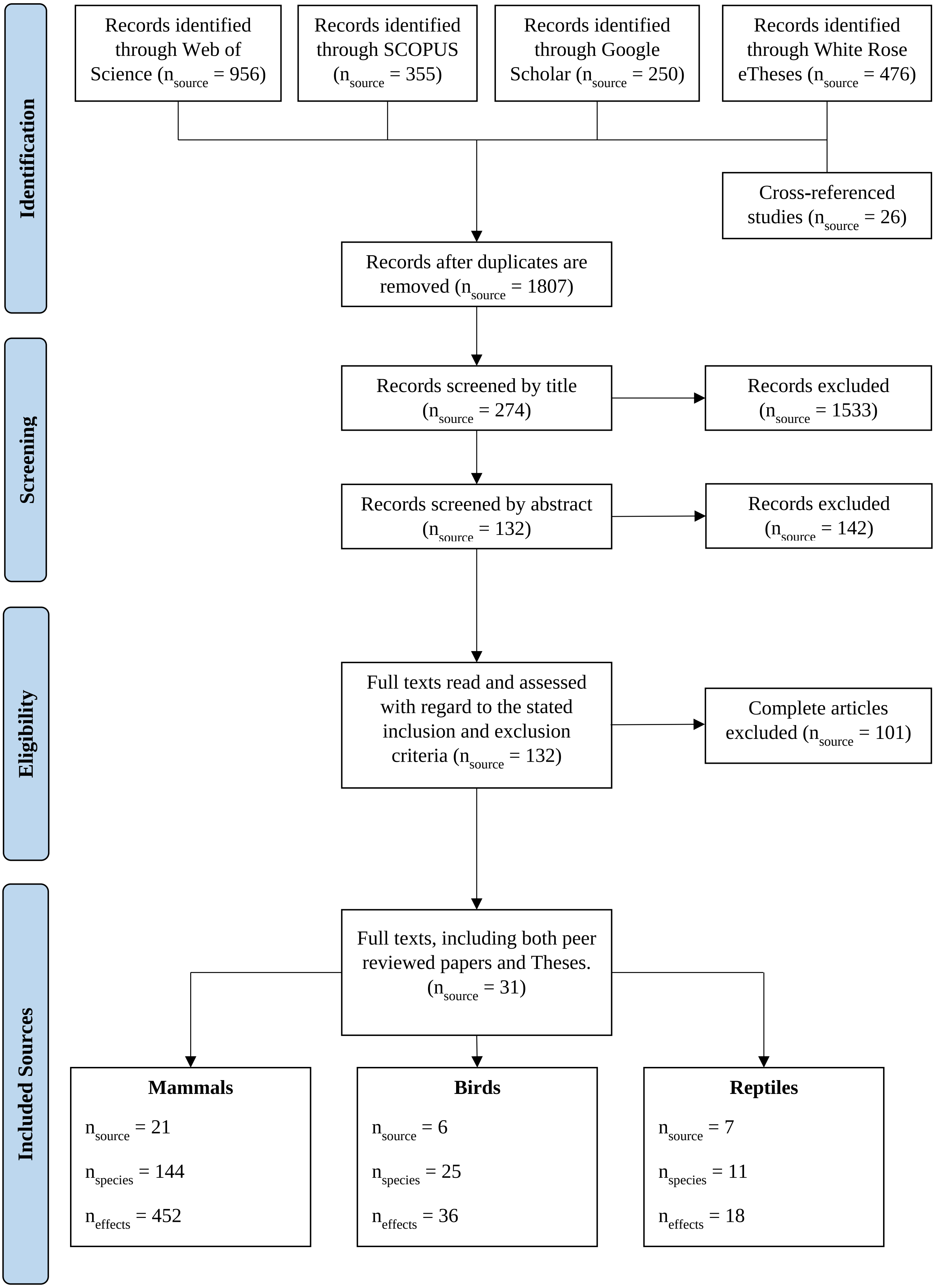
2.6 Data availability

The data used in this study are publicly available in an institutional repository at https://doi.org/10.15131/shef.data.13525679.

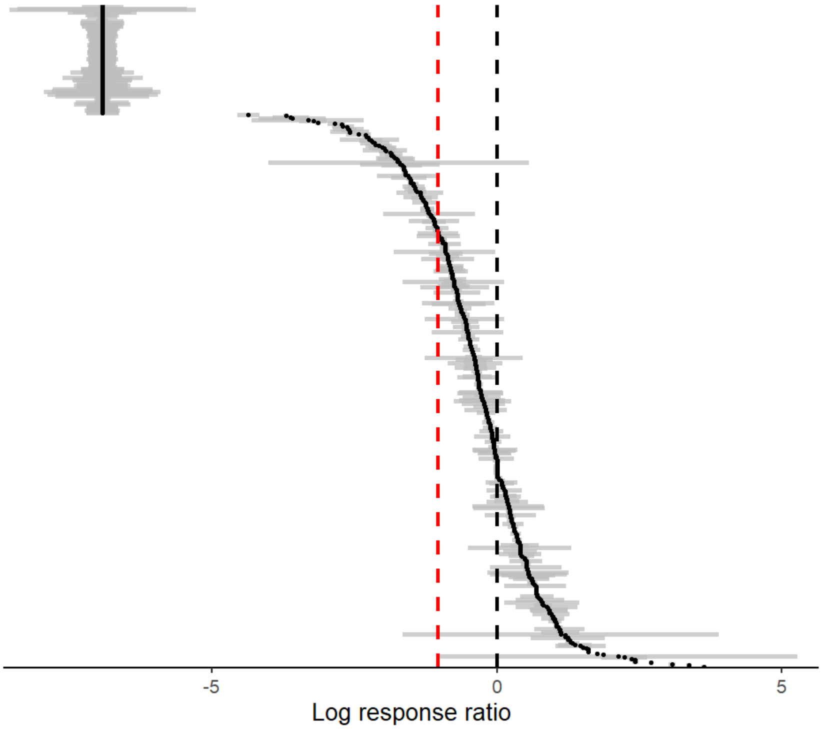
2.7 Supplementary materials



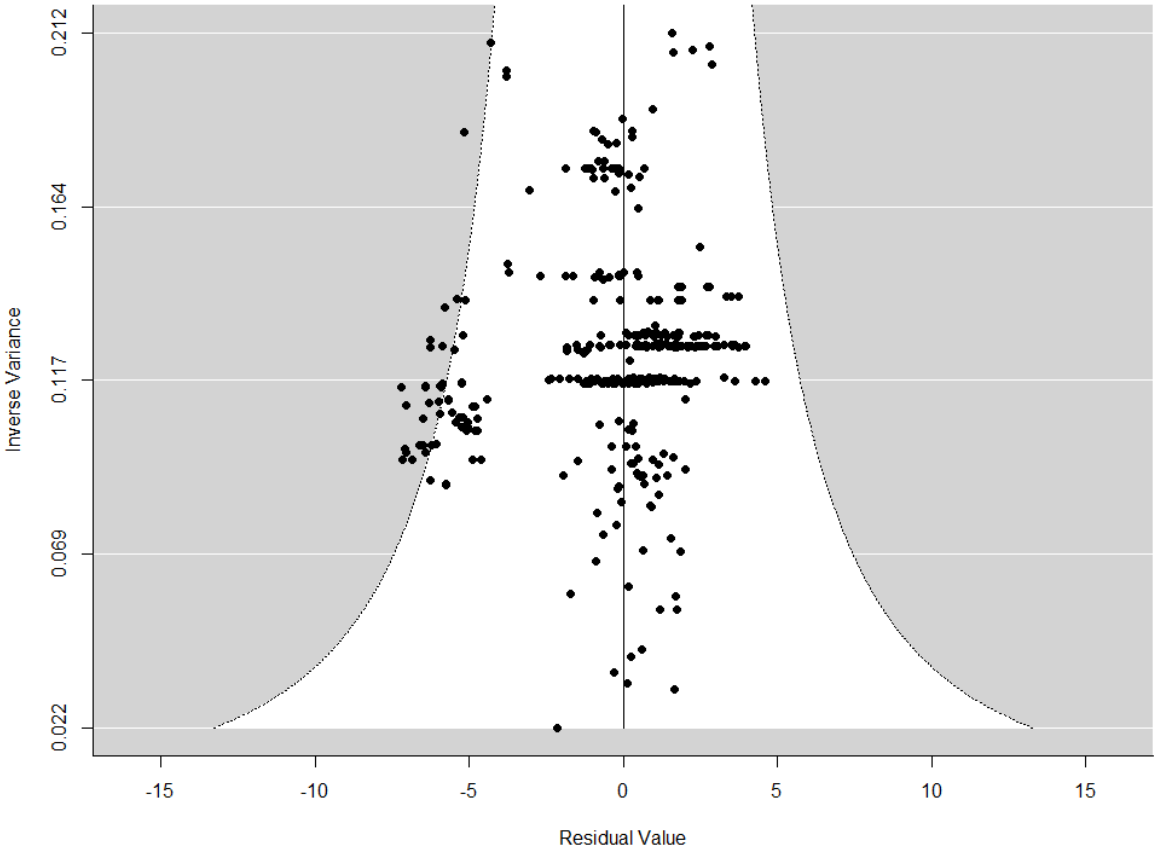
Supplementary Figure 1. Hypothetical spatial distribution of treatment and control (C and T) sites around a single common settlement (**S**) for two studies (1 and 2).



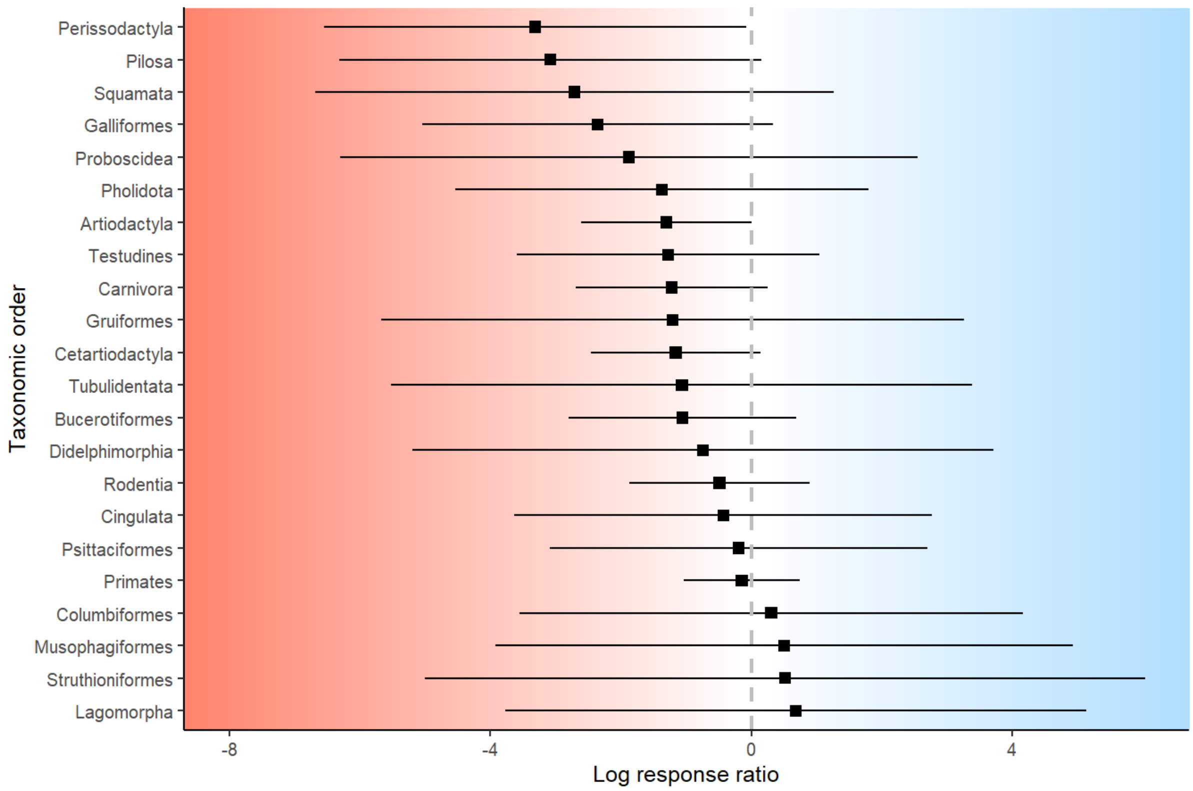
Supplementary Figure 2. PRISMA flow chart of the completed search process.



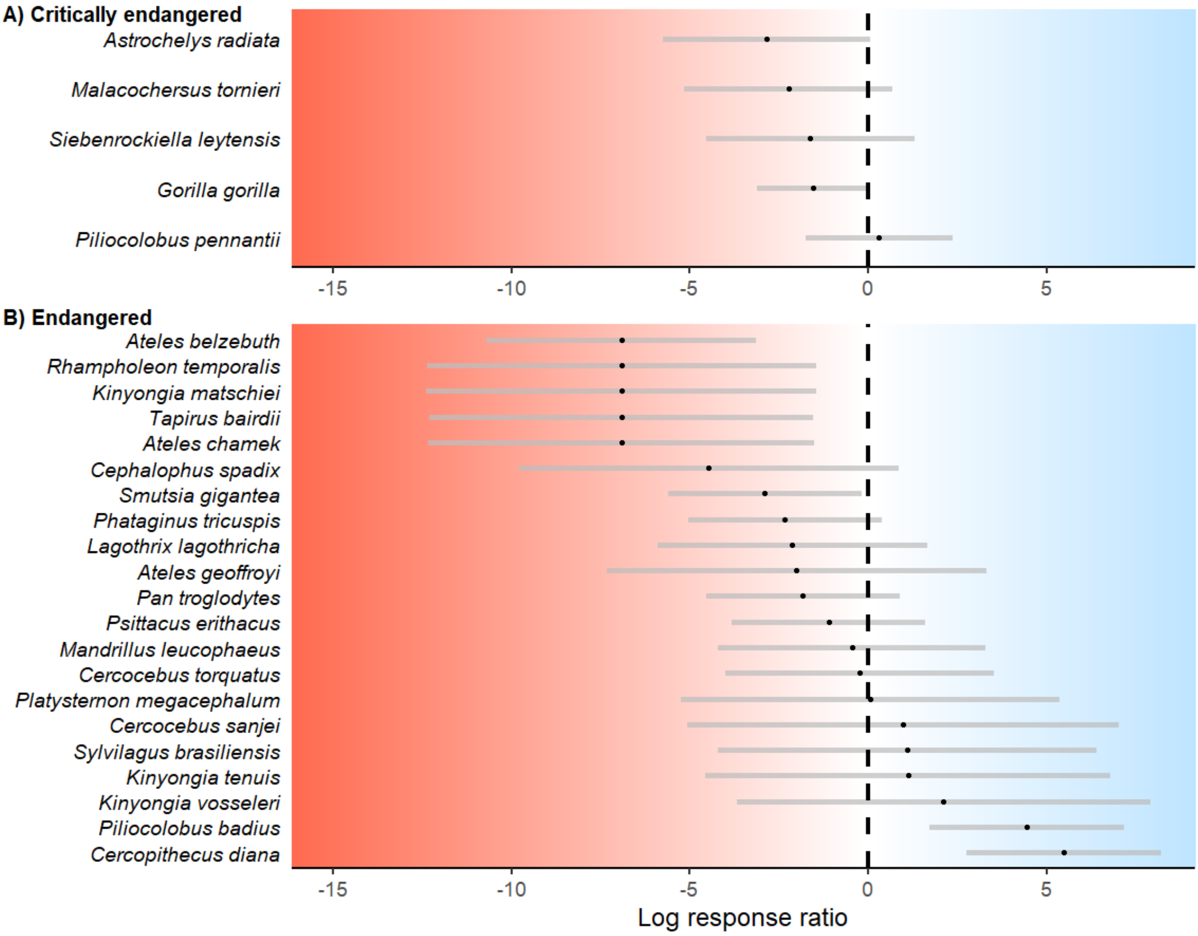
Supplementary Figure 3. Effect sizes and sampling variances as recalculated using total transect length per study. 506 taxa wide effect size estimates showing the 95% confidence interval. Overall weighted population declines of 64.2% (95% CI: 23.1 – 83.3%) are shown by the dashed red line. Points show weighted means and lines 95% confidence intervals. Dashed black line at zero denotes no impact of trade. Estimate obtained through random-effects meta-regressions. Extremely negative results indicate where traded populations were locally extirpated (population declines of 100%), see Supplementary Methods for details.



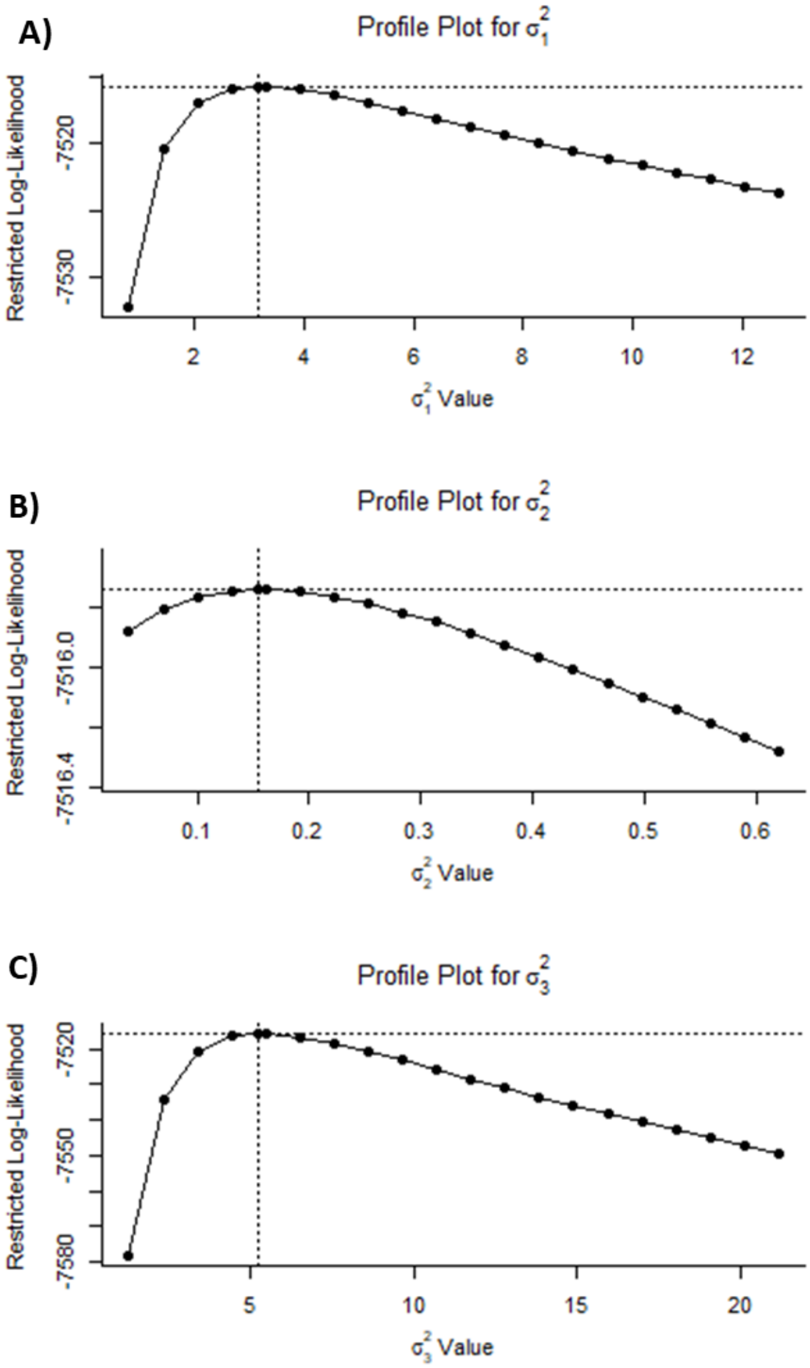
Supplementary Figure 4. Funnel plot for complete dataset showing the meta-analysis residuals and the inverse variance for the complete dataset.



Supplementary Figure 5. Effect size estimates of taxonomic order. Bars show the effect size estimate 95% confidence intervals. Estimates obtained using single mixed meta-regressions (Q_M = 21.5824, df = 22, P = 0.4850).



Supplementary Figure 6. Effect size estimates of A) critically endangered and B) endangered species. Bars show the effect size estimate 95% confidence intervals. Estimates obtained using single mixed meta-regressions.



Supplementary Figure 7. Profile likelihood plots of the variance components included in the optimal multiple meta-regression. A) Study level variability. B) Taxonomic order level variability. C) Nested species within order level variability. The clear peaks corresponding to the model REML estimates indicate the models are not over parametrized. If they were over parametrized, we would expect to see sections of the profile likelihood or its entirety running flat. Which would suggest some parameters are largely arbitrary and cannot be clearly identified.

Supplementary Table 1. List of included studies. Includes the source type (e.g. peer-reviewed article or doctoral thesis), country the research was conducted in, the taxonomic class studied and the number of unique species the study covered.

Source	Type	Country	Class	Number of species
(Aquino and Calle, 2003)	Article	Peru	Mammalia	14
(Aquino et al., 2016)	Article	Peru	Mammalia	3
(Carrillo et al., 2000)	Article	Costa Rica	Mammalia	20
(Cronin, 2013)	Doctoral thesis	Equatorial Guinea	Mammalia	6.
(Dasgupta and Hilaluddin, 2012)	Article	India	Aves	5
(Davies et al., 2008)	Chapter	Sierra Leone	Mammalia	8
(De Thoisy et al., 2005)	Article	French Guiana	Mammalia	6
(Espinosa-Andrade, 2012)	Doctoral thesis	Ecuador	Mammalia and Aves	10 and 2 species
(Fay, 1991)	Article	Central African Republic	Mammalia	1
(Gamble and Simons, 2004)	Article	USA	Reptilia	1
(Gonzalez, 2003)	Article	Peru	Aves	11
(Gray and Phan, 2011)	Article	Cambodia	Mammalia	2

(Hall et al., 1997)	Article	Democratic Republic of the Congo	Mammalia	1
(Klemens and Moll, 1995)	Article	Tanzania	Reptilia	1
(Kümpel et al., 2008)	Article	Equatorial Guinea	Mammalia	4
(Linder and Oates, 2011)	Article	Cameroon	Mammalia	7
(Magige et al., 2009)	Article	Tanzania	Aves	1
(Maldonado et al., 2009; Maldonado and Peck, 2014)	Article	Peru	Mammalia	Aggregate of species.
(Muchaal and Ngandjui, 1999)	Article	Cameroon	Mammalia	17
(Nunez, 2007)	Doctoral thesis	Peru	Mammalia and Aves	35 and 3 species (including 3 aggregate classes of unidentified primates by size).
(O’Brien et al., 2003)	Article	Madagascar	Reptilia	1
(Patrick et al., 2011)	Article	Tanzania	Reptilia	5

(Poulsen et al., 2011)	Article	Democratic Republic of the Congo	Mammalia and Aves	11 and 8 species.
(Remis and Kpanou, 2010)	Article	Central African Republic	Mammalia	8
(Rist et al., 2009)	Article	Equatorial Guinea	Mammalia	14
(Rovero et al., 2012)	Article	Tanzania	Mammalia	5
(Schoppe et al., 2010)	Article	Philippines	Reptilia	1
(Segura and Acevedo, 2019)	Article	Morocco	Reptilia	1
(Sung et al., 2013)	Article	China	Reptilia	1
(Topp-Jorgensen et al., 2009)	Article	Tanzania	Mammalia	11
(Yasuoka, 2006)	Article	Cameroon	Mammalia	2

Supplementary Table 2. Moderator variables used for single and multiple mixed meta-regressions.

Moderator variable		Units/levels	Source
Species-level			
Body mass		Kg	EltonTraits 1.0 (Wilman et al., 2014) and Slavenko et al (2016).
Purpose of trade	*Bushmeat, Pet, Assorted (traditional medicine, ivory, laboratory, etc.).*	4	The corresponding data source.
Current IUCN threat status	DD, LC, NT, VU, EN, CR.	7	(IUCN, 2019)
Trophic guild	Herbivore, Carnivore, Omnivore, Frugivore, Insectivore.	5	EltonTraits 1.0 (Wilman et al., 2014)
Study level			
Continent	Africa, Asia, Central America, North America, South America.	5	The corresponding data source.
Trade level	Local, National, International.	3	The corresponding data source.
Travel time to large settlement (population > 5000)		Minutes *(by both treatment and control)*	(Nelson et al., 2019)
Protected area status (as per WDPA)	Yes, No	2	
Local protection (i.e. guards, patrols etc)	Yes, No.	2	The corresponding data source.

Presence of logging in both treatment and control sites.	Yes, No.	2	The corresponding data source.
Presence of agriculture in both treatment and control sites.	Yes, No.	2	The corresponding data source.

Supplementary Table 3. Random effects structure selection. Random effects structures were compared without the fixed effects structures. Final effects structures were compared using the second-order Akaike Information Criterion (AICc). Bayesian Information Criterion (BIC) and first-order Akaike Information Criteria (AIC) presented for reference. BIC values in bold show the final random effects structure used for each taxa.

Effects structure	**Complete Dataset**			***Mammalia Subset***		
	BIC	AIC	AICc	***BIC***	*AIC*	*AICc*
~ 1 | 1	60171.16	60166.93	60166.94	37944.43	37940.32	37940.33
~ 1 | Study	54227.20	54218.75	54218.78	34131.25	34123.03	34123.06
~ 1 | Source	55123.92	55115.47	55115.50	35035.69	35027.47	35027.50
~ 1 | Species	24073.91	24065.46	24065.48	22533.80	22525.58	22525.61
~ 1 | Order	54063.58	54055.14	54055.16	36302.50	36294.28	36294.31
~ 1 | Source/Study	54228.73	54216.05	54216.10	34139.43	34127.10	34127.15
~ 1 | Order/Species	24014.82	24002.15	24002.20	22474.83	22462.50	22462.56
~ 1 | Source + 1 | Order	50281.28	50268.61	50268.65	33475.99	33463.66	33463.71
~ 1 | Study + 1 | Order	49332.25	49319.58	49319.63	32519.39	32507.07	32507.12
~ 1 | Source + 1 | Species	21804.20	21791.52	21791.57	20287.04	20274.72	20274.77
~ 1 | Study + 1 | Species	21456.56	21443.89	21443.94	19925.90	19913.57	19913.62
~ 1 | Source/Study + 1 | Order	49333.68	49316.79	49316.87	32527.59	32511.16	32511.25
~ 1 | Source/Study + 1 | Species	21461.28	21444.38	21444.46	19930.29	19913.85	19913.94
~ 1 | Source + 1 | Order/Species	21765.23	21748.34	21748.42	20248.03	20231.59	20231.68
~ 1 | Study + 1 | Order/Species	**21419.73**	21402.83	21402.91	**19888.80**	19872.36	19872.45
~ 1 | Source/Study + 1 | Order/Species	21424.75	21403.63	21403.75	19893.58	19873.04	19873.17

Supplementary Table 4. Trade level subset random effects structure selection. Random effects structures were compared without the fixed effects structures. Final effects structures were compared using the second-order Akaike Information Criterion (AICc). Bayesian Information Criterion (BIC) and first-order Akaike Information Criteria (AIC) presented for reference. BIC values in bold show the final random effects structure used for each taxa.

Effects structure	**Local**			**National**			**International**		
	BIC	AIC	AICc	**BIC**	AIC	AICc	**BIC**	AIC	AICc
~ 1 | 1	43155.95	43152.36	43152.37	15944.19	15940.81	15940.83	430.04	429.15	429.40
~ 1 | Study	39522.17	39514.99	39515.03	14323.32	14316.56	14316.61	375.92	374.14	374.94
~ 1 | Source	39600.73	39593.55	39593.59	15155.21	15148.45	15148.51	366.24	364.46	365.26
~ 1 | Species	14905.92	14898.73	14898.78	7981.80	7975.04	7975.09	**295.04**	293.26	294.06
~ 1 | Order	37452.66	37445.48	37445.52	12178.21	12171.45	12171.51	391.99	390.21	391.01
~ 1 | Source/Study	39526.00	39515.22	39515.31	14328.70	14318.56	14318.67	369.13	366.46	368.17
~ 1 | Order/Species	14911.49	14900.71	14900.80	7987.86	7977.72	7977.83	297.93	295.26	296.98
~ 1 | Source + 1 | Order	34623.56	34612.79	34612.88	11981.07	11970.93	11971.04	368.48	365.81	367.52
~ 1 | Study + 1 | Order	34543.81	34533.03	34533.12	11605.35	11595.21	11595.32	378.17	375.50	377.22
~ 1 | Source + 1 | Species	**13766.18**	13755.41	13755.50	7123.59	7113.45	7113.56	297.93	295.26	296.98
~ 1 | Study + 1 | Species	13766.48	13755.70	13755.79	**6768.42**	6758.28	6758.40	297.93	295.26	296.98
~ 1 | Source/Study + 1 | Order	34547.78	34533.41	34533.57	11610.73	11597.21	11597.40	371.37	367.81	370.88

~ 1 | Source/Study + 1 | Species	13766.68	13752.32	13752.47	6773.80	6760.28	6760.47	300.82	297.26	300.34
~ 1 | Source + 1 | Order/Species	13774.10	13759.74	13759.89	7132.33	7118.81	7119.00	300.82	297.26	300.34
~ 1 | Study + 1 | Order/Species	13774.38	13760.02	13760.17	6777.28	6763.76	6763.95	300.82	297.26	300.34
~ 1 | Source/Study + 1 | Order/Species	13774.61	13756.66	13756.89	6782.66	6765.76	6766.05	303.71	299.26	304.26

Supplementary Table 5. Single mixed-effects meta-regression coefficients and effect size estimates. Significance denotes whether results are significantly different from zero i.e. the null hypothesis that trade has no effect on species abundance (effect size = 0).

Fixed effect	Mean effect size	95% Confidence interval		Significance	Test of Moderators (Q_M)
		Lower	Upper		
TravelTime$_{(T)}$					
Intercept	-3.0616	-3.9369	-2.1862	**<0.001**	**Q_M = 2868.5561, P = 0.0001**
TravelTime$_{(T)}$	0.3509	0.3380	0.3637	**<0.001**	
Trade purpose					
Bushmeat	-0.9091	-1.6859	-0.1324	**<0.05**	**Q_M = 8.2729, P = 0.0407**
Pet	-1.3066	-2.2264	-0.3868	**<0.001**	
Assorted	-0.9036	-2.4901	0.6830		
Trade level					
Local	-0.6347	-1.4584	0.1890		**Q_M = 10.9366, p = 0.0121**
National	-1.4390	-2.4342	-0.4437	**<0.01**	
International	-1.0720	-2.0194	-0.1247	**<0.05**	
WDPA status					
No	-1.2334	-2.0297	-0.4370	**<0.01**	**Q_M = 789.0634, p = 0.0001**
Yes	-0.8220	-1.6183	-0.0258	**<0.05**	

Local PA status					
No	-1.0395	-1.7731	-0.3059	**<0.01**	**Q_M = 25.0662, p = 0.0001**
Yes	-0.4920	-1.2543	0.2703	**<0.05**	
Where trade co-occurs with logging					
No	-1.1353	-1.8599	-0.4107	**<0.01**	**Q_M = 153.1707, p = 0.0001**
Yes	0.1348	-0.6103	0.8799		
Where trade co-occurs with agriculture					
No	-0.9473	-1.6811	-0.2136	**<0.05**	**Q_M = 9.0256, p = 0.0110**
Yes	-1.0856	-1.8363	-0.4448	**<0.01**	
IUCN status					
DD	-0.4867	-3.6916	2.7181		**Q_M = 17.2544, p = 0.0084**
LC	-0.5756	-1.4547	0.3035		
NT	-0.8763	-1.9699	0.2172		
VU	-1.2027	-2.2926	-0.1129	**<0.05**	
EN	-1.6712	-2.9107	-0.4318	**<0.01**	
CR	-2.1640	-4.4259	0.0980		

Supplementary Table 6. Multiple regression global model selection. Fixed effects structures were compared using the optimal random effects structure as shown in Supplementary Table 2. Final effects structures were compared using the Bayesian Information Criterion (BIC). First and second-order Akaike Information Criteria presented for reference. P denotes the degrees of freedom in each structure.

Model	**BIC**	**AIC**	**AICc**	**P**
Human				
Hypothesis – Trade level will have a significant impact on species abundances, with international trade being more detrimental than local trade.				
Null	21419.73	21402.83	21402.91	1
TradeLevel	21420.13	21394.81	21394.98	3
TradeLevel + ControlTraded	21420.26	21390.73	21390.96	4
TradeLevel + TradePurpose	21423.16	21376.84	21377.39	8
TradeLevel + TradePurpose + TradeLevel*TradePurpose	21425.65	21370.97	21371.72	18
TradeLevel + TradePurpose + TradeLevel*TradePurpose + ControlTraded	21425.45	21366.59	21367.46	19
TradeLevel + TradePurpose + Agriculture	21428.16	21377.66	21378.30	9
TradeLevel + TradePurpose + Agriculture + Logging	**21288.71**	21234.03	21234.78	10
Species				

Hypothesis – Species with a larger bodymass are more likely to traded and impacted due to their conspicuousness.				
Null	21419.73	21402.83	21402.91	1
Bodymass	21352.41	21331.30	21331.42	2
Guild	21369.34	21335.61	21335.90	5
Bodymass + Guild	**21322.15**	21284.22	21284.58	**6**
Spatial				
Hypothesis – The effects of trade would be greatest where there is the shortest travel time to human settlements and where the land is not protected (WDPA or Local PA).				
TravelTime$_{(T)}$	17418.26	17397.61	17397.74	2
TravelTime$_{(T, C)}$	17275.74	17250.98	17251.17	3
TravelTime$_{(T, C)}$ + LocalPA	17276.35	17247.47	17247.72	5
TravelTime$_{(T, C)}$ + WDPA	16497.23	16468.36	16468.61	4
TravelTime$_{(T, C)}$ + Continent	17271.70	17234.61	17235.02	7
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*PA + PA	17275.06	17242.08	17242.40	7

TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + WDPA	15317.74	15284.76	15285.09	5
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + PA + WDPA	15319.43	15278.25	15278.75	9
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA	**15316.82**	15263.37	15264.21	13
Global Model*				
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA	15316.82	15263.37	15264.21	11
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA + Bodymass	15214.96	15157.43	15158.39	12
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA + TradeLevel + TradePurpose	15325.95	15235.95	15238.36	24
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA + Guild	15263.04	15193.43	15194.73	15
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA + TradeLevel* TravelTime$_{(T)}$	15308.17	15238.43	15239.85	15
TravelTime$_{(T, C)}$ + TravelTime$_{(T)}$*WDPA + TravelTime$_{(T)}$*PA + Continent + PA + WDPA + Guild + Logging + Agriculture	**15147.34**	15069.47	15071.26	17

Supplementary Table 7. Optimum global model coefficients. Approximate residual heterogeneity was calculated using Cochran's Q (Q_E), and a Wald type Omnibus test of parameters was used to assess the heterogeneity explained by the combination of moderator variables (Q_M).

Fixed effect	**Estimate**	**Standard error**	**Z value**	**Lower 95% CI**	**Upper 95% CI**	**P-value estimate**
Intercept	-5.74927	1.075287	-5.34673	-7.85679	-3.64175	0.0000
TravelTime$_{(T)}$	0.164002	0.008662	18.93254	0.147024	0.18098	0.0000
TravelTime$_{(C)}$	0.408501	0.050406	8.10427	0.309708	0.507294	0.0000
LocalPA (Yes)	2.624566	3.235707	0.811126	-3.7173	8.966435	0.4173
WDPA (Yes)	-2.03738	0.072741	-28.0087	-2.17995	-1.89481	0.0000
Continent (Asia)	0.736568	1.793299	0.410733	-2.77823	4.25137	0.6813
Continent (Central America)	0.41486	1.870166	0.221831	-3.2506	4.080317	0.8244
Continent (South America)	-1.95424	0.932906	-2.09478	-3.7827	-0.12577	0.0362
Guild (Frugivore)	2.304816	0.975835	2.361892	0.392216	4.217417	0.0182
Guild (Herbivore)	1.262718	1.03483	1.220217	-0.76551	3.290948	0.2224
Guild (Insectivore)	0.913619	1.209922	0.755106	-1.45778	3.285023	0.4502
Guild (Omnivore)	1.910277	0.976298	1.956653	-0.00323	3.823786	0.0504
Logging (Yes)	1.216157	0.107452	11.31812	1.005554	1.426759	0.0000
Agriculture (Yes)	0.123521	0.08975	1.37628	-0.05239	0.299428	0.1687
TravelTime$_{(T)}$*LocalPA (Yes)	-0.47578	0.646324	-0.73614	-1.74256	0.790989	0.4616
TravelTime$_{(T)}$*WDPA (Yes)	0.425064	0.012355	34.40351	0.400848	0.449279	0.0000

$Q_M = 5191.1$ ($P < 0.0001$), $Q_E = 50937.1$ ($P < 0.0001$), McFadden's pseudo-$R^2 = 0.297$ (df = 19), McFadden's pseudo adjusted-$R^2 = 0.296$ (df = 19)

Supplementary Table 8. Fail-safe numbers for the taxa wide dataset and the mammal subset. Assuming a target significance level of 0.05

	Fail-safe Method	
	Rosenthal	**Rosenberg**
Taxa wide	928169	177789
Mammal Subset	*905220*	*317815*
Trade level Subsets		
Local	*278882*	*47036*
National	*134127*	*35101*
International	*4715*	*3480*

Supplementary Table 9. Results of Geary diagnostic tests. Percentage declines are shown for a reanalysis after the removal of studies that failed the diagnostic methods, and remain highly similar to our overall estimates (61.6%, 95% CI: 20.0 – 81.6%).

	Estimate	**Lower CI**	**Upper CI**
Original Geary diagnostic	64.49	19.83	84.27
Small sample adj Geary diagnostic	63.93	17.65	84.20

Supplementary Table 10. Estimated trade induced declines using three different methods to fill in missing standard deviations. We used the most conservative, Bracken1992 imputation approach for our analysis.

Imputation method used	**Estimate**	**95% CI**		**Percentage declines (95% CI)**
		Lower	**Upper**	
Poisson assumption	-1.532	-2.289	-0.774	78.4 (53.4 – 89.9%)
Bracken (Bracken, 1992)	-0.958	-1.693	-0.224	61.6 (20.0 – 81.6%)
HotDeck_NN (Rubin and Schenker, 1991)	-1.332	-2.077	-0.587	73.6 (44.4 – 87.5%)

Supplementary Table 11. Examination of significantly positive individual effect-sizes for potential conservation insights. These effect sizes comprise 15.3% of our dataset. For this purpose significance was defined as effect sizes where the 95% confidence interval did not cross below zero.

Source	Country	Class	Species	Guild	Estimate	Lower CI	Upper CI	Relevant conservation information
Sung2013	China	Reptilia	*Platysternon megacephalum*	Omnivore	0.513	0.102	0.924	Authors state despite trapping occurring at this site, no traps were observed during their study period so potential for recent, unrecorded cessation of trapping. This is compared to the other sites where traps were observed during the study period.
Rist2009	Equatorial Guinea	Mammalia	*Cercopithecus cephus*	Frugivore	1.204	0.999	1.410	Authors state coarse-scale interactions between habitat heterogeneity, hunting, logging roads and agricultural proximity each may confound the species level impacts of hunting on abundance.
Rist2009	Equatorial Guinea	Mammalia	*Cercopithecus nictitans*	Frugivore	0.273	0.067	0.478	
Rist2009	Equatorial Guinea	Mammalia	*Mandrillus sphinx*	Frugivore	0.511	0.306	0.717	
Rist2009	Equatorial Guinea	Mammalia	*Pan troglodytes*	Frugivore	0.917	0.711	1.122	
Rist2009	Equatorial Guinea	Mammalia	*Pan troglodytes*	Frugivore	1.042	0.836	1.247	
Rist2009	Equatorial Guinea	Mammalia	*Cephalophus ssp*	Herbivore	0.244	0.038	0.449	
Rist2009	Equatorial Guinea	Mammalia	*Cephalophus ssp*	Herbivore	0.694	0.488	0.899	

Rist2009	Equatorial Guinea	Mammalia	*Potamochoerus porcus*	Omnivore	3.638	3.432	3.843	
Rist2009	Equatorial Guinea	Mammalia	*Potamochoerus porcus*	Omnivore	3.367	3.162	3.573	
Rist2009	Equatorial Guinea	Mammalia	*Potamochoerus porcus*	Omnivore	2.708	2.503	2.913	
Rist2009	Equatorial Guinea	Mammalia	*Syncerus caffer*	Herbivore	0.442	0.237	0.648	
Rist2009	Equatorial Guinea	Mammalia	*Cricetomys emini*	Omnivore	1.036	0.831	1.242	
Rist2009	Equatorial Guinea	Mammalia	*Cricetomys emini*	Omnivore	0.799	0.594	1.004	
Rist2009	Equatorial Guinea	Mammalia	*Cricetomys emini*	Omnivore	0.636	0.431	0.842	
Rist2009	Equatorial Guinea	Mammalia	*Phataginus tricuspis*	Insectivore	0.891	0.686	1.097	
Rist2009	Equatorial Guinea	Mammalia	*Phataginus tricuspis*	Insectivore	0.224	0.019	0.429	
Yasuoka2006	Cameroon	Mammalia	*Cephalophus ssp*	Herbivore	0.337	0.047	0.628	No reason suggested why this species had a positive effect when others were negative.
Aquino2003	Peru	Mammalia	*Cebus apella*	Omnivore	0.287	0.146	0.429	No reason suggested why these species had a positive effect when others were negative.
Aquino2003	Peru	Mammalia	*Saimiri boliviensis*	Omnivore	0.398	0.256	0.540	

Magige2009	Tanzania	Aves	*Struthio camelus*	Herbivore	0.511	0.425	0.598	Authors state current populations are high within the Serengeti, so potentially protected and unprotected areas are buffered by this. However, the prominence of ostrich-derived products for sale to tourists indicate it may be a developing problem likely to get worse.
Linder2011	Cameroon	Mammalia	*Cercopithecus erythrotis*	Frugivore	1.329	0.919	1.740	Authors state the ecological flexibility of the two positively affected species, compared to the specialists suffering declines allow these species to proliferate through competitive release.
Linder2011	Cameroon	Mammalia	*Cercopithecus pogonias*	Frugivore	0.511	0.101	0.922	
Dasgupta2012	India	Aves	*Ducula badia*	Frugivore	1.014	0.896	1.132	Authors state the ecological flexibility of the *Ducula* pigeons, allow this species to proliferate through competitive release, where hornbill species abundances decline.
Davies2008	Sierra Leone	Mammalia	*Cercopithecus diana*	Omnivore	0.300	0.170	0.430	Authors state that as species are traded a considerable distance from where they are extracted certain species such as these *Cercopithecus sp* are less sought after compared to species such as *Piliocolobus sp* as their meat is more oily and therefore difficult to transport.
Davies2008	Sierra Leone	Mammalia	*Cercopithecus diana*	Omnivore	0.300	0.170	0.430	
Davies2008	Sierra Leone	Mammalia	*Cercopithecus campbelli*	Frugivore	0.167	0.037	0.297	
Davies2008	Sierra Leone	Mammalia	*Cercopithecus campbelli*	Frugivore	0.300	0.170	0.430	
Davies2008	Sierra Leone	Mammalia	*Cercopithecus diana*	Omnivore	1.050	0.920	1.180	

Davies2008	Sierra Leone	Mammalia	*Cercopithecus petaurista*	Omnivore	0.344	0.214	0.474	
deThoisy2005	French Guiana	Mammalia	*Cebus apella*	Omnivore	0.723	0.312	1.133	Authors state commercial hunters preferentially target *Allouatta* and *Ateles sp* for markets, suggesting that potentially these listed species are subjected to reduced pressures.
deThoisy2005	French Guiana	Mammalia	*Cebus olivaceus*	Omnivore	1.764	1.353	2.174	
deThoisy2005	French Guiana	Mammalia	*Cebus olivaceus*	Omnivore	1.504	1.094	1.915	
deThoisy2005	French Guiana	Mammalia	*Cebus olivaceus*	Omnivore	0.511	0.101	0.922	
deThoisy2005	French Guiana	Mammalia	*Cebus olivaceus*	Omnivore	1.872	1.461	2.283	
deThoisy2005	French Guiana	Mammalia	*Pithecia pithecia*	Omnivore	0.917	0.506	1.327	
deThoisy2005	French Guiana	Mammalia	*Pithecia pithecia*	Omnivore	0.965	0.555	1.376	
deThoisy2005	French Guiana	Mammalia	*Pithecia pithecia*	Omnivore	0.486	0.075	0.897	
deThoisy2005	French Guiana	Mammalia	*Saguinus midas*	Frugivore	0.694	0.283	1.104	
deThoisy2005	French Guiana	Mammalia	*Saguinus midas*	Frugivore	1.253	0.842	1.664	
deThoisy2005	French Guiana	Mammalia	*Saguinus midas*	Frugivore	2.354	1.943	2.765	

Espinosa-Andrade2012	Ecuador	Mammalia	*Tayassu pecari*	Frugivore	1.106	1.025	1.187	Authors state that despite the extraction being modelled as over sustainable levels, population viability among species is maintained via the immigration of individuals from inaccessible areas of the reserves.
Espinosa-Andrade2012	Ecuador	Mammalia	*Tapirus terrestris*	Herbivore	0.527	0.446	0.608	
Espinosa-Andrade2012	Ecuador	Mammalia	*Mazama americana*	Herbivore	0.196	0.115	0.277	
Espinosa-Andrade2012	Ecuador	Mammalia	*Mazama gouazoubira*	Herbivore	0.979	0.898	1.060	
Espinosa-Andrade2012	Ecuador	Mammalia	*Cuniculus paca*	Omnivore	0.530	0.448	0.611	
Espinosa-Andrade2012	Ecuador	Mammalia	*Cuniculus paca*	Omnivore	0.149	0.066	0.232	
Espinosa-Andrade2012	Ecuador	Mammalia	*Eira barbara*	Carnivore	1.289	1.208	1.370	
Espinosa-Andrade2012	Ecuador	Mammalia	*Eira barbara*	Carnivore	0.620	0.539	0.700	
Espinosa-Andrade2012	Ecuador	Mammalia	*Eira barbara*	Carnivore	0.083	0.000	0.166	
Espinosa-Andrade2012	Ecuador	Aves	*Penelope jacquacu*	Frugivore	3.076	2.995	3.157	
Espinosa-Andrade2012	Ecuador	Aves	*Penelope jacquacu*	Frugivore	2.428	2.347	2.508	
Espinosa-Andrade2012	Ecuador	Aves	*Penelope jacquacu*	Frugivore	2.428	2.345	2.511	

Espinosa-Andrade2012	Ecuador	Mammalia	*Priodontes maximus*	Insectivore	0.102	0.021	0.183	
Espinosa-Andrade2012	Ecuador	Mammalia	*Priodontes maximus*	Insectivore	0.228	0.148	0.309	
Poulsen2011	Republic of the Congo	Mammalia	*Funisciurus lemniscatus*	Frugivore	0.700	0.595	0.806	Authors state that the targeted extraction of larger bodied species shifted the community composition to favour smaller frugivorous mammals and birds. Which despite being hunted proliferate via competitive release.
Poulsen2011	Republic of the Congo	Mammalia	*Protoxerus stangeri*	Frugivore	0.755	0.554	0.956	
Poulsen2011	Republic of the Congo	Aves	*Bycanistes albotibialis*	Frugivore	0.546	0.473	0.619	
Poulsen2011	Republic of the Congo	Aves	*Bycanistes fistulator*	Frugivore	0.587	0.481	0.693	
Poulsen2011	Republic of the Congo	Aves	*Ceratogymna atrata*	Frugivore	0.782	0.638	0.925	
Poulsen2011	Republic of the Congo	Aves	*Corythaeola cristata*	Frugivore	1.598	1.482	1.715	

Poulsen2011	Republic of the Congo	Aves	*Psittacus erithacus*	Frugivore	0.609	0.511	0.707	
Poulsen2011	Republic of the Congo	Aves	*Lophoceros fasciatus*	Frugivore	0.245	0.100	0.390	
Remis2010	Central African Republic	Mammalia	*Philantomba monticola*	Frugivore	1.116	0.008	2.223	Authors state the secondary forest mosaic habitat preferred by *Duiker* species currently can support high abundances, maintaining population viability despite hunting pressures. However, the authors caution that the growing trend for gun and night hunting in the region may place these species in jeopardy.
Remis2010	Central African Republic	Mammalia	*Cephalophus ssp*	Herbivore	1.367	0.375	2.359	
Nunez2007	Peru	Mammalia	*Puma concolor*	Carnivore	0.694	0.283	1.104	Authors state that these herbivore species may be benefiting from competitive release as slower breeding species suffer decreases disproportionately faster. Additionally the prevalence of nearby refuges may also act as buffers for these species.
Nunez2007	Peru	Mammalia	*Nasua nasua*	Frugivore	0.694	0.283	1.104	
Nunez2007	Peru	Mammalia	*Tapirus terrestris*	Herbivore	0.694	0.283	1.104	
Nunez2007	Peru	Mammalia	*Sylvilagus brasiliensis*	Herbivore	1.099	0.688	1.510	
Nunez2007	Peru	Mammalia	*Dasypus novemcinctus*	Insectivore	0.848	0.437	1.258	
Nunez2007	Peru	Mammalia	*Didelphis marsupialis*	Carnivore	0.848	0.437	1.258	

Nunez2007	Peru	Mammalia	*Saguinus fuscicollis*	Frugivore	1.275	0.855	1.696	
Nunez2007	Peru	Mammalia	*Saimiri sciureus*	Omnivore	1.038	0.530	1.546	
Nunez2007	Peru	Mammalia	*Aotus nigriceps*	Omnivore	0.410	0.163	0.657	
Nunez2007	Peru	Mammalia	*Potos flavus*	Frugivore	0.686	0.413	0.959	
Nunez2007	Peru	Mammalia	*Sciurus spadiceus*	Frugivore	0.686	0.440	0.933	
Cronin2013	Equitorial Guinea	Mammalia	*Piliocolobus pennantii*	Herbivore	1.569	1.332	1.806	Authors state the niche speciality of certain species predispose them to be particularly vulnerable to over exploitation and conversely certain generalists can exploit these extraction-induced declines.
Cronin2013	Equitorial Guinea	Mammalia	*Cercopithecus pogonias*	Frugivore	1.071	0.834	1.308	
Cronin2013	Equitorial Guinea	Mammalia	*Cercopithecus erythrotis*	Frugivore	0.486	0.196	0.777	
Fay1991	Central African Republic	Mammalia	*Loxodonta africana*	Herbivore	1.017	0.606	1.427	Authors state despite high hunting pressures at the site, its densely forested nature impedes easy hunter access and provides a refuge for the local elephant population.

Chapter 3:

Mixed protection of threatened species traded under CITES

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3.1 Abstract

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates international legal trade to prevent detrimental harvest of wildlife. We assess volumes of threatened and non-threatened bird, mammal, amphibian, and reptile species in CITES-managed trade and how this trade responded to species changing IUCN Red List categories between 2000 and 2018. In this time, over a thousand wild-sourced vertebrate species were commercially traded. Species of least conservation concern had the highest yearly volumes (excluding birds), while species in most Red List categories showed an overall decrease in reoccurrence and volume through time, with most species unlikely to reoccur in recent trade. Charismatic species with populations split-listed between Appendices I and II were traded in substantially lower yearly volumes when sourced from more-threatened Appendix I populations. Species trade volumes did not systematically respond to changes in Red List category, with 31.0% of species disappearing from trade before changing category and the majority of species revealing no difference in trade volume pre- to post-change. Just 2.7% (12/432) of species volumes declined and 2.1% (9/432) of volumes increased after a category change. Our findings highlight non-threatened species dominate trade, but reveal small numbers of highly threatened species in trade and a disconnect between species trade volumes and changing extinction risk. We highlight potential drawbacks in the current regulation of trade in listed species and urgently call for open and accessible assessments—non-detriment findings—robustly evidencing the sustainable use of threatened and non-threatened species alike.

3.2 Introduction

International wildlife trade spans the tree of life, involving thousands of species and millions of individuals per year (Harfoot et al., 2018a; Scheffers et al., 2019). Effective management of wildlife trade is a necessity for human health, livelihoods, and species persistence. This management requires multifaceted processes, including population assessments, global economic investment, law enforcement, and livelihood considerations along the supply chain (Blair et al., 2017).

For over 40-years, the legal international trade in many species has been regulated by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). As a binding international agreement, CITES mandates the protection of "*wild fauna and flora against over-exploitation through international trade*" (CITES, 1973). Since 1994, CITES Parties have applied the precautionary principle (Dickson, 1999), advocating the prohibition of trade that threatens any negative impacts on species, even where there is scientific uncertainty regarding the severity of impacts (CITES, 2004). CITES lists species in two Appendices with differing constraints on trade (plus Appendix III where Parties seek cooperation to prevent unsustainable trade). Appendix I prohibits commercial trade in species threatened with extinction that are or may be affected by trade (except in special circumstances, e.g., captive breeding), while Appendix II covers species that may become threatened if trade is not appropriately managed (plus look-alikes that could be misidentified as a listed species). Where different populations of a single species face varied levels of threat from trade, they can be split-listed between Appendix I and II, aiming to prevent detriment to at-risk populations while allowing sustainable use of others.

Parties to the Convention are required to only allow the export of Appendix I and II species (or populations) after a positive Non-Detriment Finding (NDF), and only then in the volumes evidenced to be non-detrimental. There is currently no central repository nor peer-reviewed assessment of NDFs outside of Parties own scientific authorities (excluding species-specific quotas set directly by the Conference of Parties or Scientific Committees). Given that NDFs are the basis for legally trading CITES-listed species their accuracy is critical, especially since CITES trade should be sustainable and this rests predominantly on NDF's. However, some self-regulated NDFs have been criticized for lacking evidence, incorrectly affirming sustainability, and facilitating detrimental trade (Castello and Stewart, 2010). Given CITES' central role in the legal international trade, appropriate processes to prevent harmful trade are paramount.

The presence of threatened species (Vulnerable [VU], Endangered [EN], or Critically Endangered [CR], as defined by the International Union for Conservation of Nature-IUCN) in trade does not inherently equate to trade-induced threat nor unsustainable trade. However, trade in threatened species can directly drive population losses and inflate extinction risk (Morton et al., 2021). Trading threatened species can also compound concurrent non-trade threats. For instance, avifaunal species primarily threatened by deforestation suffer exacerbated population declines when exploited for the cage bird trade (Symes et al., 2018), while threatened species with inherently small populations have increased risk of stochastic extinction potentially exacerbated by harvesting for trade (Mace et al., 2008). A non-detriment finding in such cases must indicate that the removal of individuals from an already threatened population will neither further threaten that population nor exacerbate synergistic threats (Smith et al., 2011). Anecdotal evidence of trends or abundances cannot accurately forecast the impact of compounded threats, instead requiring complex consideration and offtake modelling (Foster and Vincent, 2021).

Where high levels of potentially unsustainable trade have already occurred, the Parties have previously overlooked the externalities and implications of decisions. Asian pangolin species were historically threatened by high levels of both legal and illegal trade, thus triggering their inclusion in the Review of Significant Trade (RST) process in 1988 (Challender et al., 2015b). Consequently, zero-export quotas were established for all wild-sourced Asian species in 2000 at CoP11. This reduced wild-sourced legal trade, but was ineffective at tackling the illegal trade threat. It was not until 2010 this was further addressed, and until 2016 that the Parties again paid concerted attention to both legal and illegal trade by issuing a reporting mandate for all Parties to submit data on illegal pangolin trade (Challender et al., 2015b). Similarly, when species face a multitude of threats an understanding of these is essential. The Appendix II-listed *Arapaima gigas* is concurrently threatened by habitat degradation, by-catch, and overfishing for local subsistence and aquaculture, with current populations and trends unknown (Castello and Stewart, 2010). This paucity of baseline data and the magnitude of threats led to scepticism that positive NDFs for the species were evidence based, despite its presence in international trade (Castello and Stewart, 2010), and local extirpations have occurred outside of management areas (Sinovas et al., 2017). Considering the negative externalities and interactions between trade and non-trade threats is crucial when determining offtake and policy (Cooney et al., 2021).

Understanding and effectively managing legal wildlife trade is a conservation priority and global necessity to achieve wider sustainable-use and development goals. We apply a multi-level Bayesian modelling framework to provide a data-driven assessment of patterns of threat (as defined by IUCN Red List categories) in the wild-sourced, commercial trade in CITES-listed vertebrate species between 2000 and 2018. We first hypothesise that trade volume under CITES should be dominated by non-threatened species as extinction-threatened species are less likely to demonstrate the requisite positive NDF and, where they do, it would likely be for smaller numbers of individuals. Where species populations are split-listed, we hypothesise more threatened Appendix I populations to be less likely to appear in trade and when they are, it would be in smaller volumes. Lastly, we hypothesise that proactive, precautionary trade management under CITES would be responsive to species becoming more threatened (as assessed by IUCN Red list category changes). We hypothesise this regardless of whether a Red List change was due to trade threat, since species becoming rarer due to any driver are less likely to endure the previous levels of exploitation and thus the NDF recommendation would likely be for smaller volumes than it would be absent other threats.

3.3 Results

Threatened species in trade

Birds, mammals, amphibians, and reptiles in trade are dominated by least concern (LC) species, with ten or fewer EN or CR species from each taxa present annually since 2000 (Figure 1A-D). Most species (47.6%, 488/1025) were traded for the first time as LC, with 13.7% (140/1025) classed as threatened (VU, EN, CR) when first traded (Figure 1A-D).

On average, IUCN Red List categories showed either decreasing or uncertain trends through time for probability of occurrence in trade (*hu*) and volumes when traded (*mu*) (Figure 1E – H). For birds, trade occurrence and volume of LC and NA (Not evaluated + DD categories) decreased over time (Figure 1E, Table S2), reflected in steep declines in their joint estimates (Figure 1I), whereas trade occurrence and volumes for NT, VU, EN, and CR remained stable (Figure 1E). Here, volumes were comparatively low over time (Figure 1I). For mammals, LC and VU had decreasing presence in trade through time (Figure 1F and J, Table S2), while trends for all other categories remained stable (Figure 1F) at similar volumes (Figure 1J). For amphibians, trade volumes of threatened and NA groups (Figure 1G and K, Table S2), and trade presence of EN species decreased through time (Table S2), whereas LC and NT had increasing and stable volumes in trade, respectively (Figure 1K). Similarly, CR, EN, and NA reptiles showed decreasing volume trends (Figure 1H and L). LC reptiles had increasing, and NT and VU reptiles had stable volume trends over time (Figure 1L).

These results support our hypothesis that trade under CITES is dominated by non-threatened species. Nevertheless, the presence of threatened species in trade since 2000 necessitates rigour in evidencing non-detriment, especially for those at highest risk of extinction (Morton et al., 2021). In specific instances, trade has proved an effective conservation management tool, especially where local collectors and stakeholders are incorporated as species managers (Robinson et al., 2018). Underpinned by federal regulation designating '*Threatened'* status under the US Endangered Species Act in 1987, persistent trade, monitoring, and management of American alligator (*Alligator mississippiensis*) led to increasing wild populations (currently non-threatened; LC) and large economic returns for stakeholders (J. Nickum et al., 2018). Developing sustainable use thus has the potential to protect wild populations and incentivise conservation, but this must be evidenced and enforced.

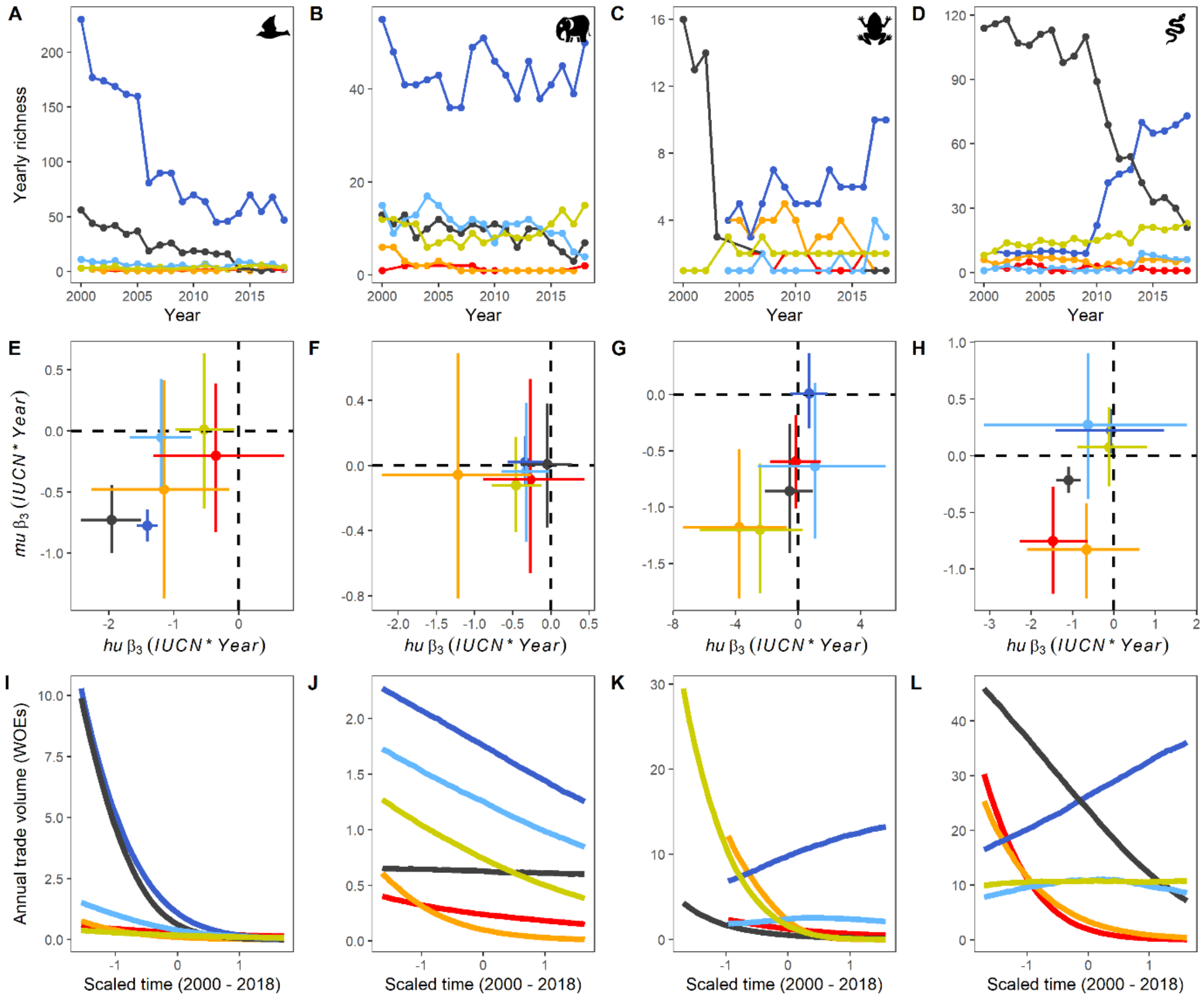

Figure 1. Summary of CITES trends through time. A- D, summary plot of traded species richness per year. E – H, slope coefficients for IUCN Red List categories through time (IUCN*Year) for *hu* (probability of occurrence in trade) and *mu* (volume when traded in WOE's – whole organism equivalent) distributional parameters. Points are medians, solid lines the 90% highest density continuous interval (HDCI), and dashed lines at 0. I – L, joint hurdle-distribution estimates of traded volume through time for the average species in whole organism equivalents (WOE's), lines show the median values. The lagged volume term was fixed at the Red List category mean per class. IUCN categories are respectively coloured dark grey (Not assessed or Data deficient - NA), red (Critically endangered - CR), orange (Endangered-EN), yellow (Vulnerable-VU), pale blue (Near-threatened-NT), and dark blue (Least concern-LC). See also Table S2.

Overall, 54.2% (504/930) of species commercially traded from a wild source that were still listed in the Appendices in 2018 had median estimated volumes below 1 in 2018, suggesting that the majority of species across taxa and IUCN categories are no longer traded. Despite the richness of CITES-traded birds since 2000, the majority of these species (76.3%, 305/401) had estimated median volumes less than 1 in 2018 (Figure 2A). Only 6.7% (27/401) of bird species were estimated to still occur in volumes >100, and only Orange-winged Amazon (*Amazona amazonica*), Red-fronted Parrot (*Poicephalus gulielmi*), and Senegal Parrot (*Poicephalus senegalus*) (0.7%, 3/401) occurred in volumes >1000, each popular in pet trade (Gonzalez, 2003; Rowan O Martin, 2018). Similarly, 42.1% of mammal species (85/202) had estimated median volumes less than 1 in 2018 (Figure 2B), but a larger proportion of species traded in higher volumes, with 13.4% (27/202) estimated in volumes >100 and 5.0% (10/202) in volumes >1000 (Figure 2B). This includes VU White-lipped Peccary (*Tayassu pecari*), whose populations are declining and threatened by a combination of subsistence and commercial hunting, deforestation, and fragmentation (Keuroghlian et al., 2013).

Despite the relatively low number of amphibian species in trade, 34.1% (15/44) are estimated in volumes >100 and three LC Malagasy *Mantella* (6.8%, 3/44) in volumes >1000 (Figure 2C). Reptiles have 42.0% of species (119/283) estimated at volumes >100 and 18.4% (52/283) in volumes >1000 (Figure 2B). Of these, 67.3% (35/52) were LC species. However, the VU Southeast Asian Box Turtle (*Cuora amboinensis*) was traded in volumes >17,000 WOE’s annually since 2000, and in 2020 was reassessed as EN due to “*widespread intensive exploitation*” for pets, food, and traditional Chinese medicine (Cota et al., 2020).

Only 19.7% of species (183/930) retained a high probability of reoccurring in recent trade (in 2018, $hu > 0.9$) and 62.3% (114/183) of these species were classed as LC. Why species appear and disappear from trade remains unclear for the majority of cases. Attempts to predict which species may be traded in the future have used phylogenetic and trait-based interpolation (e.g.,(Scheffers et al., 2019)), but linking this to real-world drivers remains a research frontier. Predicting trade volumes is an even greater challenge, particularly considering future unknowns – including zero quotas, sudden novel demand, economic development, and societal change, all occurring across regional to international scales (Nijman and Nekaris, 2017).

Across taxa, on average LC species had the highest median volumes (except in birds). LC mammal and amphibian species were traded in substantially higher volumes than CR, EN, or VU species (Table S3, Figure 2F and G), while LC reptile species were traded in substantially higher volumes than CR and EN species (Table S3, Figure 2H). Volumes traded for birds remained low across all Red-list categories (Table S3). These results (Figure 1 and 2) suggest that non-threatened species dominate CITES trade in richness, reoccurrence, and volume.

The low reoccurrence and volume of most species in trade could result from at least three starkly contrasting drivers. First, altered supply of species owing to overexploitation and reduced accessibility; for instance, in southern Sumatra, extensive field surveys revealed several threatened, sought-after species for the cagebird trade were depleted across a remoteness gradient (Harris et al., 2017). Second, changing demand, where preferences drive changes in demand; for example, songbird ownership in Java has seen a decadal shift to non-native species (H. Marshall et al., 2020a). Third, effective national or international legislative protection can remove or limit trade, such as the EU wild-caught bird import ban (Cardador et al., 2019) – although such approaches often do not stop trade entirely and may shift global trade patterns (both spatially and to illicit forms) (Reino et al., 2017). Trade will be further influenced by other interconnected regional to international factors, such as supply and demand infrastructure, economic development, and social change.

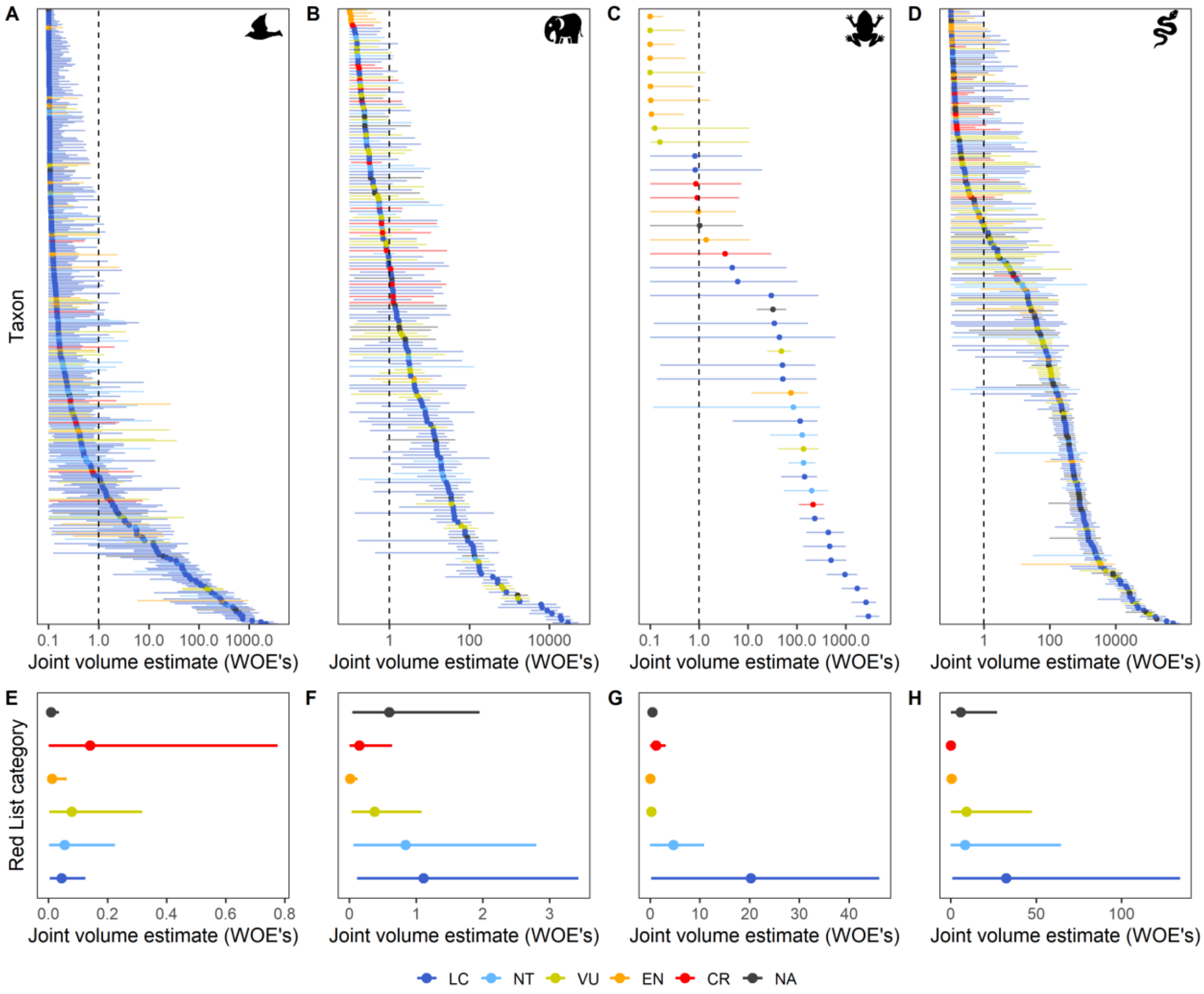

Figure 2. Estimated volumes in trade across both species and Red-list categories. A – D provide species-level joint distributional estimates for all CITES-traded species in 2018 for bird (A, n = 401), mammal (B, n = 202), amphibian (C, n = 44), and reptile (D, n = 283) species, respectively. An adjustment of 0.1 was added to the entire posterior to aid visualisation of species estimated at volumes approaching 0. E-H show joint distributional volume estimates in WOE's for each Red List category in 2018, excluding species-level variability, for birds, mammals, amphibians and reptiles respectively. Red List category is coloured dark grey (Not assessed or Data Deficient - NA), red (Critically endangered - CR), orange (Endangered-EN), yellow (Vulnerable-VU), light blue (Near threatened-NT), and dark blue (Least concern-LC), respectively. Points denote median volumes and lines the 90% HDCI. See also Table S2.

Managing differentially threatened populations

Split-listed species represent some of the most charismatic megafauna traded, including Southern white rhinoceros (*Ceratotherium s. simum*), African lion (*Panthera leo*), African elephant (*Loxodonta africana*), and Nile crocodile (*Crocodylus niloticus*). For all nine split-listed species evaluated, estimated median traded volumes for the Appendix I populations were lower than for Appendix II populations in 2018 (Figure 5A, *median difference* = -16.11, 90% HDCI: -63.77 to -0.91, *pd* = 99.90%). For crocodilian species, this difference in volume was at least three orders of magnitude (Figure 3A). Overall, Appendix I and Appendix II populations show stable trends through time in probability of trade occurrence (Figure 3A and C) and volume when traded (Figure 3B and C). However, Appendix I populations retained median probabilities of reoccurrence less than 0.16, whereas Appendix II populations always had a probability greater than 0.99. In 2018, Appendix I populations are estimated to be 92% (90% HDCI -1.00 to -0.79, *pd* = 99.83%) less likely to be present in trade.

This indicates threatened populations of split-listed species are less likely to be traded plus likely to be traded in lower volumes. Split-listing has clear potential to achieve synergistic benefits, protecting at-risk populations while providing livelihood benefits and legal supply (Lewis, 2009). Robust mechanisms are needed to differentiate between populations of a species in trade, and traceability is complex to guarantee and enforce (Bauer et al., 2018; Doukakis et al., 2009). Therefore, while split-listing suggests CITES policy can provide population-specific protection and management, the tools and infrastructure to identify individuals to specific populations are absent for many taxa. Species can have populations that are better or worse suited to utilisation (including split-listed species), but for the vast majority of species spatial variation in suitability for harvesting between populations is not considered. Thus, relatively common species could experience local extirpations if smaller declining populations are overexploited, even if their global population trends are stable (Marsh et al., 2021). Considerations of the resilience of individual populations of species through space and time remains a research and policy frontier. By including only species that were wild-sourced and commercially traded at least once in both Appendices during our timeframe, we exclude certain split-listed species (e.g. *Vicugna vicugna*) only traded under Appendix II (thus the more threatened Appendix I populations were not traded at all) (Lewis, 2009), suggesting that the effectiveness of split listing may be even greater.

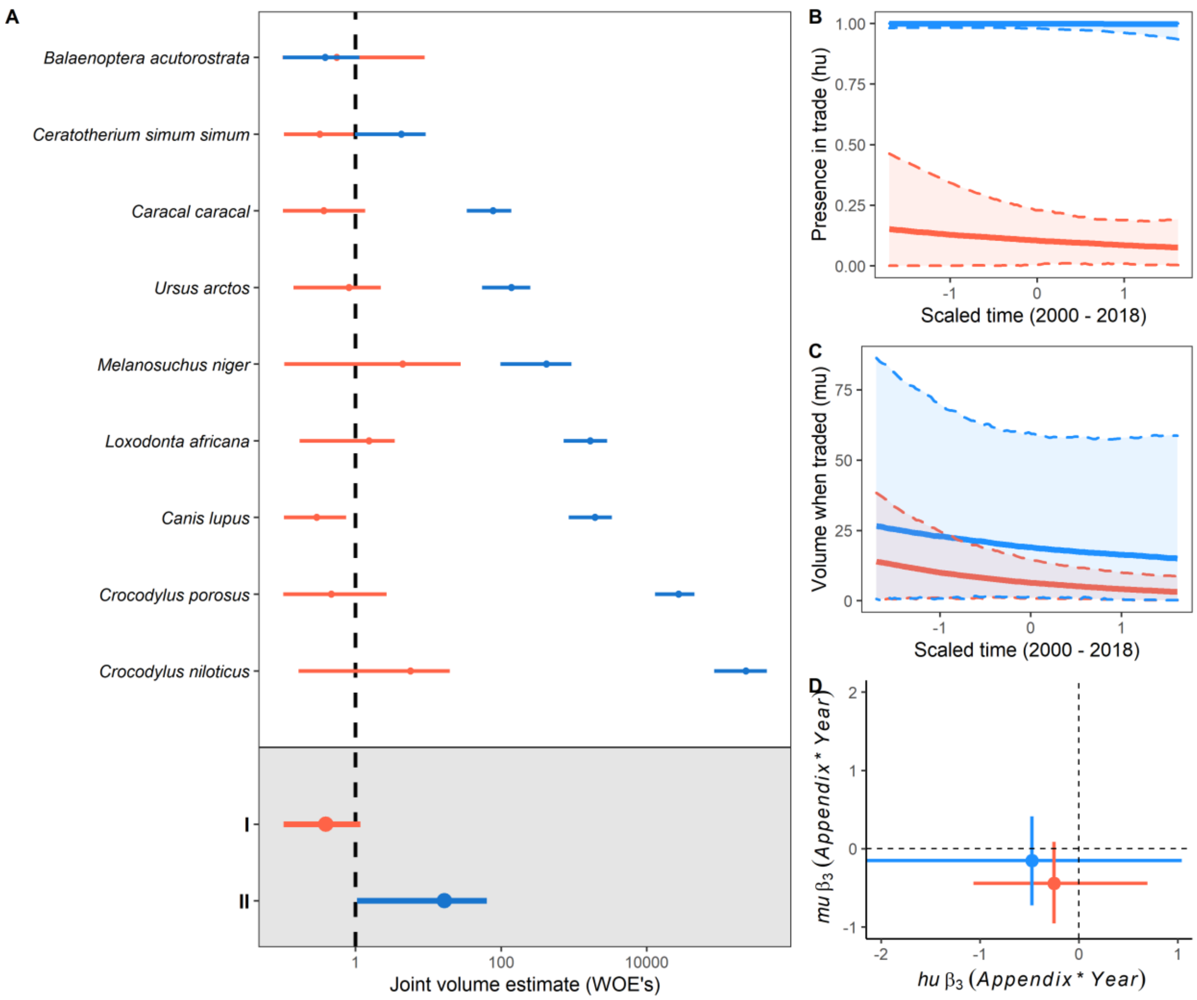

Figure 3. Effect of split listing species populations. A. Joint distributional volume estimates per listing for each split listed species in 2018. Grey lower panel shows population-level estimates for Appendix I (red) and II (blue) groups, excluding species-level variability. Points are medians and the interval is the 90% HDCI. The x-axis on a $\log_{10}$ scale for clarity (an adjustment of 0.1 was added to the entire posterior to aid visualisation of species estimated at volumes approaching 0), the dashed line shows a yearly volume of 1 WOE. B. Estimated probabilities of occurring in trade (*hu*) through time for Appendix I and II listed populations. C. Estimated volumes when traded (*mu*) through time for Appendix I and II listed populations. D. Population-level slope coefficients for populations listed in Appendix I and II through time (Appendix*Year) for both *hu* (probability of being traded) and *mu* (volume when traded) distributional parameters.

CITES response to changing extinction risk

The final key step in examining CITES-listed trade considers whether trade responds to changes in IUCN Red List categories. Species change Red List category to reflect updated knowledge of populations, threats, or previous errors. Between 2000 and 2018, 395 wild-sourced species commercially traded under CITES changed or were given their first Red List assessment, equating to 432 species-level category changes (35 species changed Red List category more than once). There was substantial variation in volumes traded pre- to post-change in Red List category (Figure 4A – H). However, contrary to our hypothesis that species would be less likely to reoccur or occur in smaller volumes after becoming threatened, changes in volume were not broadly associated with changes in Red List category, irrespective of change type, and individual species responses varied greatly (Figure 4A - D).

On average, only birds and reptiles revealed any pre- to post-changes in volume, with birds that became non-threatened slightly increasing in volume (median difference = 0.3, 90% HDCI: 0.0 to 0.7, *pd* = 99.84%) and reptiles that became threatened decreasing in volume (median difference = -8.0, 90% HDCI: -32.6 to -0.11, *pd* = 99.76%) (Figure S1A-D and Table S4). Similarly, there was limited evidence that changing category relative to species that did not change category led to a difference in volume for the average species (Figure S1E-H and Table S4). Birds that became non-threatened were estimated to reappear in higher volumes than those that did not change (Table S4). Mammals and reptiles that stayed threatened and amphibians that stayed non-threatened or became threatened were estimated to be traded in lower volumes in 2018 than those that did not change category (Table S4).

Of individual Red List category changes, 45.8% (198/432) showed minimal change in traded volume pre- to post-change (-1 < median difference < 1, clustered on the dashed zero lines in Figure 4). This can largely be attributed to 31.0% of changes (134/432) having a median pre- and post-change volume of < 1, suggesting the species presence in trade had already declined to near zero before an Red List category change (stopped being traded) or while CITES-listed had not yet been traded. Also contributing to the apparent lack of change in volumes are species that remained traded at similar volumes pre- to post-change. For instance, Madagascar Big-headed Turtle (*Erymnochelys madagascariensis*) had no identifiable change in volume after a reassessment from EN to CR in 2008 (median difference = -0.23 90% HDCI: -23.7 to 22.6). Similarly, Saker falcon (*Falco cherrug*) remained traded in the hundreds (median difference = 273.8, 90% HDCI: -261.4 to 936.6) following reassessment from LC to EN in 2004 with “*inadequately controlled capture for the falconry trade*” given as explanation for the reassessment (BirdLife International, 2004). As hypothesised for many species that became or stayed non-threatened, there was no change in volumes post-change. For example, after Northern red-shouldered macaw (*Diopsittaca nobilis*) was first assessed in 2014 (as LC) it remained traded in the hundreds (median difference = 225.3, 90% HDCI: -207.7 to 749.3) with trade not considered to be a threat (Birdlife International, 2016a; Herrera and Hennessey, 2007).

In 2.7% (12/432) of species-level changes, volumes fell pre- to post-change (negative lower and upper 90% HDCI bounds). For example, Grey parrot (*Psittacus erithacus)* median volumes decreased by 3588.3 (90% HDCI: -8419.9 to -437.7) after reassessment from VU to EN in 2016. Conversely, only 2.1% (9/432) of species-level changes were associated with increased volumes, the majority of which had stayed or became non-threatened. For instance, Common long-tailed macaque (*Macaca fascicularis*) volumes increased sharply immediately after reassessment from NT to LC in 2008 (difference = 2833.4, 90% HDCI: 430.0 to 6696.7). Volumes have since decreased, with the species reassessed in 2020 as VU owing to declines from hunting (local consumption) and extraction for international trade (taken for breeding or directly exported) (Eudey et al., 2020).

It is important to consider both these static changes in volumes pre- to post-change, with the associated changes in volume and occurrence trends through time (Wauchope et al., 2020). Such an approach is necessary as volumes may remain constant just after a change, but there may be longer-term changes in volumes through time, e.g., post-change the volumes may gradually decrease. We considered these trend differences in both presence (*hu*) and volume (*mu*) using species-level trend coefficients. Only five species category changes (1.2%) displayed negative occurrence-trend (*hu*) differences (90% HDCI below zero), i.e., a species is decreasing in occurrence probability more rapidly post- than pre-change (Figure 4E – H). Thirty-eight species (8.8%) had substantial positive difference in occurrence trends (HDCI above zero), suggesting species presence trends were more positive after a change than before. For example, although Golden mantella (*Mantella aurantiaca*) decreased substantially in traded volume when reassessed from VU to CR, it shifted from a declining occurrence trend pre-change to an increasing trend post-change. Care must be taken with interpretation where species-level reoccurrences asymptotically approach either 0 or 1 e.g. a pre-change trend towards zero (negative trend), and a post-change trend asymptotic with zero (flat trend), would also have a positive trend difference (post-change trend – pre-change trend), hence trend changes must be cross-referenced with the absolute values. Only 0.4%

(2/432) of species saw negative volume trend-differences, i.e., volumes falling faster post- than pre-change. For Southern lechwe (*Kobus lechwe*), volumes were low (<100 WOE's year^{-1}) and stable prior to reassessment from NT to LC in 2008, but immediately post-change volumes peaked in the hundreds then rapidly fell. Conversely, 2.7% of species (12/432) had positive volume-trend differences suggesting volumes increased at a faster rate post-change; in all but one case (VU to NT), the move was from not assessed to LC or NT.

Recently, numerous species have been reassessed by the IUCN into a higher threat categories with trade given as justification following rigorous assessment of species populations or threats and open-access, peer-review (Birdlife International, 2018, 2016b). Despite IUCN assessments reflecting changing trade impacts, we find an unclear response from CITES. NDFs are not publically available, in part owing to a lack of central data-basing (excluding 36 NDFs and 29 NDF Guidelines), making it impossible to scrutinise the evidence or methods used in creating an NDF. Updating NDFs in light of changing threats or population trends is a key step for proactive trade management. Crucially, this could reduce the risk that species highly threatened by anthropogenic stressors are additionally traded and suffer subsequent Allee effects or stochastic extinction. For example, vulture species critically endangered by poisoning are still being traded (Mateo-Tomás and López-Bao, 2020). Well-managed trade in threatened species is crucial to long-term conservation goals, making sharing and building on successful NDF approaches of utmost importance (Aylesworth et al., 2020; Foster and Vincent, 2021).

Our analyses are limited to the legal wild-sourced commercial trade, which is regulated, quantified, and aims to promote sustainable use. However, this represents only a fraction of trade, overlooking all illicit international trading and all legal or illegal within-country trade. Patterns of threat in illegal trade could plausibly run opposite to the patterns we find in legal trade (Courchamp et al., 2006). The same could be true for captive trade, as the general volume and presence decline across species in the wild-sourced trade (Figure 1) could be indicative of a shift to captive sources, as found in previous studies (Harfoot et al., 2018a).

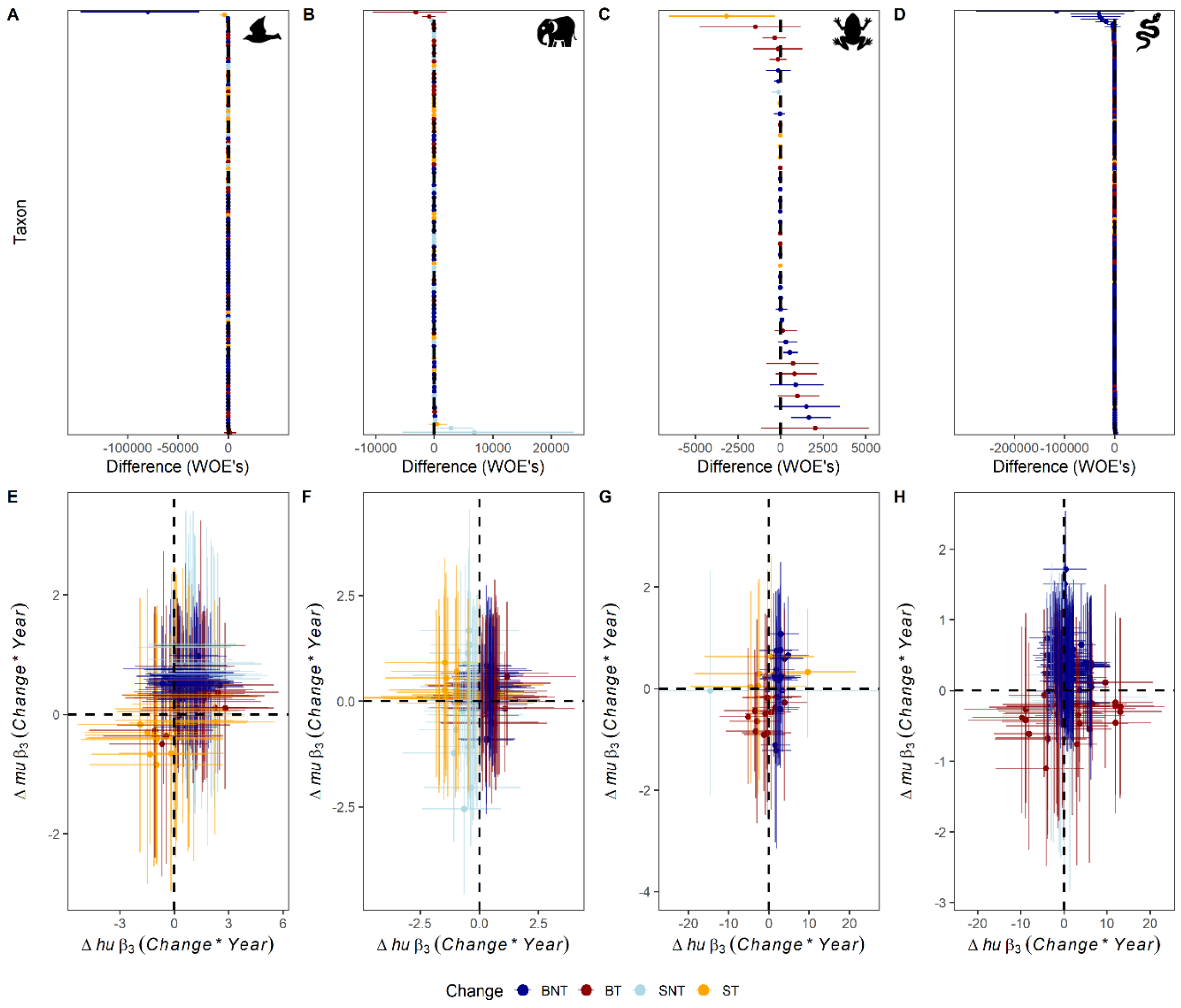

Figure 4. Differences in trends and volumes pre- to post Red List category change. A – D. Species-level estimated volume differences 1-year pre- to 1-year post-change. Each point represents a species-level change for birds (n = 127), mammals (n = 103), amphibians (n = 39), and reptiles (n = 163) respectively. Negative values denote an estimated decrease in traded volume pre- to post-change, vice versa for positive values. E – H. Difference in species-level slope coefficients (Change*Year) pre- to post-change per change for both *hu* and *mu* distributional parameters. Negative values denote the change is associated with a decreasing trend (for *mu* – decreasing volume, for *hu* – decreasing presence) through time relative to the species prior category trend, vice versa for positive values. Points are posterior medians, error bars the 90% HDCI per point and legend acronyms are as follows: BNT - became non-threatened, SNT - stayed non-threatened, BT- became threatened, and ST - stayed threatened. Points along the dashed lines denote no difference in *hu* or *mu* trends, or joint distributional volume estimates. See also Table S4

3.4 Discussion

Implications for CITES-regulated trade

Our study highlights that less-threatened species, including split-listed Appendix II populations, dominate CITES trade in richness, occurrence, and volume. However, we find limited evidence that when individual species became or remained threatened they were less likely to appear in future trade or be traded at lower volumes. Legal trade in threatened species places considerable onus on the accuracy and robustness of the CITES NDF procedure. A process that has been effectively used to bolster conservation efforts and species recovery (e.g. for Southern white rhino (Amin et al., 2006) and American alligator (J. Nickum et al., 2018)), but has also been plagued with controversy concerning its rigour and transparency (Castello and Stewart, 2010; Cohen et al., 2020; Nijman, 2015). Since 2008, Thailand has been subject to a CITES Review of Significant Trade (RST), where the NDF's have been queried for four heavily exported seahorse species to assess whether such export was evidenced as non-detrimental. Ultimately, Thailand was unable to produce positive NDF's for the species (Aylesworth et al., 2020) and their trade was classed as "*urgent concern*" by the CITES Animal Committee (CITES, 2014). Compounding the validity of NDF's is whether they exist at all. Work examining African rosewood (*Pterocarpus erinaceus*) trade from Ghana found no up-to-date scientific NDF, despite this species' presence in trade – a non-compliance issue in clear contradiction of the Convention (Dumenu, 2019).

A 2020 CITES Report of the Secretariat on Non-detriment Findings examined the 36 publically available NDFs, concluding standards vary greatly (CITES, 2020b). Only 44% (16/36) fully considered non-trade threats and the overall threats to species, 42% (15/36) considered species-specific biology or life-history factors influencing their vulnerability, 36% (13/36) clearly considered the precautionary principle, and just 17% (6/36) fully considered historical and current patterns of harvest and mortality. A single NDF considered the role of the species in the ecosystem, and no NDF's reached three or more robustness targets ("*good*" data, multiple indicators, triangulation, or peer-review/stakeholder consultation). Given this and our results, we urgently call for greater transparency and gradual transition to publishing all NDFs.

Processes such as the RST exist to identify and respond to species/populations at risk of unsustainable CITES trade, but this makes two problematic assumptions: 1) that unsustainable trade can be recognized by other Parties; and 2) acting *after* trade has occurred is an appropriate response. Discerning unsustainable or ecologically harmful trade from trade data alone (i.e., independent of population-level data) is almost impossible, yet that is the main data source used to identify species for the RST (UNEP-WCMC, 2020). We posit that unsustainable offtake for trade should be recognized *prior* to its occurrence. This could be achieved through a review of NDF documents confirming the analyses include robust evidence, demonstrate that relevant ecological information was used, and ultimately justify offtakes appropriate to ensure species survival. Open-access NDF's would be a step closer to this. There are clear logistical challenges, primarily that under the current Convention there is no provision for making NDF data, methods, or results available and any change would require a considerable amendment to the Convention text. Similarly, there are risks to sharing species data openly, but geographic data can be anonymized (Nguyen et al., 2019). Additionally, there are major challenges to sourcing the necessary expertise and finances to perform NDF reviews. Reviewers could potentially be found within the research community or Scientific Authorities of other Parties, but acquiring the funding and standardising the process would be non-trivial. While ideally the process would be managed within individual Parties, the initialisation and oversight would need to come via the Animal and Plant Committees. Given the challenges, we suggest this would be developed gradually, starting initially with sharing and reviewing methods, and culminating in results being open access. As individual Parties have autonomy to implement the Convention and make NDFs as they see appropriate, the review would represent a judgement of the validity of an NDF, flagging where it is inaccurate. Exporting Parties could appeal with evidence if they believed the review was in error, and in such cases decisions to sanction or not could come from a panel from the Animal and Plants Committees. Any trade undertaken by a Party that was justified by an inaccurate NDF could then be viewed in breach of the Convention (lack of a valid NDF) and subject to follow-up action including sanctions. However, initially these reviews would be used to build capacity and develop consistent methods; trade could be allowed under inaccurate NDFs for a set number of years while processes and methods were fully developed.

Making space for controversy and debate

Wildlife trade science is diverse. It spans those focusing on protecting species from overexploitation to those working to ensure continued livelihoods. From researchers utilising large quantitative datasets to those using qualitative evidence. And from independently supported researchers to those at least in part supported by the trade industry (e.g., the luxury fashion industry (Natusch et al., 2021)), with associated risks of the "science for profit" model (Legg et al., 2021), or by animal welfare groups and their potentially anti-trade stance. Such a diversity of researchers offers great potential to overcome one of the greatest challenges faced by biodiversity and humanity – how to deliver sustainable offtake that protects species whilst delivering on societal needs. At present, this diversity has resulted in increasingly entrenched and polarised viewpoints about how to assess and manage wildlife trade.

Some of the approaches, recommendations, and discussion points we highlight contradict the opinions of others, in particular our integration and interpretation of the IUCN Red List with CITES trade data, and the suggestion of reforms to CITES NDF policies. We have emphasised that threatened species (VU, EN, or CR) can appear in wild-sourced trade and not be threatened as a result. However, we need greater consideration of how concurrent threats to species are considered. It is robustly evidenced that habitat loss and extraction (for trade or consumption) (Romero-Muñoz et al., 2020, 2019; Symes et al., 2018), and climate change and extraction (Chen et al., 2015) can drive synergistic declines in target species. There is a need to evidence, not assume, that exploiting a species for which trade is not the primary driver of loss will not *further* contribute to declines. This is embodied in the Text of the Convention *"Trade in specimens ... must be subject to particularly strict regulation in order not to endanger further their survival"* (CITES, 1973).

It has become common to see examples of species benefiting from legal trade (predominantly of large, commercialised reptiles) (Joanen et al., 2021; Natusch et al., 2016) held up as counterpoints to the risk of unsustainability and thus the need for regulatory reforms. Sustainability must be evidenced; an example from a different species (or indeed Class) merely highlights that for most species there is no available evidence of benefits or declines (Morton et al., 2021). The precautionary principle mandates caution in the absence of evidence.

Reforms to CITES are not a new phenomenon (for examples see (Challender et al., 2015b; Frank and Wilcove, 2019; Rivera et al., 2021)), but reforms or amendments take time to disseminate and enforce. The Bonn and Gaborone amendments were proposed in 1979 and 1983, respectively, but currently are only accepted by 149 and 102 of the 183 Parties, respectively. An amendment requiring Parties to submit the methods and results of all NDF's would be complicated and controversial. But the mere fact that the Review of Significant Trade (RST) process has uncovered instances of detrimental trade and missing NDFs highlights that assuming these documents are robust and up to date is insufficient (Dumenu, 2019; Foster and Vincent, 2021). The logistical and political difficulties of implementing change should not censure criticism of regulatory processes nor debate of the status quo. Rather, it should offer space for constructive collaboration across the diversity of wildlife trade scientists to ensure that Parties to CITES deliver on its mission.

Conclusions

The dynamic nature of international wildlife trade and the huge diversity of species involved necessitates a nuanced consideration of trade. While we apply novel analytical methods and indicators to find that CITES trade is dominated by non-threatened species, with unclear responses in trade to changing species threat category, this is no substitute for transparent, accurate, and up-to-date NDF procedures evidencing the population-level effects of trade for all species. Indeed, trade can promote species recovery (J. Nickum et al., 2018), but this cannot be assumed *a priori* for all species without data-driven justification – conservation outcomes must be evidenced to avoid compounding species extinction risk.

3.5 Acknowledgements

We thank Simon Mills for methodological advice, members of the IUCN Red List Unit Cambridge, CITES, and the UNEP-WCMC for responding to our queries so helpfully, and to Mark Auliya and three anonymous reviewers whose comments enhanced this manuscript.

3.6 Author contributions

O.M, B.R.S, T.H and D.P.E. conceived the study idea; O.M collated the data; O.M. analyzed the data and produced the figures with input from B.R.S, T.H and D.P.E; and O.M. wrote the first draft of the manuscript, with all co-authors substantially contributing to revisions.

3.7 STAR Methods

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Oscar Morton (omorton1@sheffield.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

All data used in this analysis are from publically available sources and no new datasets are generated. Code to reproduce the analysis have been deposited in a freely available institutional repository (10.15131/shef.data.17151449) available upon publication. Any additional information is available from the lead contact upon request.

Experimental model and subject details

CITES data extraction

The CITES Trade database stores all reported wildlife trade (exports and imports) by CITES Parties. These reports are compiled in official annual reports and deposited in the CITES Trade Database. All deposited records were downloaded in bulk (version 2020.1, https://trade.cites.org/), which resulted in a database with 21,635,430 unidirectional trade records. Comprehensive detail of the data structure can be found at the point of access.
We follow established protocols for cleaning and preparing the data (Harfoot et al., 2018a; Robinson and Sinovas, 2018). For a full summary of the data curation pipeline see Table S1. In summary, all re-exports were removed to avoid double counting (keeping only original exports, where the exporter matches the recorded origin), because where trades ultimately pass through multiple countries they may be reported multiple times artificially inflating their presence in the data. Similarly, we focused only on exporter-reported values as it is known that import permits are not required for Appendix II species and as such can lead to underreported figures for these species if trade is not reported (Robinson and Sinovas, 2018). However, there is not one (‘correct’) standardised approach to analysing CITES trade data, and using only exports could be viewed as an overestimation if some records reflect granted

permits, but not realised trade. Therefore, we include a complete re-analysis of all hypotheses using import data (processed identically to the export data). In the supplementary methods we present all main text figures replicated using importer-based values and all supplementary results tables are marked (*, **, etc.) where values differ to those from the exporter-based data. We find no systematic differences between the datasets that affect our overall conclusions.

We also removed all records where species were not traded under any specific Appendix (I, II or III), coded "N". All trades were classed as either wild-sourced or not, using the reported "Source" codes. We follow established criteria and only assign records as wild-sourced where the source code is W, X or R (this respectively includes "Specimens taken from the wild", "Specimens taken in the marine environment not under the jurisdiction of any State", and "Ranched specimens: specimens of animals reared in a controlled environment, taken as eggs or juveniles from the wild, where they would otherwise have had a very low probability of surviving to adulthood") (Harfoot et al., 2018b). Records listed as "U" (Unknown) or [Blank] could also refer to wild sourced records. However, they may also refer to records sourced from non-wild sources but lacking documentation. Retrospectively, we cannot know with certainty the reasons enforcement officers around the globe recorded these thus they are also excluded. All subsequent analyses focus solely on these wild-sourced trade records. Records with a source code of C, D, A, F, I, O, U or [Blank], were all excluded at this point. Similarly, as species are traded through CITES for a range of reasons including scientific research and reintroduction, we focus only on trade reported as being for a commercial or personal purpose (purpose codes 'T' and 'P'), which we subsequently term commercial. We include personal following previous studies to potentially capture wild-sourced pet trades (Bush et al., 2014). As a result, we exclude the codes B, E, G, H, L, M, N, Q, S, Z or [Blank]. Some commercial movements may potentially be excluded under the medical code (M) or the circus trade (Q), but equally these codes can represent non-commercial trades. Due to this uncertainty, M and Q are excluded. Therefore, all subsequent reference to the data or trade data is in reference to only the wild-sourced and commercially traded records. We limit our time frame to 2000 – 2018 to best understand recent trade. Despite data being present in the CITES data for up to 2021 we conservatively only include records up to and including 2018.

Trade quantities are reported in many “Terms” (teeth, skulls, skin fragments, carvings etc.), which make comparisons of “Quantity” misleading. For example, four skulls represent four individuals, but four small leather pieces or four teeth could represent anything from one to four individuals. Therefore, all records were standardised to whole organism equivalents (WOE’s) following the methodologies outlined by (Harfoot et al., 2018a). This allows a more robust comparison across trade records as one WOE represents one individual, regardless of taxa or original term. Building on a published WOE conversion protocol (Harfoot et al., 2018a), we use their published vertebrate conversion factors and add five additional terms which each denote 1 WOE (gall bladder, eggs, eggs (live), specimen and trunk). We applied this conversion protocol to records where the “Unit” term was specified as *NA* denoting “number of specimens”. Records are reported in various other “Unit” terms including bags, bottles, flasks, kilograms, cubic feet, sets, etc. but reconciling this unit diversity remains a research frontier. In total 19.67% of vertebrate records could not be converted to WOE’s. These unconvertable records were removed. We then further focused on bird, mammal, amphibian and reptilian trade data from 2000 – 2018 and removed all records where species were reported as clearly unknown such as *Falco* spp. or *Felis* spp.

Species presence in trade is highly variable with some species being traded consistently each year (2000 – 2018) and others only being traded certain years. This can be attributed to two distinct processes: 1) the species may not have been (reported) in trade that year; or 2) the species was not formally CITES listed prior to (or after) a particular date and as such its trade was not recorded. We cross-referenced the historical CITES listings, which record the year individual species, genera, families, or orders are listed, and matched this information to the processed CITES trade data. Species were marked as absent from trade (a traded volume of 0) if they were not recorded traded but were CITES listed in that year, while species that were added to CITES, deleted from CITES, or added, deleted, and added again to the Appendices have shorter time series. For example, if a species was recorded in trade from 2010, but was listed in 2003, we record that species’ time series as beginning in 2003 (not 2000), its traded volume being 0 for the years 2003 – 2009, and then the reported trade volume from 2010 onwards.

Method details

IUCN data

We obtained IUCN assessments (including all historical assessments) for all wild-sourced commercially trade terrestrial vertebrates (2000 – 2018) using the "*rredlist*" package. We converted pre-2000 codes (lr/cd/nt) and removed all other older notations (such as "*rare*" or "*CT*", commercially threatened) as more recent assessments before 2000 had been done. The pre-2000 codes were converted were converted thusly "lr" (least concern), "cd" (near-threatened) and "nt" (near-threatened). All species that were returned as not assessed were checked manually for spelling conventions, synonym use or older classification style. Species that had genuinely not been assessed or had been taxonomically split were included as not assessed. As the IUCN assessment data includes the year the assessment was published, species that were in trade preceding a full IUCN assessment were coded as Not evaluated until the year their assessment was published. We also grouped assessments that concluded a species was Data deficient (DD) with the Not evaluated species as a DD finding infers that there was inadequate information to make an assessment and subsequently refer to this group as "Not assessed". All species assessments were read in full as part of this process.

We removed one Extinct species (*Chelonoidis niger*) as a likely misidentification, as assessments of wild and captive populations show all individuals have <80% of the *Chelonoidis niger* genome. We removed one Extinct in the Wild (EW) species (*Oryx dammah* – only 4 records). The records may have been listed as not bred in captivity if the captive breeding did not meet the stringent requirements for CITES classification as bred in captivity. We also removed all instances where species were identified as hybrids such as "*Felis* hybrid" or "*Bison* hybrid" (8 different hybrid types were removed). The reviewed database of species assessments through time were then incorporated into our database of wild-sourced commercial CITES trade, giving a database of species traded volumes (WOEs) and presence in trade through time with up to date IUCN assessment (LC, NT, VU, EN, CR and Not assessed) data for each year. Of the 1053 taxa present in the data, 491 were first traded as LC, 71 as NT, 83 as VU, 36 as EN, 26 as CR and 346 were either not evaluated/recognized or assessed as DD (1025/1053 could be included in the final models, species were lost where they could be resolved for inclusion in the phylogenetic matrices, see Table S1). All references to threat categories made in the main text are solely based on the IUCN Red List, i.e., Endangered refers to the Red List category not species classed under the US Endangered Species Act or other authority. Similarly, we explicitly use the terms threatened to describe species assessed as Vulnerable, Endangered or Critically Endangered by the IUCN Red List, and non-threatened to include species assessed as Least Concern or Near-threatened.

To examine whether trade presence is responsive to perceived changes in species threatened categories, we assessed the difference between species preceding presence and subsequent presence. IUCN changes were modelled with 6 levels, no-change i.e. species that did not change categories at all, pre-change i.e. for species that do change the time period preceding the first change, (changed but) stayed threatened i.e. EN to CR, (changed but) stayed non-threatened i.e. NT to LC, (changed and) became threatened i.e. LC to VU and (changed and) became non-threatened i.e. EN to NT. We considered that when species not assessed or assessed as DD by the IUCN were in trade and then changed or were assessed for the first time this change could either be became threatened (i.e. DD to VU or not assessed to VU) or became non-threatened (i.e. DD to LC or not assessed to NT). We classed a species transition from Not evaluated to DD as ‘No-change’ as this still infers that there was inadequate information to make a full assessment. However, we removed the three species that transitioned from an assessed state (LC, NT, VU, EN or CR) to DD from this analysis, as this cannot be classed as a change in perceived threat. In total 113 birds (127 unique changes), 87 mammals (103 unique changes), 33 amphibians (39 unique changes) and 162 reptiles (163 unique changes) changed or was assessed for the first time between 2000 and 2018 (totalling 395 species and 432 changes). Of the 127 changes in birds, 62 became non-threatened, 26 became threatened, 18 changed but stayed non-threatened and 21 changed but stayed threatened. Of the 103 changes in mammals, 33 became non-threatened, 24 became threatened, 29 changed but stayed non-threatened and 17 changed but stayed threatened. Of the 39 changes in amphibians, 19 became non-threatened, 13 became threatened, 1 changed but stayed non-threatened and 6 changed but stayed threatened. Of the 163 changes in reptiles, 119 became non-threatened, 33 became threatened, and 11 changed but stayed threatened. In total, 1000 species (including those classed as “No change”) could be included in the final models, species were lost where they could be resolved for inclusion in the phylogenetic matrices and where species changed status to DD or only had 1 year of trade data pre- or post-change, see Table S1. In the supplementary information, we present the methods and results of a simplified analysis considering simply where species ‘Increase’ or ‘Decrease’ in extinction risk, crucially these results do not contradict our main text analysis.

We hypothesise that becoming threatened would lead to a decrease in trade presence in some cases and more often a reduction in volume relative to the preceding state and vice versa for becoming non-threatened. We hypothesised there to be a weak or null effect of staying threatened or non-threatened relative to a species previous state. This approach allowed us to infer multiple changes in a single species relative to that species preceding state. For example, a species could be pre-change (2000 – 2009), stay non-threatened (2010 – 2014) and become threatened (2015 – 2018). Here we would assess the two changes relative to the preceding (pre-change – to staying non-threatened and then staying non-threatened to becoming threatened). We did not centre each species time-series change year to the year zero, as numerous species changed category multiple times.

CITES split-listing

All species reported in trade in >1 CITES Appendix in the processed wild-sourced commercially traded CITES database were subsetted, as potentially being split listed. Each species in this subset was then manually checked to confirm its split listed status via the historic CITES listings data portal (https://checklist.cites.org/#/en). Species appearing in two Appendices because they had reservations taken out by member parties were excluded, this occurs when a party declares it will not be bound by the Convention for trade concerning a given species. Although parties with active reservations are treated as non-member states with regard to that species, such species could appear in multiple Appendices if they were an Appendix I species and the party with a reservation agreed to report trade as if the species was listed in Appendix II. A small number of species were also listed in multiple Appendices with no explanation or reason found in the historic listings and such species were also excluded. This checking process resulted in the inclusion of time series for explicitly split-listed species traded at least once in both Appendices at least once since 2000 (9 species). We summed WOE’s, per species, per Appendix for the timeframe each species was both split-listed and CITES listed.

Limitations of the CITES trade data

All analyses using CITES data could be subject to unknown reporting errors, unfulfilled permits or trades reported in the subsequent year (Robinson and Sinovas, 2018). Here we attempt to standardize the data and our approach to get as wider picture of trade while ensuring accuracy. By converting the data to WOE’s, following established methods (Harfoot et al., 2018a), we standardise a wide variety of the terms used by CITES Parties and the final data values represent number of individual animals. However, a great many terms and units cannot be converted unavoidably meaning we do fail to capture some reported trade.

Similarly, data-handling choices have the potential to unintentionally bias the interpretation of trade data. Rather than attempt to reconcile importer and exporter reported values as a single "true" value, we present the exporter reported analysis results in the main text and in the supplement we provide the importer reported analysis results (Table S2-4, Figure S2 and 3).

Quantification and statistical analysis

Data analyses

All trade data was modelled in a Bayesian framework. This approach was selected due to the high number of individual species, the need to incorporate the known phylogenetic signal of species threatened category with multiple observations (González-del-Pliego et al., 2019; Jetz and Freckleton, 2015) and to allow derived difference calculations of the posterior. We included species phylogenetic relatedness in our models due to the sheer number of species traded, as these are not truly independent units as they come from the same phylogenetic tree. Thus, the dependency between species should be considered. Conventionally applied phylogenetic least squares (PGLS) analyses of the type implemented in the "*caper"* package (Orme et al., 2018) do not handle repeated measurements per species (i.e. trade presence for a given species across a number of years) or the additional inclusion of taxon as an independent group effect. Multiple Bayesian packages have since been developed to accommodate this (Bürkner, 2017; Hadfield, 2010). Accordingly, all phylogenetic multilevel models were implemented using the "*brms*" package (Bürkner, 2017).

The amphibian, avian (Ericson) and mammalian phylogenies of species in our database were generated from 250 sampled trees which were then used to generate a consensus tree (phylogenies available from http://vertlife.org/phylosubsets/ see also (Jetz et al., 2012; Jetz and Pyron, 2018; Upham et al., 2019)). A reptile phylogeny of the species traded was sourced from http://timetree.org/ (Kumar et al., 2017). The phylogenetic correlation matrices (where diagonal elements are equal to 1 (de Villemereuil and Nakagawa, 2014)) for each class were computed using the *"ape"* package (Paradis and Schliep, 2019). A small number of reptilian species names could not be resolved and could not be included in subsequent analyses (detailed in Table S1). The taxonomic species names listed in the Appendices were conserved throughout the data pipeline. Where the CITES Appendices records a number of taxa separately, that are resolved to a single species in the phylogenies, we maintained the yearly volume structure for individual CITES taxa and incorporated their variation dependant on phylogeny under the phylogenetically recognized species. For example, CITES lists the Marco polo argali, Tianshan argali, and the Gobi argali subspecies separately (so we track these yearly records separately for each species), thus their variation independent of phylogeny is modelled separately (taxa-level group effect). However, as their exact relatedness is not quantified in the phylogenies available, the variation dependant on phylogeny for the three subspecies was included via the recognized species *Ovis ammon* (Argali).

All data, across hypotheses, were modelled using the hurdle negative binomial (HNB) distribution. This is parametrised by $n \sim HNB(hu, mu, shape)$, where n is the outcome, *hu* is the probability of a non-zero value (presence), *mu* is the mean or location parameter of a negative binomial distribution and *shape* (or *phi*) is the over dispersion. The processed CITES trade data contains a high proportion of zeros (years where a species is listed but did not appear in the data). The HNB models the absence of trade and the volume of trade as two distinct processes. A Bernoulli regression (parametrised by *hu*) estimates the probability of being in trade ($n \geq 1$). A truncated negative binomial regression then estimates the volumes when trade occurs (i.e. $n > 0$). The distributional parameters *hu* and *mu* are distinctly estimated as a unique function of predictors (details below), and shape we only constrain to be positive. The joint estimates of the response (HNB) distribution therefore incorporate two key features: 1) whether a species is likely to be traded at all, and 2) if traded what volume this would be in.

Weakly informative priors were specified for each model parameter (see equation details below). All models were visually assessed to ensure chains were mixing and had achieved stable convergence. All Rhat (potential scale reduction factor) values were checked to be <1.05, indicating between and within chain estimates had converged. Post predictive checks were also completed using the predictive distribution, such checks were only used to assess individual model adequacy and check for systemic discrepancies between features of the real and simulated data (Gelman et al., 2013).

Traded presence/volume across Red list categories – probabilities of $n > 0$ (hu -$\hat{P}$) and volumes when $n > 0$ ($mu -\ \mu$) are modelled as functions of the standardised lagged-volume traded the previous year, yearly Red List category (IUCN) and Year (2000 – 2018, reduced to 0 – 18 and standardised), and the interaction of IUCN category and Year. Taxon-level variance independent of phylogeny was included as a distinct group effect (indexed by j for $\hat{P}$ and k for μ). IUCN, Year, and their interaction were incorporated as phylogenetically independent group effects (Equation 1). We incorporated variation dependant on phylogeny via phylogenetic correlation matrices as a separate group effect for both (*hu* and *mu*) distributional parameters (matrices omitted from Eq. 1 for clarity). Weakly informative priors were specified for model slope (β), intercept (α) and standard deviation (σ) (a default *lkj(1)* prior was used for the correlations between grouping factors – not shown here). This model was run for a total of 4000 iterations, including 2000 warm-up iterations, for 4 chains with no thinning per taxonomic class. We note when checking the reptile model, we identified a single species the model overestimated traded volumes, *Podocnemis unifilis*, exponentially increased in traded volumes starting from 8 in 2002 (0 for 2000 and 2001), to 623444 in 2017, with volumes regularly more than doubling between years. Therefore, in 2018, our model does predict this continued growth, but the volumes actually decline to 363363. For clarity, we removed this species from the Figure 2D plot.

Trade volumes were contrasted for the average species in each IUCN threat category by using only the population-level effects and excluding the species-level variability. For contrasts the year was set at 2018 to most closely represent recent trade, and the lagged volume was held at the threat category average per taxonomic class (Table S3). Slope coefficients through time in both occurrence and volume for the average species of each class (β_3) where extracted for the whole posterior and then summarised.

$$
\begin{aligned}
\text{n} \quad & \sim \text{Hurdle-NB}(\hat{P}, \mu, \phi) \\
\text{Logit}(\hat{P}) \quad & = \alpha_j^1 + \beta_j^1(\text{Year}) + \beta_{2j}^1(\text{IUCN}) + \beta_{3j}^1(\text{Year} \times IUCN) + \ \beta_4^1(\text{lag}) \\
\begin{pmatrix} \alpha_j \\ \beta_{1j} \\ \beta_{2j} \\ \beta_{3j} \end{pmatrix} \quad & \sim N\left(\begin{pmatrix} \nu_{\alpha_j} \\ \nu_{\beta_{1j}} \\ \nu_{\beta_{2j}} \\ \nu_{\beta_{3j}} \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha_j}^2 & \rho_{\alpha_j\beta_{1j}} & \rho_{\alpha_j\beta_{2j}} & \rho_{\alpha_j\beta_{3j}} \\ \rho_{\beta_{1j}\alpha_j} & \sigma_{\beta_{1j}}^2 & \rho_{\beta_{1j}\beta_{2j}} & \rho_{\beta_{1j}\beta_{3j}} \\ \rho_{\beta_{2j}\alpha_j} & \rho_{\beta_{2j}\beta_{1j}} & \sigma_{\beta_{2j}}^2 & \rho_{\beta_{2j}\beta_{3j}} \\ \rho_{\beta_{3j}\alpha_j} & \rho_{\beta_{3j}\beta_{1j}} & \rho_{\beta_{3j}\beta_{2j}} & \sigma_{\beta_{3j}}^2 \end{pmatrix}\right), \text{for Taxon j} = 1, \ldots, \text{J} \\
\text{Log}(\mu) \quad & = \alpha_k^2 + \beta_k^2(\text{Year}) + \beta_{2k}^2(\text{IUCN}) + \beta_{3k}^2(\text{Year} \times IUCN) + \ \beta_4^2(\text{lag}) \\
\begin{pmatrix} \alpha_k \\ \beta_{1k} \\ \beta_{2k} \\ \beta_{3k} \end{pmatrix} \quad & \sim N\left(\begin{pmatrix} \nu_{\alpha_k} \\ \nu_{\beta_{1k}} \\ \nu_{\beta_{2k}} \\ \nu_{\beta_{3k}} \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha_k}^2 & \rho_{\alpha_j\beta_{1k}} & \rho_{\alpha_j\beta_{2k}} & \rho_{\alpha_k\beta_{3k}} \\ \rho_{\beta_{1k}\alpha_k} & \sigma_{\beta_{1k}}^2 & \rho_{\beta_{1j}\beta_{2k}} & \rho_{\beta_{1k}\beta_{3k}} \\ \rho_{\beta_{2k}\alpha_k} & \rho_{\beta_{2k}\beta_{1k}} & \sigma_{\beta_{2k}}^2 & \rho_{\beta_{2k}\beta_{3k}} \\ \rho_{\beta_{3k}\alpha_k} & \rho_{\beta_{3k}\beta_{1k}} & \rho_{\beta_{3k}\beta_{2k}} & \sigma_{\beta_{3k}}^2 \end{pmatrix}\right), \text{for Taxon k} = 1, \ldots, \text{k} \\
\text{Log}(\phi) \quad & = \alpha \\
\alpha \quad & \sim \text{Normal}(0,1) \\
\beta \quad & \sim \text{Normal}(0,1) \\
\phi \quad & \sim \text{Gamma}(0.01, 0.01) \\
\alpha_{j,k} \quad & \sim \text{Normal}(0, \sigma_{j,k}) \\
\sigma_{j,k} \quad & \sim \text{Normal}(0,1)
\end{aligned}
$$

Equation 1

Trade presence/volume per appendix for split listed species - probabilities of *n* > 0 (*hu* -$\hat{P}$) and volumes when *n* > 0 (*mu*− μ) are modelled as functions of the standardised lagged-volume traded the previous year, population Appendix and Year (2000 – 2018, reduced to 0 – 18 and standardised), and the interaction of Appendix and Year. Taxon-level variance independent of phylogeny was included as a distinct group effect (indexed by *j* for $\hat{P}$ and *k* for μ). IUCN, Year, and their interaction were incorporated as phylogenetically independent group effects (Equation 2). As split-listed species in trade are few in number and range across classes, we analysed all classes in one model without incorporating phylogeny. Weakly informative priors were specified for model slope (β), intercept (α) and standard deviation (α) (a default *lkj(1)* prior was used for the correlations between grouping factors – not shown here). These models were run for a total of 2000 iterations, including 1000 warm-up iterations, for 4 chains with no thinning.

$$
\begin{aligned}
\text{n} &\sim \text{Hurdle-NB}(\hat{P}, \mu, \phi) \\
\text{Logit}(\hat{P}) &= \alpha_j^1 + \beta_j^1(\text{Year}) + \beta_{2j}^1(\text{Appendix}) + \beta_{3j}^1(\text{Year} \times \text{Appendix}) + \beta_4^1(\text{lag}) \\
\begin{pmatrix} \alpha_j \\ \beta_{1j} \\ \beta_{2j} \\ \beta_{3j} \end{pmatrix} &\sim N\left(\begin{pmatrix} \nu_{\alpha_j} \\ \nu_{\beta_{1j}} \\ \nu_{\beta_{2j}} \\ \nu_{\beta_{3j}} \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha_j}^2 & \rho_{\alpha_j\beta_{1j}} & \rho_{\alpha_j\beta_{2j}} & \rho_{\alpha_j\beta_{3j}} \\ \rho_{\beta_{1j}\alpha_j} & \sigma_{\beta_{1j}}^2 & \rho_{\beta_{1j}\beta_{2j}} & \rho_{\beta_{1j}\beta_{3j}} \\ \rho_{\beta_{2j}\alpha_j} & \rho_{\beta_{2j}\beta_{1j}} & \sigma_{\beta_{2j}}^2 & \rho_{\beta_{2j}\beta_{3j}} \\ \rho_{\beta_{3j}\alpha_j} & \rho_{\beta_{3j}\beta_{1j}} & \rho_{\beta_{3j}\beta_{2j}} & \sigma_{\beta_{3j}}^2 \end{pmatrix}\right), \text{for Taxon j} = 1, \ldots, \text{J} \\
\text{Log}(\mu) &= \alpha_k^2 + \beta_k^2(\text{Year}) + \beta_{2k}^2(\text{Appendix}) + \beta_{3k}^2(\text{Year} \times \text{Appendix}) + \beta_4^2(\text{lag}) \\
\begin{pmatrix} \alpha_k \\ \beta_{1k} \\ \beta_{2k} \\ \beta_{3k} \end{pmatrix} &\sim N\left(\begin{pmatrix} \nu_{\alpha_k} \\ \nu_{\beta_{1k}} \\ \nu_{\beta_{2k}} \\ \nu_{\beta_{3k}} \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha_k}^2 & \rho_{\alpha_j\beta_{1k}} & \rho_{\alpha_j\beta_{2k}} & \rho_{\alpha_k\beta_{3k}} \\ \rho_{\beta_{1k}\alpha_k} & \sigma_{\beta_{1k}}^2 & \rho_{\beta_{1j}\beta_{2k}} & \rho_{\beta_{1k}\beta_{3k}} \\ \rho_{\beta_{2k}\alpha_k} & \rho_{\beta_{2k}\beta_{1k}} & \sigma_{\beta_{2k}}^2 & \rho_{\beta_{2k}\beta_{3k}} \\ \rho_{\beta_{3k}\alpha_k} & \rho_{\beta_{3k}\beta_{1k}} & \rho_{\beta_{3k}\beta_{2k}} & \sigma_{\beta_{3k}}^2 \end{pmatrix}\right), \text{for Taxon k} = 1, \ldots, \text{k} \\
\text{Log}(\phi) &= \alpha \\
\alpha &\sim \text{Normal}(0,1) \\
\beta &\sim \text{Normal}(0,1) \\
\phi &\sim \text{Gamma}(0.01, 0.01) \\
\alpha_{j,k} &\sim \text{Normal}(0, \sigma_{j,k}) \\
\sigma_{j,k} &\sim \text{Normal}(0,1)
\end{aligned}
$$

Equation 2

Trade presence after species change Red list categories – probabilities of $n > 0$ (*hu* -$\hat{P}$) and volumes when $n > 0$ (*mu*– μ) are modelled as functions of the standardised lagged-volume traded the previous year, species change category (Change) and Year (2000 – 2018, reduced to 0 – 18 and standardised), and the interaction of Change and Year. Taxon-level variance independent of phylogeny was included as a distinct group effect (indexed by j for $\hat{P}$ and k for μ). Change, Year, and their interaction were incorporated as phylogenetically independent group effects (Equation 1). We incorporated variation dependant on phylogeny via phylogenetic correlation matrices as a separate group effect for both (*hu* and *mu*) distributional parameters (matrices omitted from Eq. 1 for clarity). Weakly informative priors were specified for model slope (β), intercept (α) and standard deviation (σ) (a default *lkj(1)* prior was used for the correlations between grouping factors – not shown here). This model was run for a total of 4000 iterations, including 2000 warm-up iterations, for 4 chains with no thinning per taxonomic class.

In the Supplementary Methods we also present a simplified precautionary re-analysis considering only whether species “increased” or “decreased” in threat category. Full details of this approach and the results are detailed there (Figure S4), crucially these are in line with the method we present here.

$$\begin{aligned}
\text{n} &\sim \text{Hurdle-NB}(\hat{P}, \mu, \phi) \\
\text{Logit}(\hat{P}) &= \alpha_j^1 + \beta_j^1(\text{Year}) + \beta_{2j}^1(\text{Change}) + \beta_{3j}^1(\text{Year} \times \text{Change}) + \ \beta_4^1(\text{lag}) \\
\begin{pmatrix} \alpha_j \\ \beta_{1j} \\ \beta_{2j} \\ \beta_{3j} \end{pmatrix} &\sim N\left(\begin{pmatrix} \nu_{\alpha_j} \\ \nu_{\beta_{1j}} \\ \nu_{\beta_{2j}} \\ \nu_{\beta_{3j}} \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha_j}^2 & \rho_{\alpha_j\beta_{1j}} & \rho_{\alpha_j\beta_{2j}} & \rho_{\alpha_j\beta_{3j}} \\ \rho_{\beta_{1j}\alpha_j} & \sigma_{\beta_{1j}}^2 & \rho_{\beta_{1j}\beta_{2j}} & \rho_{\beta_{1j}\beta_{3j}} \\ \rho_{\beta_{2j}\alpha_j} & \rho_{\beta_{2j}\beta_{1j}} & \sigma_{\beta_{2j}}^2 & \rho_{\beta_{2j}\beta_{3j}} \\ \rho_{\beta_{3j}\alpha_j} & \rho_{\beta_{3j}\beta_{1j}} & \rho_{\beta_{3j}\beta_{2j}} & \sigma_{\beta_{3j}}^2 \end{pmatrix}\right), \text{for Taxon j} = 1, \ldots, \text{J} \\
\text{Log}(\mu) &= \alpha_k^2 + \beta_k^2(\text{Year}) + \beta_{2k}^2(\text{Change}) + \beta_{3k}^2(\text{Year} \times \text{Change}) + \ \beta_4^2(\text{lag}) \\
\begin{pmatrix} \alpha_k \\ \beta_{1k} \\ \beta_{2k} \\ \beta_{3k} \end{pmatrix} &\sim N\left(\begin{pmatrix} \nu_{\alpha_k} \\ \nu_{\beta_{1k}} \\ \nu_{\beta_{2k}} \\ \nu_{\beta_{3k}} \end{pmatrix}, \begin{pmatrix} \sigma_{\alpha_k}^2 & \rho_{\alpha_j\beta_{1k}} & \rho_{\alpha_j\beta_{2k}} & \rho_{\alpha_k\beta_{3k}} \\ \rho_{\beta_{1k}\alpha_k} & \sigma_{\beta_{1k}}^2 & \rho_{\beta_{1j}\beta_{2k}} & \rho_{\beta_{1k}\beta_{3k}} \\ \rho_{\beta_{2k}\alpha_k} & \rho_{\beta_{2k}\beta_{1k}} & \sigma_{\beta_{2k}}^2 & \rho_{\beta_{2k}\beta_{3k}} \\ \rho_{\beta_{3k}\alpha_k} & \rho_{\beta_{3k}\beta_{1k}} & \rho_{\beta_{3k}\beta_{2k}} & \sigma_{\beta_{3k}}^2 \end{pmatrix}\right), \text{for Taxon k} = 1, \ldots, \text{k} \\
\text{Log}(\phi) &= \alpha \\
\alpha &\sim \text{Normal}(0,1) \\
\beta &\sim \text{Normal}(0,1) \\
\phi &\sim \text{Gamma}(0.01,0.01) \\
\alpha_{j,k} &\sim \text{Normal}(0, \sigma_{j,k}) \\
\sigma_{j,k} &\sim \text{Normal}(0,1)
\end{aligned}$$

Equation 3

We contrasted the absolute difference in expected posterior volumes between 2-years pre and 1-year post-change at the species level (if a species was reassessed in 2010 we contrast 2008 with 2011). We specify these periods pre- and post-change rather than the whole pre and post-change series per species as we are specifically assessing the impact of change. Therefore, each species category-change has its own comparison timeframe. Comparing between the whole pre- and post-change time series' could lead to erroneous conclusions. For example, take a species that was present in trade for 5-years, then absent for 5-years before increasing in perceived threat category and then remaining absent for the remainder of the series. Comparing the entire pre- and post-change posterior at all year values would reveal overall the species was less present post-change when actually the change was irrelevant as the species was already absent from trade prior to the change.

We further estimated the difference in trend or slope through time between pre- and post-change. This approach aims to detect changes in trend before and after a change e.g. whether a species was increasing in traded volumes through time and then post-change volumes decreased through time. We extracted both species-level distributional coefficients (*hu* and *mu*, $\beta_{3\,j,k}$) for each change type. The difference was then calculated between the species pre-change slope coefficient through time and the species post-change coefficient through time (Δ Change *Year $_{\text{Post - Pre}}$). All differences were calculated from the full posterior.

We additionally contrasted population-level estimates assessing the impact of change on the average species. This took two forms. Firstly, we contrasted whether for the average species if changes associated with any change in volume pre- to post-change. Each change was contrasted at the class average year of change for each change type. Secondly, whether species that changed category were traded in different volumes to those that remained unchanged in 2018. Thus, assessing whether volumes traded after a change was different to the baseline across species that did not change. This final comparison examines whether species that changed category were systematically present in different volumes to those species that did not change category (Figure S1 and Table S4). Both comparisons here were using the population-level effects only to consider a category change for the average species.

We assess directional differences between Red List categories, before and after a change, and between the CITES Appendices for split-listed species, using the direct probability of direction (*pd*) (Makowski et al., 2019b, 2019a). The *pd* provides evidence of directional effect existence (or the certainty that effect goes in a particular direction, i.e. if endangered species are more likely to reoccur in trade than least concern species in a given year). We term substantial to denote a *pd* >97.5%, a value highly correlated with a two-sided *p*-value of 0.05 (Makowski et al., 2019b, 2019a). The *pd* is calculated from the difference of the full posterior, not a sample or summary. For example, the difference between the population-level posterior volume of the average least concern and vulnerable reptile in a given year. For the presence and split listing analysis we set the year at 2018 – the most recent year in CITES records. We present 90% HDCI's (highest density continuous intervals) to reflect this uncertainty not 95% intervals, as 90% has been deemed more stable (Kruschke, 2014).

All statistical analyses were carried out using R version 4.0.2 (R Core Team, 2020). Data curation and processing were carried out using "*dplyr*" 1.0.2 (Wickham et al., 2021), plotting using "*ggplot2*" 3.3.2 (Wickham, 2016), figure arrangement using "*egg*" 0.4.5 (Auguie,

2019) and “*png*” 0.1.7 (Urbanek, 2013). .All phylogenies were handled using “*ape*” 5.4.1 (Paradis and Schliep, 2019). Model fitting, checking and post-processing was done using “*brms*” 2.15.0 (Bürkner, 2017), “*bayestestr*” 0.8.0 (Makowski et al., 2019a) and “*tidybayes*” 2.3.1 (Kay, 2020).

Precautionary re-analyses

The method presented in Eq. 3 and Figure 4, using the post-change categories, “Becomes threatened”, Becomes non-threatened”, “Stayed threatened” and “Stayed non-threatened”, picks up important nuance on directional change and whether the change moves the species to a threatened or non-threatened category. The key result of this analysis is that a change does not systematically change species reoccurrence. To confirm this we ran a simpler model solely considering a directional change. Here we modelled the following categories, “Pre-change”, “Increase” and “Decrease”. Pre-change here denotes the same as in the main methods. Here “Increase” refers to an increase in extinction risk (i.e. LC to VU, NT to CR, etc.). Conversely, “Decrease” is any decrease in extinction risk (i.e. VU to LC, CR to EN etc.). The simplicity of these models required a number of species (changes) to be removed. All species that changed category more than once were removed, all species changing to or from Data Deficient (DD) or changing from Not evaluated (NE) were also removed as changes to or from DD or NE should not be considered an increase or decrease in extinction risk. Therefore, this re-analysis focused only on the most well-understood species that were reassessed into a different category, with full assessments pre and post-change. As before the same criteria as applied in the main text models applied here mainly all species must have at least 2-years data pre- or post-change. The number of species modelled was therefore severely reduced (36 birds, 42 mammals, 3 amphibians and 16 reptiles, totalling 97 species). The basic structure of the models remained the same as that in the main text. Due to the reduced number of species, this model does not account for relatedness between species we do however account for species variation and class level differences by nesting species within taxonomic classes in the models group-level effects (see Equation 5). The smaller number of species meeting the prerequisites for this reanalysis prevent a more nuanced analysis fully separating classes and accounting for species non-independence.

$$
\begin{aligned}
n &\sim \text{Hurdle-NB}(\hat{P}, \mu, \phi) \\
Logit(\hat{P}) &= \alpha^1_{j,k} + \beta^1_{j,k}(\text{Year}) + \beta^1_{2j,k}(\text{Change}) + \beta^1_{3j,k}(\text{Year} \times \text{Change}) + \ \beta^1_4(\text{lag}) \\
\begin{pmatrix} \alpha_j \\ \beta_{1j} \\ \beta_{2j} \\ \beta_{3j} \end{pmatrix} &\sim N\left(\begin{pmatrix} \mu_{\alpha_j} \\ \mu_{\beta_{1j}} \\ \mu_{\beta_{2j}} \\ \mu_{\beta_{3j}} \end{pmatrix}, \begin{pmatrix} \sigma^2_{\alpha_j} & \rho_{\alpha_j\beta_{1j}} & \rho_{\alpha_j\beta_{2j}} & \rho_{\alpha_j\beta_{3j}} \\ \rho_{\beta_{1j}\alpha_j} & \sigma^2_{\beta_{1j}} & \rho_{\beta_{1j}\beta_{2j}} & \rho_{\beta_{1j}\beta_{3j}} \\ \rho_{\beta_{2j}\alpha_j} & \rho_{\beta_{2j}\beta_{1j}} & \sigma^2_{\beta_{2j}} & \rho_{\beta_{2j}\beta_{3j}} \\ \rho_{\beta_{3j}\alpha_j} & \rho_{\beta_{3j}\beta_{1j}} & \rho_{\beta_{3j}\beta_{2j}} & \sigma^2_{\beta_{3j}} \end{pmatrix}\right), for\ Species{:}\, Class\ j \ = \ 1, \dots , \\
\begin{pmatrix} \alpha_k \\ \beta_{1k} \\ \beta_{2k} \\ \beta_{3k} \end{pmatrix} &\sim N\left(\begin{pmatrix} \mu_{\alpha_k} \\ \mu_{\beta_{1k}} \\ \mu_{\beta_{2k}} \\ \mu_{\beta_{3k}} \end{pmatrix}, \begin{pmatrix} \sigma^2_{\alpha_k} & \rho_{\alpha_k\beta_{1k}} & \rho_{\alpha_k\beta_{2k}} & \rho_{\alpha_k\beta_{3k}} \\ \rho_{\beta_{1k}\alpha_k} & \sigma^2_{\beta_{1k}} & \rho_{\beta_{1k}\beta_{2k}} & \rho_{\beta_{1k}\beta_{3k}} \\ \rho_{\beta_{2k}\alpha_k} & \rho_{\beta_{2k}\beta_{1k}} & \sigma^2_{\beta_{2k}} & \rho_{\beta_{2k}\beta_{3k}} \\ \rho_{\beta_{3k}\alpha_k} & \rho_{\beta_{3k}\beta_{1k}} & \rho_{\beta_{3k}\beta_{2k}} & \sigma^2_{\beta_{3k}} \end{pmatrix}\right), for\ Class\ k \ = \ 1, \dots , K \\
\text{Log}(\mu) &= \alpha^2_{l,m} + \beta^2_{l,m}(\text{Year}) + \beta^2_{2l,m}(\text{Change}) + \beta^2_{3l,m}(\text{Year} \times \text{Change}) + \ \beta^2_4(\text{lag}) \\
\begin{pmatrix} \alpha_l \\ \beta_{1l} \\ \beta_{2l} \\ \beta_{3l} \end{pmatrix} &\sim N\left(\begin{pmatrix} \mu_{\alpha_l} \\ \mu_{\beta_{1l}} \\ \mu_{\beta_{2l}} \\ \mu_{\beta_{3l}} \end{pmatrix}, \begin{pmatrix} \sigma^2_{\alpha_l} & \rho_{\alpha_l\beta_{1l}} & \rho_{\alpha_l\beta_{2l}} & \rho_{\alpha_l\beta_{3l}} \\ \rho_{\beta_{1l}\alpha_l} & \sigma^2_{\beta_{1l}} & \rho_{\beta_{1l}\beta_{2l}} & \rho_{\beta_{1l}\beta_{3l}} \\ \rho_{\beta_{2l}\alpha_l} & \rho_{\beta_{2l}\beta_{1l}} & \sigma^2_{\beta_{2l}} & \rho_{\beta_{2l}\beta_{3l}} \\ \rho_{\beta_{3l}\alpha_l} & \rho_{\beta_{3l}\beta_{1l}} & \rho_{\beta_{3l}\beta_{2l}} & \sigma^2_{\beta_{3l}} \end{pmatrix}\right), for\ Species{:}\, Class\ l \ = \ 1, \dots , L \\
\begin{pmatrix} \alpha_m \\ \beta_{1m} \\ \beta_{2m} \\ \beta_{3m} \end{pmatrix} &\sim N\left(\begin{pmatrix} \mu_{\alpha_m} \\ \mu_{\beta_{1m}} \\ \mu_{\beta_{2m}} \\ \mu_{\beta_{3m}} \end{pmatrix}, \begin{pmatrix} \sigma^2_{\alpha_m} & \rho_{\alpha_m\beta_{1m}} & \rho_{\alpha_m\beta_{2m}} & \rho_{\alpha_m\beta_{3m}} \\ \rho_{\beta_{1m}\alpha_m} & \sigma^2_{\beta_{1m}} & \rho_{\beta_{1m}\beta_{2m}} & \rho_{\beta_{1m}\beta_{3m}} \\ \rho_{\beta_{2m}\alpha_m} & \rho_{\beta_{2m}\beta_{1m}} & \sigma^2_{\beta_{2m}} & \rho_{\beta_{2m}\beta_{3m}} \\ \rho_{\beta_{3m}\alpha_m} & \rho_{\beta_{3m}\beta_{1m}} & \rho_{\beta_{3m}\beta_{2m}} & \sigma^2_{\beta_{3m}} \end{pmatrix}\right), for\ Class\ m \ = \ 1, \dots , M \\
\text{Log}(\phi) &= \alpha \\
\beta &\sim Normal(0,1) \\
\alpha &\sim Normal(0,1) \\
\phi &\sim \text{Gamma}(0.01,0.01) \\
\alpha_{j,k,l,m} &\sim\sim \text{Normal}(0, \sigma_{j,k,l,m}) \\
\sigma_{j,k,l,m} &\sim \text{Normal}(0,1)
\end{aligned}
$$

Equation 5

This simplified approach has merit but also severe limitations as LC to NT, NT to VU, or EN to CR are all classed equally as “Increases” extinction risk, a factually correct, but very limited interpretation as it is dubious all changes are equally likely to prompt policy or management measures. Crucially, these results mirror our main text findings. There is no systematic change in species traded volumes after pre- to post-IUCN change. This was true across species and for the average species changing to a more-threatened (Increase) or less threatened (Decrease) status, there was no substantial directional effect on traded volumes (Figure S4). There are a number of reasons why species may show no response to a change, namely that species presence is ephemeral and that species may have ceased to be traded (but remain listed) years before the IUCN reassessment and status change.

3.8 Supplementary materials

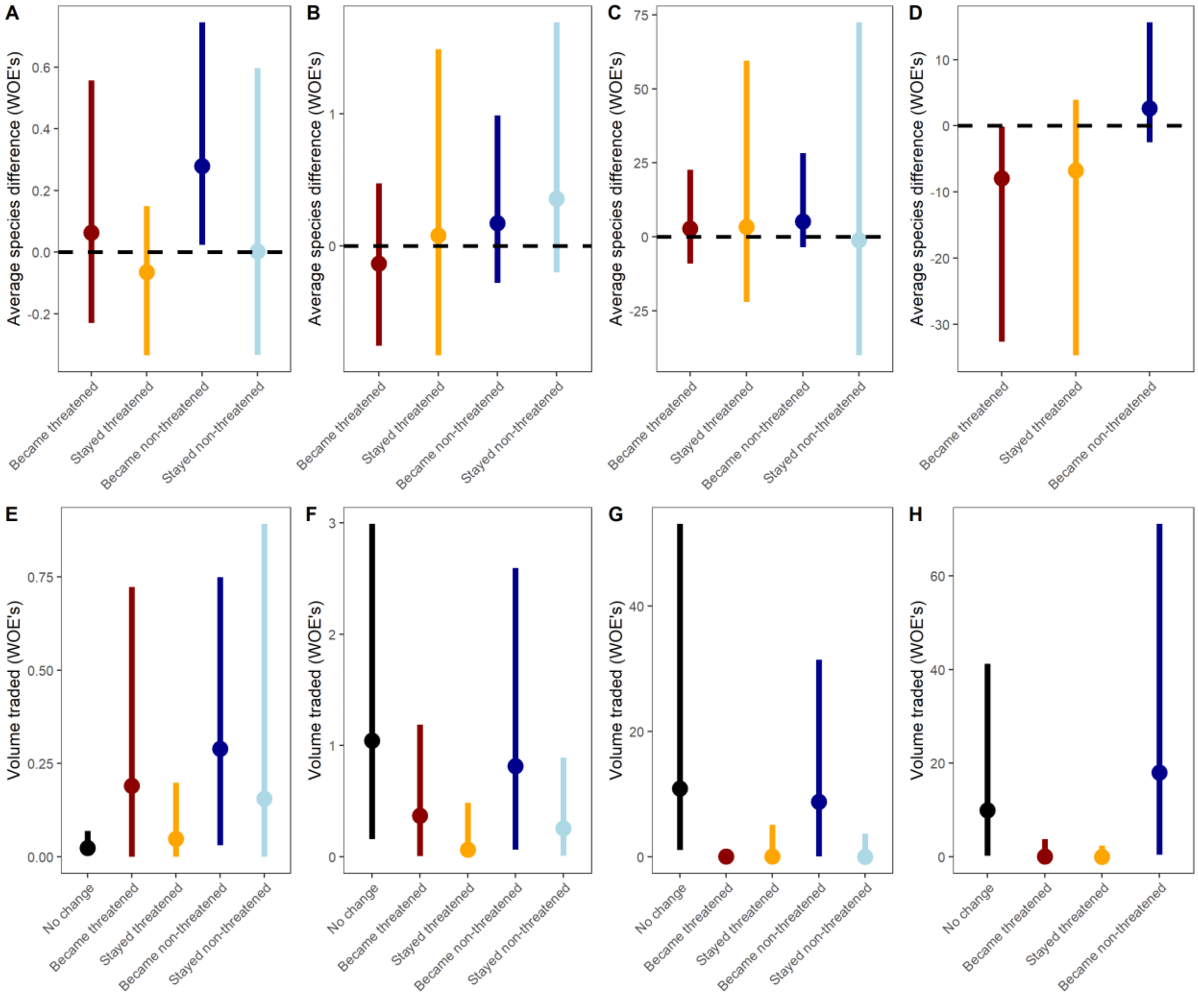

Figure S1. Average (population-level) results, columns represent Aves, Mammals, Amphibians and Reptiles respectively. Related to Figure 4. A – D. Represent the volume difference 1-year pre- to 1-year post-change for each change type. Change year modelled as the most common change year per class (Aves – 2013, Mammals – 2007, Amphibians – 2003, Reptiles – 2010), lagged volume fixed at the Class median. E – H. Estimated volumes traded in 2018 for each change type and those that did not change, lagged volume fixed at the Class median. Points are medians and lines the 90% HDCI, calculated from the entire posterior.

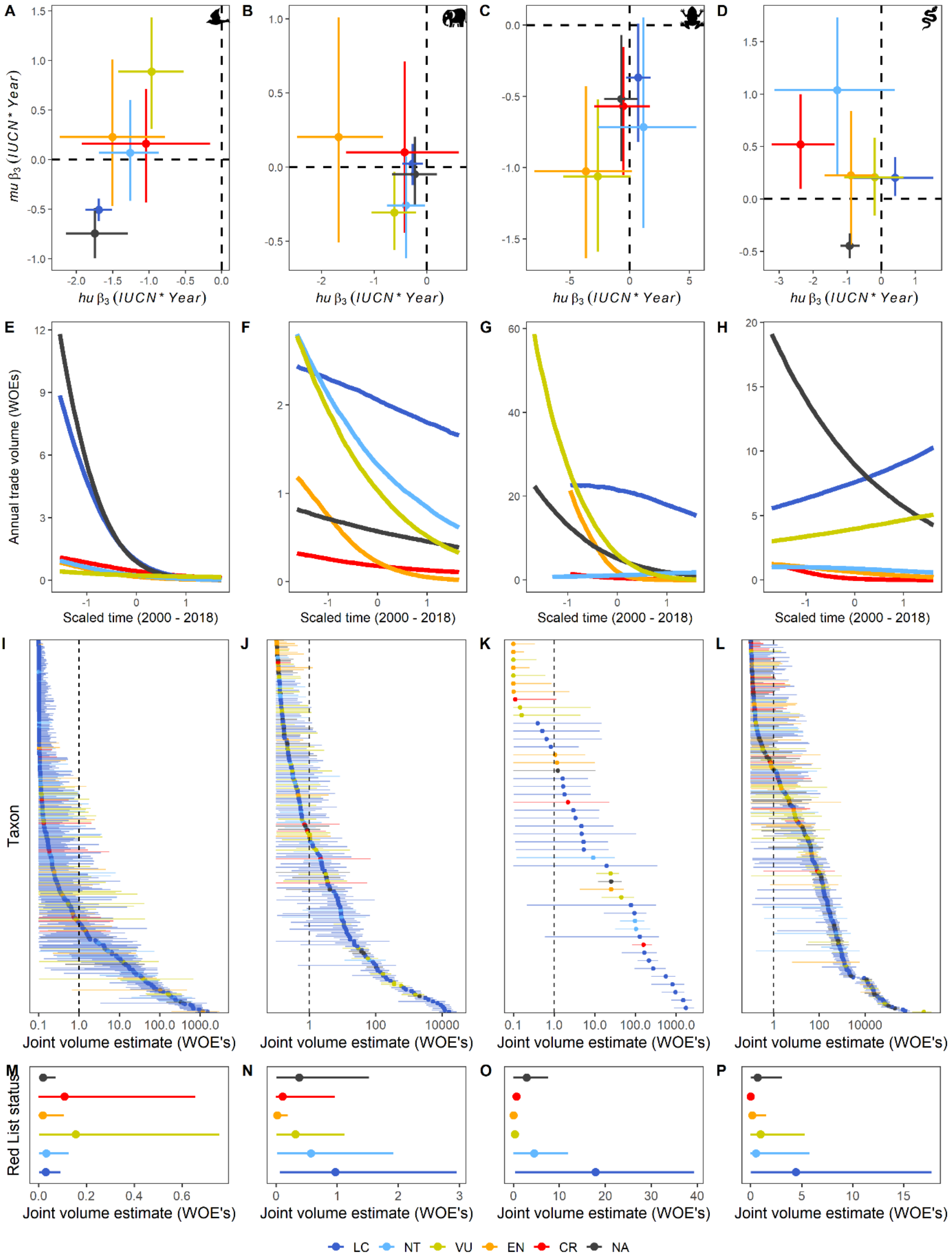

Figure S2. Replication of main text findings (Figures 1 and 2) using the Importer reported results (rather than exporter). Related to STAR Methods. Points are medians and lines the 90% HDCI, calculated from the entire posterior.

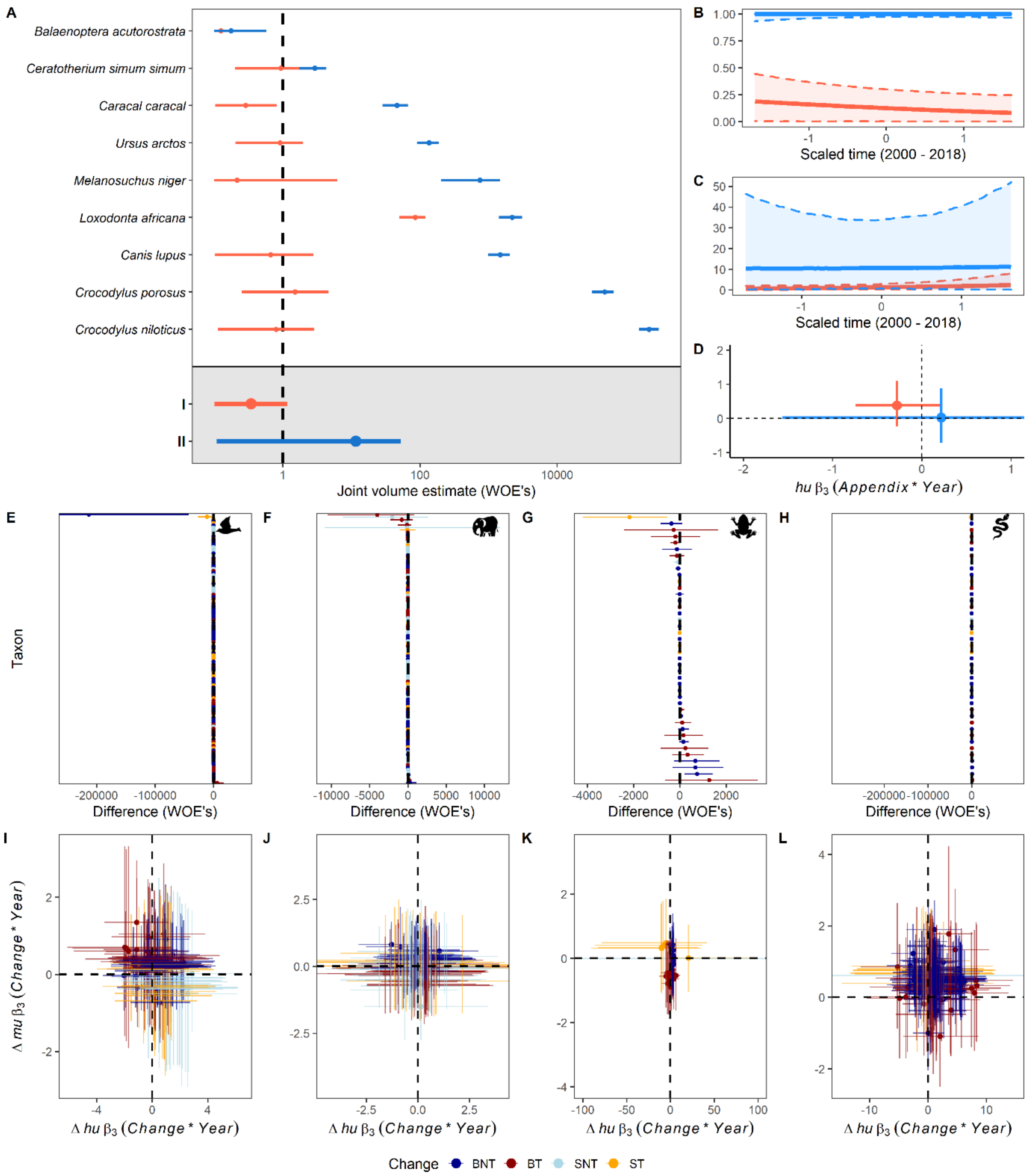

Figure S3. Replication of main text findings (Figures 3 and 4) using the Importer reported results (rather than exporter). Related to STAR Methods. Points are medians and lines the 90% HDCI, calculated from the entire posterior.

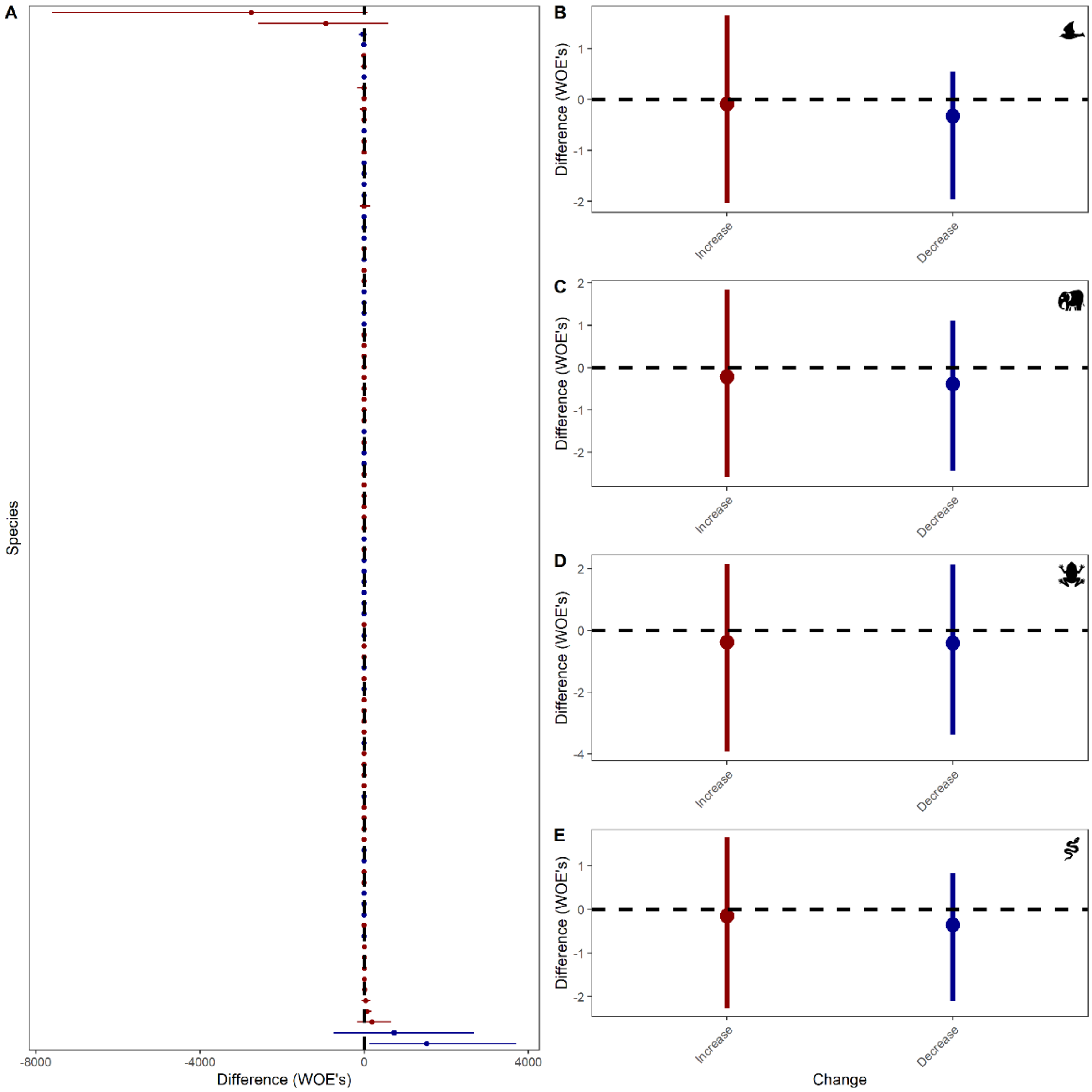

Figure S4. Simplified analysis of trade volumes pre- to post-change using only “Increase” or “Decrease”. Related to STAR Methods. A. Species level estimates for differences in volume pre- to post-change. C – F. Differences pre-post change for the average species. Change year was specified as the most common change year per Class. Colours denote Increases (red) and Decreases (blue) in IUCN extinction risk, see supplementary methods for details. Points are medians and lines the 90% HDCI, calculated from the entire posterior.

Preliminary cleaning steps

Step	Description	Records	Notes
1	CITES Trade database Version 2021.1	22,616,522	
2	Remove all re-exports	12,880,243	
3	Focus on target Classes	3,770,437	
4	Convert records to woes	3,015241	80.0% of records could be converted. By Class 5.7% of Amphibian, 2.6% of bird, 19.8% of Mammal and 34.5% of Reptile records could not be converted.
5	Focus on 2000 to 2018	1,864,275	
6	Focus on Exporter data	991,417	872,858 Importer records
7	Focus on the wild sourced commercial trade	284,091	Commercial and not wild-sourced = 350,491. Non-commercial and not wild-sourced = 67,129. Non-commercial and wild-sourced = 289,706.

Final dataset species numbers

	Total species present in CITES data	**Total that could be resolved to include in the model**	**%**
Presence (Figure 1 and 2)			
Aves	486	486	100.0
Mammalia	207	207	100.0
Amphibia	44	44	100.0
Reptilia	316	288	91.1
Total	**1053**	**1025**	
IUCN change (Figure 4)			
Aves	482	482	100.0
Mammalia	201	201	100.0
Amphibia	40	40	100.0
Reptilia	301	277	92.0
Total	**1024**	**1000**	

Table S1. Summary of the CITES data curation pipeline and numbers of species present in the data and the number that could be included in the phylogenetic models. Related to STAR Methods. Initial data download accessed here https://trade.cites.org/. Species were lost from the Presence (Figure 2) analysis only if they could not be resolved to a phylogeny. Care was taken to check for incorrect naming, updated names etc. We used the CITES naming as the authority so we retained sub-species names in the phylogenetically independent group effects but the sub-species where grouped under the known species name for the phylogenetically dependent group effect. But some species still could not be included. Note – while 1024 could be modelled, when discussing species in recent trade (2018) we only consider the 926 species still listed in the Appendices at that point. Species were lost from the IUCN change (Figure 4) analysis for the same reason, but additionally where species changed status to DD or only had 1 year of trade data pre- or post-change.

Class	**IUCN**	***mu***	**90% HDCI**	***pd***	***hu***	**90% HDCI**	***pd***
Aves	CR	-0.20	-0.83 to 0.39	70.21	-0.35	-1.32 to 0.69	72.16*
	EN	-0.48	-1.37 to 0.41	80.41	-1.15	-2.27 to -0.15	97.32*
	LC	-0.78	-0.90 to -0.64	100.00	-1.41	-1.57 to -1.25	100.00
	NA	-0.73	-1.00 to -0.44	100.00	-1.96	-2.43 to -1.51	100.00
	NT	-0.05	-0.46 to 0.43	57.66	-1.19	-1.68 to -0.73	100.00
	VU	0.01	-0.64 to 0.63	51.26*	-0.53	-0.97 to -0.07	97.27*
Mammalia	CR	-0.09	-0.66 to 0.53	58.92	-0.27	-0.89 to 0.44	75.46
	EN	-0.06	-0.82 to 0.69	55.17	-1.22	-2.21 to -0.26	98.21
	LC	0.02	-0.13 to 0.18	58.81	-0.34	-0.56 to -0.11	99.08
	NA	0.01	-0.38 to 0.38	50.90	-0.05	-0.39 to 0.27	59.13
	NT	-0.04	-0.47 to 0.38	55.75	-0.32	-0.64 to -0.01	95.33
	VU	-0.12	-0.41 to 0.18	74.94	-0.46	-0.78 to -0.12	99.02
Amphibia	CR	-0.59	-1.01 to -0.20	98.40	-0.15	-1.83 to 1.32	56.65
	EN	-1.18	-1.81 to -0.53	99.35	-3.77	-7.11 to -0.71	99.25
	LC	0.01	-0.30 to 0.34	51.80	0.71	-0.39 to 1.94	84.85
	NA	-0.86	-1.40 to -0.28	98.92**	-0.54	-2.11 to 0.85	74.22
	NT	-0.64	-1.28 to 0.08	93.03	1.09	-2.52 to 5.31	71.83
	VU	-1.20	-1.72 to -0.61	99.10	-2.45	-6.08 to 0.28	94.33
Reptilia	CR	-0.75	-1.22 to -0.27	99.33[+]	-1.47	-2.27 to -0.64	99.90
	EN	-0.83	-1.26 to -0.42	99.85[+]	-0.66	-2.10 to 0.62	80.97[++]
	LC	0.22	0.02 to 0.41	97.50[+]	-0.07	-1.42 to 1.22	53.57
	NA	-0.22	-0.33 to -0.10	99.83	-1.09	-1.40 to -0.81	100.00
	NT	0.27	-0.39 to 0.90	75.25[+]	-0.62	-3.14 to 1.76	67.70
	VU	0.07	-0.27 to 0.42	63.80	-0.11	-0.89 to 0.80	57.90

Table S2. Slope coefficients for IUCN statuses through time. Related to Figure 1. Coefficients were derived for each status for both volumes when traded (*mu*) and for presence in trade (*hu*). The 90% HDCI is calculated from the entire posterior draw of coefficients. The *pd* is used to show the certainty of direction, whether a slope coefficient is increasing, decreasing or uncertain. We colours slope values with *pd*'s > 97.50% indicating a very high certainty of direction. Those that decrease are coloured red, those that increase blue.

*Importer based results suggests that the relative me trend through time for VU is increasing (pd > 97.5%) and the *hu* trend through time for CR, EN and VU species is also substantially negative in direction (>97.50%).

** Importer based results suggest that the relative *mu* trend through time for NA species is no longer substantially negative, however the pd remains at 97.25%.

[+] Importer based results suggests that the relative *mu* trend through time for CR, EN and LC species is no longer clearly positive or negative (pd < 97.50%). Additionally the mu trend for NT species is now substantially positive.

[++] Importer based results suggests that the relative h*u* trend through time for EN species is now substantially negative (pd > 97.50%)

Class	**Status contrast**	**Absolute difference (WOE's, 90% HDCI)**	***Pd (%)***
Birds	CR - LC	0.09 (-0.10 to 0.73)	80.87
	CR - NT	0.07 (-0.18 to 0.80)	74.01
	EN – LC	-0.03 (-0.12 to 0.04)	87.47
	EN – NT	-0.04 (-0.23 to 0.05)	87.53
	VU – LC	0.03 (-0.06 to 0.25)	77.54
	VU - NT	0.02 (-0.16 to 0.28)	65.08
Mammalia	CR - LC	-0.88 (-3.09 to 0.01)	**98.65***
	CR - NT	-0.62 (-2.66 to 0.16)	96.08
	EN – LC	-1.07 (-3.32 to -0.1)	**99.83**
	EN – NT	-0.80 (-2.75 to -0.06)	**99.71**
	VU – LC	-0.69 (-2.57 to 0.12)	**97.88***
	VU - NT	-0.42 (-2.15 to 0.32)	91.33
Amphibia	CR - LC	-11.72 (-41.66 to 0.01)	**99.70**
	CR - NT	-1.30 (-10.28 to 2.70)	76.00
	EN – LC	-12.59 (-43.38 to -0.19)	**100.00**
	EN – NT	-2.03 (-10.55 to 0.27)	95.08
	VU – LC	-12.48 (-43.02 to -0.07)	**99.90**
	VU - NT	-1.89 (-10.52 to 1.14)	90.80
Reptilia	CR - LC	-32.37 (-134.26 to -0.98)	**100.00**
	CR - NT	-8.30 (-64.61 to 1.40)	97.08**
	EN – LC	-31.56 (-131.23 to -0.97)	**100.00**
	EN – NT	-7.38 (-65.76 to 4.72)	90.77
	VU – LC	-20.00 (-103.87 to 8.80)	95.33
	VU - NT	-0.09 (-51.49 to 53.69)	50.40

Table S3. Contrasts in traded volumes across IUCN statuses. Related to Figure 2. Contrasts taken with Year fixed at 2018 and the lagged volume term held at the status median.

* Importer based results suggests that the absolute difference between CR and LC, and VU and LC is no longer clearly positive or negative (*pd* < 97.5%) however the probability of direction for both remaining negative remains above 94.00%.

** Importer based results suggests there is an absolute difference between CR and NT traded volumes (pd = 98.12%).

Class	**Contrast**	***In 2018 relative to no change***		**Contrast**	***Pre- to post change for the average species***	
		Absolute difference (90% HDCI)	***Pd (%)***		***Absolute difference (90% HDCI)***	***Pd (%)***
Birds	NC – BT	-0.16 (-0.68 to 0.04)	96.54	BT-PC	0.06 (-0.23 to 0.56)	69.21
	NC - BNT	-0.26 (-0.69 to -0.02)	**100.00**	BNT-PC	0.28 (0.02 to 0.74)	**99.84**[+]
	NC – ST	-0.02 (-0.18 to 0.05)	72.19*	ST -PC	-0.06 (-0.34 to 0.15)	79.67
	NC – SNT	-0.13 (-0.87 to 0.06)	90.96	SNT-PC	0.00 (-0.33 to 0.60)	50.99
Mammalia	NC – BT	0.58 (-0.35 to 2.38)	91.36	BT-PC	-0.13 (-0.75 to 0.47)	73.01
	NC - BNT	0.17 (-1.22 to 1.75)	64.30	BNT-PC	0.17 (-0.28 to 0.98)	79.39
	NC – ST	0.88 (-0.01 to 2.99)	**97.50****	ST -PC	0.08 (-0.83 to 1.49)	58.11
	NC – SNT	0.70 (-0.19 to - 2.49)	96.11	SNT-PC	0.36 (-0.20 to 1.69)	90.00
Amphibia	NC – BT	10.20 (-0.08 to 49.37)	**99.76**	BT-PC	2.70 (-9.09 to 22.68)	77.80
	NC - BNT	1.23 (-20.29 to 42.00)	57.24	BNT-PC	5.12 (-3.51 to 28.30)	92.73
	NC – ST	9.12 (-6.14 to 55.92)	94.08	ST -PC	3.38 (-22.00 to 59.44)	64.49
	NC – SNT	10.40 (0.49 to 51.43)	**99.44**	SNT-PC	-1.11 (-40.09 to 72.41)	60.89
Reptilia	NC – BT	9.23 (-2.52 to 44.73)	97.39	BT-PC	-7.87 (-33.73 to - 0.15)	**99.70**
	NC - BNT	-7.04 (-52.60 to 13.12)	83.16	BNT-PC	2.60 (-2.96 to 14.90)	90.00
	NC – ST	9.44 (-1.93 to - 45.21)	**97.60**	ST -PC	-6.45 (-34.74 to 5.80)	93.15[++]

Table S4. Summary of IUCN status change differences. Related to Figure 4. Initially we contrast the volume traded for species that changed status with those that did not change. Thus assessing whether species that changed were broadly traded in any higher or lower volumes. Red shading indicates species that did change were traded in lower volumes (blue for higher volumes) than those that did change. Secondly, we contrasted the differences pre- to post-change for the average species (using the change year as the year that class most frequently changed status and the median lagged volume). Red shading indicates a decrease in volume pre- to post change and blue an increase.

* Importer based results suggests that the average species that did not change was traded in lower volumes than those that stayed threatened (*pd* = 97.85%).

** Importer based results suggests that the average species that did not change was no longer traded in substantially lower or greater volumes than those that stayed threatened (*pd* < 97.50%).

[+] Importer based results suggests that the average species no longer saw a substantial increase in volume pre- to post-change after becoming non-threatened (*pd* = 84.05%).

[++] Importer based results suggests that the average species now saw a substantial decrease in volume pre- to post-change after changing status but staying threatened (*pd* = 99.76%).

Chapter 4:

Contrasting life-history traits in captive- and wild-sourced trade over time

4.1 Abstract

The wildlife trade is a vast global business, involving millions of people, thousands of species, and tens of millions of individual organisms. Unravelling whether trade targets demographically distinct species and, in turn, how trade varies between captive and wild sources through time is a crucial question. We used a comprehensive list of traded birds and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Listings and trade records, in combination with a suite of avian demographic parameters to ask whether trade correlates with particular facets of demography. Across general trade, CITES Listing, and CITES trade, the same traits are associated with trade or listing. This includes species with relatively high longevity and body mass, and those with relatively low adult survival rates. We then used the comprehensive CITES trade database to examine the prevalence of life-history traits across time between captive and wild sources. There was limited evidence that trade volumes from captive and wild sources target different demographic facets. Captive trade was correlated with both adult survival, age at first reproduction, and species longevity, but the wild-sourced trade showed no such association. Within species, captive-sourced trade dominates and is increasing, while wild-sourced trade is declining or absent, with evidence of a switch from wild- to captive-sources in many species. While a booming captive-bred trade can reduce pressure on over-harvested and imperilled species, without transparent oversight captive-sourced trade can easily harm wild populations via laundering into captive facilities. If captive-sourced trade is the future of species utilisation, more scrutiny and oversight are needed to prevent wild populations from being adversely impacted.

4.2 Introduction

Trade in wildlife affects 24% of all terrestrial vertebrates (Scheffers et al., 2019), contributes to elevated extinction risk for many species (Marsh et al., 2021), and can correlate with declines in species abundances (Morton et al., 2021). Trade is also a vast global industry involving the movement of millions of individuals annually (Harfoot et al., 2018a) and worth billions of dollars (Haken, 2011). Consequently, trade provides crucial livelihoods and sustenance for hundreds of millions of people (Nielsen et al., 2018). Reconciling the demand and supply of species to meet societal needs with the conservation of wildlife in a changing world is one of the key challenges for our generation.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) sets regulations for Parties to the Convention to implement, to best prevent international trade from threatening the survival of listed species. CITES makes provisions for both wild- and captive-sourced trade and has advocated captive breeding as a potential conservation tool (CITES, 2010), despite criticism that illegal trade and laundering have proliferated under the guise of captive-sourced trade (TRAFFIC, 2016). Many heavily commercialized species are now predominantly traded from ranched or captive-breeding facilities (J. Nickum et al., 2018) over wild sources. Yet such a pattern is not consistent across all taxa or regions and varies temporally (Harfoot et al., 2018a; Nijman, 2010).

Presence in wild- or captive-sourced trade will vary according to species' suitability to captive breeding (Challender et al., 2019a), demand-driven preference for a particular source (Hinsley and 't Sas-Rolfes, 2020), and the relative availability and costs of either source. In certain cases, trade from captive-bred sources offers an avenue to relieve pressure on wild populations, especially those that are threatened or declining (Tensen, 2016), assuming that an increased captive supply does not cause harm by disproportionately raising demand (Tensen, 2016). For example, the continued use of wild populations to restock Siamese crocodile (*Crocodylus siamensis*) farms led to local extirpations across its range (Bezuijen et al., 2013; Tensen, 2016). A combination of traits that predispose a species to be susceptible to overharvesting, such as high ages of maturity or longevity, may make them less suitable for captive breeding. Research has considered the viability of individual species for captive breeding (Challender et al., 2019a), but a key question is whether captive- and wild-sourced trade target different dimensions of life history (e.g., whether captive trade focuses on faster reproducing or smaller species to maximize output or space). Crucially, this begs the question as to whether captive- and wild-sourced trades are compensatory on a global scale for individual species, i.e. as volumes from one source decrease is there a compensatory increase in the other, therefore maintaining a largely stable overall volume through time.

Species’ response to extraction and trade (e.g., susceptible to declines or robust to harvest), can be viewed as a combination of the level of extraction, the presence of concurrent threats, and species-specific life-history (or demographic) traits describing species reproductive output and survival. Accurately assessing sustainable offtake for either subsistence or trade can be attempted in a myriad of ways (for detail see (Milner-Gulland and Akçakaya, 2001)). However, almost all approaches require knowledge of species’ population densities or abundances, yet knowledge of targeted population parameters is scarce especially when thousands of species (and populations) are traded.

Considering whether traded species possess more or less ‘at-risk’ life-history characteristics at a global scale has not been broadly considered. Ecological theory indicates that specific combinations of traits may result in ‘faster’ and ‘slower’ life history strategies (Quetglas et al., 2016). Characteristics like early maturation, rapid growth, or large numbers of offspring (often correlated with low adult survival and longevity) typically predispose species to be robust to high offtakes. For example, reticulated pythons (*Malaypython reticulatus*) have historically been traded in the thousands (and tens of thousands) without evidence of decline, a result attributed to both their large clutches, ecological flexibility and cryptic behaviour (Shine et al., 1999). Conversely, combinations of slower traits, including high longevity, high age at maturity, and low reproductive rates can predispose species to declines from even light collection pressure (Jolly et al., 2021). Whether legal international wild- or captive-sourced trade captures a part or all of this variation in life-history traits is largely unknown.

Here, we investigate how traded demographic diversity is partitioned between captive and wild sources, which is urgently needed to guide effective conservation. We consider the association between life-history traits and trade in two parts. Firstly, we use comprehensive data on traded species (Scheffers et al., 2019), CITES listing, and presence in the legal trade to broadly consider whether life-history traits are associated with a species' probability of being traded or CITES listed. We hypothesise an increasing probability of being traded to associate with body mass as seen in previous studies, and with faster life-history trends (i.e., decreasing adult survival, ages at first reproduction and maximum longevity). Secondly, we used the comprehensive CITES trade database to examine whether trade volumes are also associated with species life-history traits; again, we hypothesise increasing volumes with broadly faster traits in both wild- and captive-sourced trade. We further consider whether yearly traded volumes vary between wild and captive sources for threatened and non-threatened species. We hypothesise a decline in wild-sourced trade and an increase in captive-sourced trade through time across threat statuses.

4.3 Methods

Data sources

We used a published dataset (Scheffers et al., 2019) of all bird species and whether they are known to be traded or not. We further downloaded the full list of all current CITES listings (December 2021 accessed from https://checklist.cites.org/#/en). For data on the wildlife trade, we used the most up-to-date version of the CITES trade database (version 2021.1), which tracks the international legal trade in CITES-listed species. This results in a database with 21,635,430 unidirectional trade records. Comprehensive detail of the data structure can be found at the point of access. A recently published database of avian life-history characteristics for all species (Bird et al., 2020) was used for species demographic traits. Four traits of particular interest were selected and used for subsequent analysis. 1) Annual adult survival is measured as a proportion, where lower values indicate a faster life history. 2) Body mass (grams), where smaller species would indicate faster life histories, but a larger size is a known correlate of hunting and trade in birds (Keane et al., 2005; Scheffers et al., 2019). 3) Age at first reproduction (years), where lower values would indicate faster life histories and a greater reproductive output all other traits held constant. 4) Maximum longevity (years), where similarly lower values would indicate faster life histories and greater reproductive output.

For incorporation in subsequent models that include species phylogenetic relatedness, we cross-referenced the updated avian taxonomy used in Scheffers et al (Scheffers et al., 2019) with the avian phylogeny developed in Jetz et al (Jetz et al., 2012). Where the updated avian taxonomy used in Scheffers et al included recently split species that can be resolved back to a single species in the phylogeny this was done. This resulted in a list of 10,254 updated bird species which all resolved back to 9839 species included in the phylogeny, thus there were multiple instances where a single species in the phylogeny links to multiple species in the updated Scheffers et al data. To this, we matched the avian life-history database. Trait data was missing for six species' longevity, age at first breeding, and adult survival values (0.06% of species), and for 45 species' body mass values (0.46% of species). We calculated the phylogenetic signal of each trait using Pagel's lambda, as per (Goolsby, 2016). All traits had a significant and strong signal ($\lambda > 0.9$, $p < 0.05$). Therefore, we used phylogenetic imputation using one maximum clade credibility tree derived from 1000 possible avian phylogenies (Jetz et al., 2012) to estimate these missing values under Brownian motion assuming uncorrelated traits. Testing for phylogenetic signal and trait imputation used the "*Rphylopars*" (Goolsby et al., 2017) package.

Data preparation

Part 1 - Traits in trade and listings

We minimally processed the CITES data to get a list of species traded each year (see Supplementary Methods for details). From this final list, we then extracted the number of unique species names traded from 2000 (historic trade, *n = 1277*) and the number of names traded since 2015 (recent trade, *n = 840*). The CITES species names extracted from the CITES database cover a range of resolutions including sub-species and sometimes multiple species are listed under a variety of synonyms, thus this naming diversity must be resolved with our processed species lists of traded species. Similarly, we resolved the names of all CITES-listed bird species (*n = 1504*), again some species considered synonymous are listed separately, and some listed names correspond to more than one recognized species. Thus, to our list of 10,254 bird species (where 4259 are recorded as traded overall), we recorded 1243 species CITES traded since 2000, 823 CITES traded since 2015, and 1473 as currently CITES listed.

Part 2 – Contrasting life history and temporal patterns in captive- and wild-sourced trade

This analysis focused on commercial trade from captive and wild sources, requiring a greater level of processing following established methods (Harfoot et al., 2018a; Morton et al., 2022; Robinson and Sinovas, 2018) (see Supplementary Methods for details). This resulted in a cleaned species-level database of yearly traded commercial volumes from captive and wild sources. Note that as part of this, and the previous analysis we use the exporter reported values in the CITES database, as these are known to differ in some cases from the importer reported values we completed a full reanalysis of all presented results using importer reported values (see Supplementary Methods and Figures S6-10. Crucially, the conclusions remained largely unchanged.

We further used the Red List API (accessed via the Red List API using the "*rredlist*" R package) to extract historical threat assessments for all traded species. Where species had pre-2000 standard codes (e.g. "*lr*", "*cd*", and "*nt*") these were converted to present standards: "*lr*" became Least Concern; and "*cd*" and "*nt*" became Near-Threatened. We converted all assessments into threatened (T) and non-threatened (NT) classes for subsequent analyses. Threatened describes species classed as Vulnerable, Endangered, or Critically endangered, and non-threatened describes Least concern and Near-Threatened assessments. For each species, we added these time-calibrated threat assessments to their captive and wild time series. We also included the period's species were not assessed and described them as not evaluated (NE). We considered species assessed as Data deficient (DD) as NE, as a DD assessment concludes there was inadequate information to make a full assessment and as such the species threatened or non-threatened status cannot be implied. All use of the terms threatened, non-threatened, and specific statuses such as vulnerable or endangered are based on the IUCN Red List assessments, not regional or country-specific terminology such as endangered or threatened as per US Endangered Species Act.

To this final dataset, we add the previously cleaned and imputed life-history trait database. This resulted in a final database of 779 traded bird species each with two series of up to 19 years each (2000 – 2018, one for captive and one for wild trade) with corresponding threat statuses calibrated through time and species-level life-history traits (final data contained 27,640 records).

Statistical analysis

Part 1 - Traits in trade and listings

To examine the first set of hypotheses - whether certain life-history traits correlate with a species probability of being traded (generally or through CITES) or CITES-listed, we modelled whether a species was traded generally, CITES-listed or CITES traded (recently since 2015, or historically since 2000) against the species life-history traits. We ran four separate models (probability of a species being traded generally, CITES-listed and CITES traded recently and historically), each assuming a Bernoulli distribution. The life-history traits modelled were log body mass, log age at first breeding, annual adult survival rates, and log maximum longevity, each was standardised prior to analysis (mean centred and standardised). All logs were taken using base two, this was done to lessen the influence of a very small number of extremely high values (Figure S1). Due to the unlikely, but possible scenario that some of our demographic traits are perfectly correlated, we assessed this prior to fitting using Pearson's correlation coefficient and found no such evidence (all correlations < 0.75), multicollinearity was assessed post-fitting see below.

In addition to these four population-level effects, we incorporated species phylogenetic non-independence. From published avian phylogenies (Jetz et al., 2012) we downloaded 1000 complete trees covering 9993 species. As described previously, we resolved our 10,254 species to 9839 distinct species in the phylogenies (resolving instances where species once considered synonymous are now split or where sub-species are now classed as separate species). From the 1000 complete trees, we resolved this to one maximum clade credibility tree and pruned this to our species list. From this, we calculated the phylogenetic variance-covariance matrix. We then fitted our model as a phylogenetic multilevel model, incorporating this describes the covariance between species as per the matrix. Such a model specifically asks whether species with a high trait (e.g., body mass) for their combination of other traits (e.g., longevity, age at first reproduction and adult survival) are more likely to be traded/listed. A commonly used alternative method to examine associations between several traits would be to fit each separately as the sole predictor, we did not do this because such a method could mask redundant associations (e.g. there is no value in also knowing trait *x* if trait *y* is known). Additionally, independent simple models ignore potentially hidden relationships common with correlated demographic traits (e.g. whether having a high body mass for your other trait values is associated with an increased probability of trade).

Priors were specified to be weakly regularising to aid convergence but 0-centred and diffuse as we had little prior certainty of direction or magnitude of effects (normally distributed, mean = 0, SD = 1). Each model was run for a total of 1000 iterations, including 500 warm-up iterations, for 4 chains with no thinning.

Convergence was visually assessed using trace plots to ensure comprehensive chain mixing. All parameter Rhat values (scale convergence factors) were further checked to be < 1.05

indicating between and within chain estimates had converged. Posterior predictive checks using the predictive distribution were used to assess individual model adequacy and check for systemic discrepancies between features of the real and simulated data. We further examined the posterior coefficient estimates of each model for evidence of multicollinearity between coefficients. Highly correlated coefficient estimates would be indicative of potentially redundant parameters and inflate variance estimates, e.g., two variables individually may affect presence (being traded) but once you know one variable's effect the other adds little. We found no evidence of this with all Pearson correlation coefficients being < 0.5 and > -0.5 in all models.

Part 2 – Contrasting life history and temporal patterns in captive- and wild-sourced trade

We formulated the simplest theory-driven model of CITES trade through time that respected the structure of the data (namely the time-series nature of observations and the hierarchical structuring of repeated observations across non-independent species). The data contained a high proportion of zeroes (years when species that have been traded are not), e.g., a species may have all zeroes for its captive sourced time series if it is only ever traded from wild sources. Similarly, a species may be traded for some years from both wild and captive sources but then not be traded at all, for example, if trade in a given species was largely banned through effective legislation. To account for this we used a hierarchical joint distributional model, accounting for two separate processes, species not being traded and species volumes when traded. The model uses a hurdle negative binomial distribution (parametrised in Eq.1), where a Bernoulli distribution is used to model species presence and absence in trade, and a truncated negative binomial distribution to model the volume species occur at when they are traded.

$$n \sim \text{Hurdle-NB}(\hat{P}, \mu, \phi) \qquad \textit{Eq. 1}$$

In our parametrisation $\hat{P}$ (subsequently termed *hu*) is the probability of a non-zero value (presence), μ (*mu*) is the mean or location parameter of a negative binomial distribution and ϕ (described as shape or *phi*) is the overdispersion. This method has particular utility to trade data, where separate patterns may associate with species occurrence and volumes, e.g. for a given species, presence may be constant through time but volume may be declining.

The minimum model necessary to respect the structure of the data was defined as the fixed effect of time (the years 2000 – 2018, reduced to 0 – 18), source (a binary variable indicating wild or captive source), threat category (a 3-level category, not-threatened, threatened and not evaluated). We further included the 3-way interaction (and lower-order 2-way interactions) of the three variables. This is necessary as previous research on a coarser scale has shown the diverging trends for captive- and wild-sourced trade (Harfoot et al., 2018a) and at the species level that threat correlates with differing temporal trends (Morton et al., 2022). Logically, this is also essential as national legislation and therefore trade, varies depending on whether the source is wild and captive and less abundant threatened species are less likely to be traded in comparable volumes to more abundant non-threatened species. We used a hierarchical structure allowing species intercepts to vary per source and the temporal year trend to vary per source within species (including the main effect of year). Again this is essential to capture the many species only traded from one source and allow species trends to vary freely, as assuming the temporal trend for all wild-sourced species to only increase or decrease (fixed effect only) is inherently flawed. To incorporate residual temporal fluctuations or shocks (such as large-scale bans e.g. EU wild bird ban or novel avian diseases e.g. H5N1), we created a categorical year variable (19 levels) and incorporated this as a group effect with varying intercepts per source. Allowing fluctuations to vary per source is logical, from a simply legislative view wild or captive sourced trade will be subject to varying legislative shocks.

To this theory-based minimum model, we added the fixed effects of our relevant life-history traits. Body mass, maximum longevity, age at first reproduction (all logged using base 2 to lessen the influence of extreme values), and adult survival. We allowed these variables to vary by source to examine whether traits associate differently by source. This is logical as certain combinations of traits are potentially less amenable to captive breeding. As discussed previously, we did not fit the traits independently in separate models, both due to the previously mentioned reasons and the structure of the data necessitating additional terms. Likewise, we don’t use variable selection for the four traits as this is known to produce biased parameter estimates, instead, we present the full model as outlined above (Forstmeier and Schielzeth, 2011; Freckleton, 2011). All continuous variables were mean-centred and standardised. We examined whether any traits were perfectly correlated prior to fitting using Pearson’s correlation coefficient, and found no such evidence (all correlations < 0.75), multicollinearity was assessed post-fitting see below. This full model structure was used to parametrise both presence (*hu*) and volume when traded (*mu*) sub-models.

We incorporated taxonomic variation dependent on phylogeny via phylogenetic covariance matrices as a separate group effect for both *hu* and *mu*. These covariance matrices were derived using the same method as discussed previously. Zero-centred, diffuse priors (normally distributed mean = 0, *SD* = 1) were specified for model slopes (β), intercepts (α), and standard deviations (σ) (a default *lkj(2)* prior was used for the correlations between grouping factors). Weakly informative zero-centred β priors were used to guard against overfitting as they reflect scepticism of large values and shrink posterior estimates towards zero (Winter and Bürkner, 2021). This model was run for a total of 4000 iterations, including 1000 warm-up iterations, for 4 chains with no thinning. See Figure S2 for a summary of the full model parameter estimates.

Convergence was visually assessed using trace plots to ensure comprehensive chain mixing. All parameter Rhat values (scale convergence factors) were equal to 1.00 indicating between and within chain estimates had converged. All effective sample sizes were in the thousands. Posterior predictive checks using the predictive distribution were used to assess individual model adequacy and check for systemic discrepancies between features of the real and simulated data. Due to the extreme spread in trade data, we paid particular attention to checking the dispersion and the proportion of predicted zeros of our predictive distribution. Standardised residuals were visually inspected to ensure no clear underlying temporal or trait-based trends were present. We further examined the posterior coefficient estimates for evidence of multicollinearity between coefficients and found no evidence of this with all Pearson correlation coefficients being < 0.5 and > -0.6 indicating no strong correlations between estimated coefficients.

Model interpretation

Part 1 - Traits in trade and listings

Estimated coefficients and their distribution were used to assess the association of traits with trade presence or presence in the CITES listings. Due to the relatedness of demographic traits, the direct association of each trait must be viewed as the estimated change when other traits are held constant. To aid visualisation we plotted the marginal effect of each trait for the average species when the other traits are held constant at the mean.

Part 2 – Contrasting life history and temporal patterns in captive- and wild-sourced trade

Estimated coefficients and their distribution were used to assess the association of variables with trade presence and volume when traded. We explored whether traits have contrasting associations between trade sources, e.g., does increasing trait *x* associate with increased captive trade presence but decreased wild trade presence for the average species. To determine whether associations differed between captive and wild trade we contrasted the fixed effects from each source (for both hu and mu separately, see Table S4 and 5).

For the temporal trend for the average species (excluding species-level variation), we calculated the marginal fixed effect of time per source and threat (e.g., wild-sourced and threatened, captive and threatened etc.). For this, we assumed the mean value of all traits. This can then be interpreted as the per standard deviation increase in year what is the change in presence or volume for the average species (direct association).

The significance of fixed effects and contrasts was assessed using both effect size and direction. The direction of an association was determined using the probability of direction (*pd*, also termed the maximum probability of effect) which evidences whether a positive or negative correlation exists. We term a substantial positive or negative effect as one with a *pd* > 97.50%, a value shown to be highly correlated with a two-sided *p*-valu*e* of 0.05 (Makowski et al., 2019b). The *pd* was always calculated from the full posterior distribution. All figures with ridge plots show the full posterior distribution, all points are posterior medians and all uncertainty intervals are the 90% highest density continuous interval (HDCI) calculated from the full posterior.

The separate parts of the model (*hu* and *mu*) are informative individually, but together the joint hurdle negative binomial distribution offers greater insight. However, as a combination of the two distributions this has no simple coefficients of its own (see *Eq. 2*). To understand the associations of increasing values of year and trait (body mass, adult survival, age at first reproduction and maximum longevity) on this joint distribution we approximated the first derivative using the finite differences approach (see methods (Simpson, 2018) and supplementary methods for details).

$$Joint\ distribution = \left(\frac{\mu}{1-\left({}^{\phi}/_{\mu+\phi}\right)^{\phi}}\right) * (1-\hat{P}) \qquad Eq.\ 2$$

All draws were used to estimate the first derivative estimates and these were then summarised to the median and 90% HDCI. The first derivatives were back-transformed from the mean-centred and standardised forms back to the relevant variable scales to aid in interpretation. Therefore, the first derivative in the year 2000 can be directly interpreted as the estimated change in volume (WOEs) when the year increases by 1-year (see Supplementary methods for details of this). The same protocol was followed for traits, with one focal trait per calculation of the first derivative, all other traits were held at their mean and year held as 2018. Representative values were selected for each trait at which the first derivative was calculated (0.3, 0.4 and 0.5 for adult survival, 100 g, 1000 g, and 10000 g for body mass, 1, 3, and 5 years for age at first reproduction and, 5, 15 and 30 years for maximum longevity). For body mass, age at first reproduction and maximum longevity the first derivative can be interpreted as the per year or gram change in volume. As adult survival is bounded by 0 and 1, a change of 1 is uninformative, we transformed the derivative here so it can be interpreted as the per 0.1 change in adult survival effect on volumes. Joint distributional plots of the posterior expectation were further made to ease visualisation. These marginal effects held each non-focal trait at its mean, and the year was held at 2018.

To examine whether trade from captive and wild sources were diverging within a species, we repeated this at the species level. The first derivatives of the joint distribution at reference years (2000, 2010 and 2018) for each species were derived. Trait values correct for each species were used. We then calculated the difference in these slopes (difference = captive slope – wild slope, per species, per reference year). Here a positive value would mean captive slopes are more positive than wild-sourced slopes and vice versa. Differences in volumes between captive and wild-sourced trade per species were calculated directly from the processed trade data for the same years. Here we assessed the slopes and differences in slopes as whether the 90% HDCI included zero.

All data handling and analysis were done using R 4.0.2. Subsequent data processing was completed using “*dplyr*” (Wickham et al., 2021), phylogenetic imputation and handling of trees used “*Rphylopars*” (Goolsby et al., 2017), and “*ape*” (Paradis and Schliep, 2019), models were fitted and assessed using “*brms*” (Bürkner, 2017), “*tidybayes*” (Kay, 2020) and “*bayestestR*” (Makowski et al., 2019a) and all plotting used “ggplot2” (Wickham, 2016).

4.4 Results

Life-history traits in trade

The association between all life-history traits and the probability of species being generally traded, CITES-listed, and CITES traded historically (2000 to 2018) or recently (2015 to 2018) remained largely consistent (Figure 1A - D). As hypothesised, species probability of occurring in general trade and CITES trade (Table S1) was greatest for low adult survival rates, and no clear association was seen with species listing. There was no clear correlation between species age at first breeding and the probability of species being in general trade, CITES-listed, or historically traded under CITES (only in recent trade was there an association). As in previous studies (Scheffers et al., 2019), body mass had a clear positive association (Figure 1A, B, C and D, Table S1), with the highest probability of being traded or listed at high body mass values (Figure 1G). Contrary to our initial hypotheses, increasing species longevity was associated with a greater probability of being in trade and CITES traded (both historically and recently). Only a CITES listing showed no clear association with species longevity (Table S1).

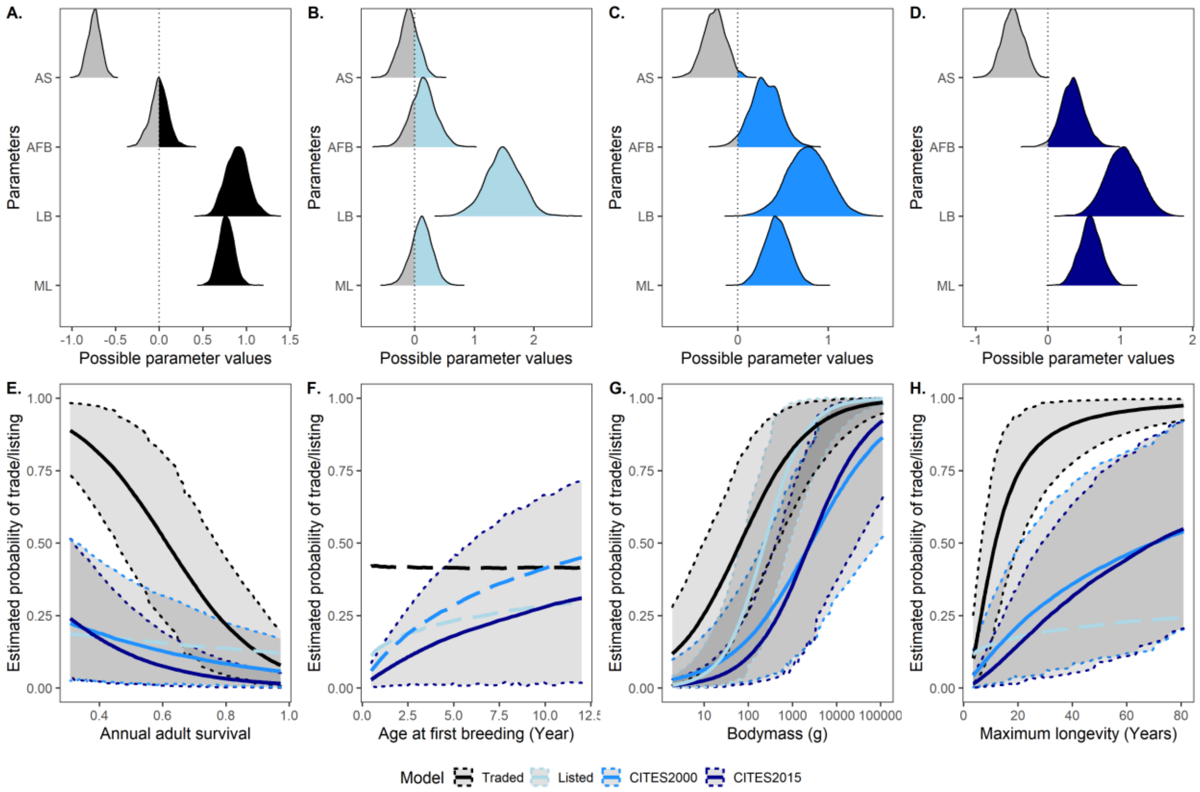

Figure 1. Association between life-history traits and species probability of trade and listing in the Appendices. A – D. Life history parameter estimates from traded (A), listed (B), CITES-traded historically (since 2000) (C) and CITES-traded recently (since 2015) (D) models. All estimates are the direct effect assuming other traits are held constant. Traits are abbreviated as follows, AS (adult survival), AFB (age at first breeding), LB (log body mass) and ML (maximum longevity). E – H. Conditional posterior probability estimates for each life-history trait: adult survival (E), age at first breeding (F), body mass (the axis is on a log10 scale for clarity, G), and maximum longevity (H). Colours denote the model, lines denote medians, and long-dash lines are used when the coefficient direction is uncertain. Grey shading shows the 90% highest density interval for those with a direction. Conditional estimates are estimated across the full range of that trait (e.g., adult survival) with the remaining traits (e.g., age at first breeding, body mass, and longevity) held at their respective mean.

Contrasting traits in CITES trade

The association between life-history traits and traded volumes varied by the source of traded species (Figures 2 and S4). For the average non-threatened species traded volumes were greatest at lower rates of adult survival. At low values of adult survival (Figure 2A and B), an increase of 0.1 in survival was associated with a decrease of 14.94 WOEs (90% HDCI: -50.54 to -0.54, *pd* = 99.89%), with this decrease shrinking at increasing values of adult survival (Figure 2B). Adult survival had no clear association with wild-sourced trade (Table S6).

Body mass had a minute and uncertain association with both captive and wild-sourced trade for the average species (Figure 2C, D and Table S7). However, within the individual reoccurrence (*hu*) and volumes when traded (*mu*) models, the average reoccurrence of a wild-sourced bird increased with body mass (Table S2 and Figure S4C).

Species age at first reproduction only correlated with volumes in captive-sourced trade, with greater volumes at lower ages (Figure 2E). An increase of 1 year (from age 1) was associated with a 1.57 WOE decrease in volume for the average non-threatened species (90% HDCI: -5.07 to 0.06, Figure 2E and F, for reference ages 3 and 5 see Table S8). Similarly, there were no clear directional correlations with reoccurrence (h*u*) for captive- or wild-sourced trade (Figure S2E, Table S2). For volumes when traded (*mu*), only captive trade showed an association, with increasing ages associated with decreasing volumes (Figure S2F, Table S3).

Maximum longevity correlated with trade from both sources, with the highest captive sourced volumes at high values and wild-sourced volumes highest at low values for the average non-threatened species (Figure 2G). Considering species reoccurrence (*hu*) and volume when traded (mu) coefficients separately, captive reoccurrences and volumes increased with increasing longevity (Figure S4 and Table S2), whereas from wild sources increasing longevity correlated with decreasing in volumes when traded (for non-threatened and threatened species, Figure S4 and Table S3). Maximum longevity was the only trait where the associations with captive- and wild-sourced trade reoccurrence increased with divergent trait values (Table S4 and S5).

There is mixed evidence that general trade (Figure 1) or CITES trade (from either captive or wild sources, Figure 2) associated specifically with biologically faster or slower reproducing species. For example, both species with high longevities for their combination of other traits (e.g., *Poicephalus* species, long-lived but comparatively smaller body-sized) and species with relatively low adult survival rates (e.g. *Agapornis* species, comparatively low survival for their longevity) are prevalent in trade.

Evidence is also mixed as to whether captive- and wild-sourced trade is associated with different spectra of species traits (Figures 2), with multiple traits associated with increasing captive volumes but fewer associated with the wild-sourced trade. This potentially reflects the greater influence of traits in determining what species are suitable to be captive-bred at scale. The starkest difference remains in the magnitude at which trade occurs, with wild-sourced trade, regardless of trait value, remaining low (Figure 2).

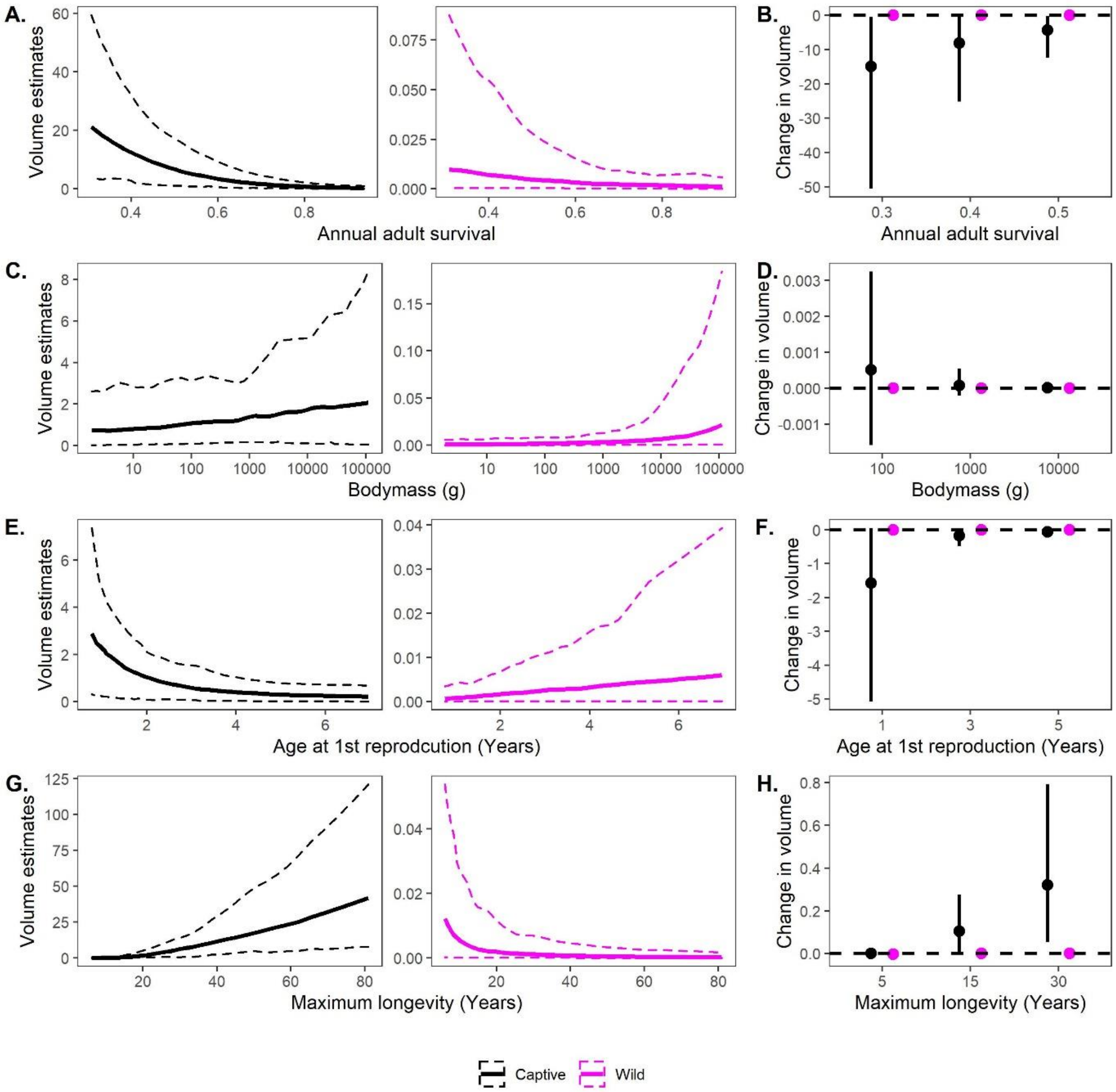

Figure 2. Joint volume estimates across trait values. The first column shows marginal effect plots for the posterior of the full model for the average non-threatened species with the year fixed at 2018, with all traits bar the focal trait held at their mean. Panels show the marginal plots for adult survival (A), body mass (C), age at first reproduction (E), and maximum longevity (G). Estimates for captive trade are in magenta and wild-sourced trade in black, these are shown in separate sub-panels for clarity due to magnitudes of difference. Traits were transformed back to their original scale with only body mass presented on a log10 scale for clarity. The second column (B, D, F H) shows the first derivative, the change in volume per 1 unit (gram or year) change in trait at reference values. For

adult survival, the change is per 0.1 increase in survival. Solid points and lines are posterior medians and dashed intervals are the posterior 90% HDCI. See Figure S4 and Tables S2 – S9 for a further breakdown of this.

Global temporal trends in the captive and wild trade through CITES

Overall, trade sees initially high wild-caught volumes declining dramatically in 2007 and then remaining low (Figure 3A), with species richness declining similarly. Threatened species have consistently comprised a low portion of both richness and volume. Captive trade did not follow the inverse pattern (Figure 3). Volumes were also initially high in 2000, before a more gradual decline to their lowest in 2007, followed by a subsequent increase. The 2007 drop in wild-sourced trade can partly be attributed to the EU wild bird ban that came into effect in October 2005, which was largely aimed at reducing the spread of avian flu and other diseases (Cardador et al., 2019).

Captive-bred richness across threat statuses remained relatively stable through time, indicating that not all species lost from the wild-sourced trade are compensated in the captive-sourced trade. This loss suggests a high temporal turnover in traded species, further highlighting the need for more research on why species disappear from wild trade and why they do or do not reappear in captive trade. Part of this is likely due to different traits more likely to occur from each source. For example, abundant shorter-lived species more common in wild-sourced trade, potentially opportunistically extracted and traded, may be less likely to make the shift to captive-sourced trade, based on the relative costs and benefits of setting up and maintaining facilities for breeding.

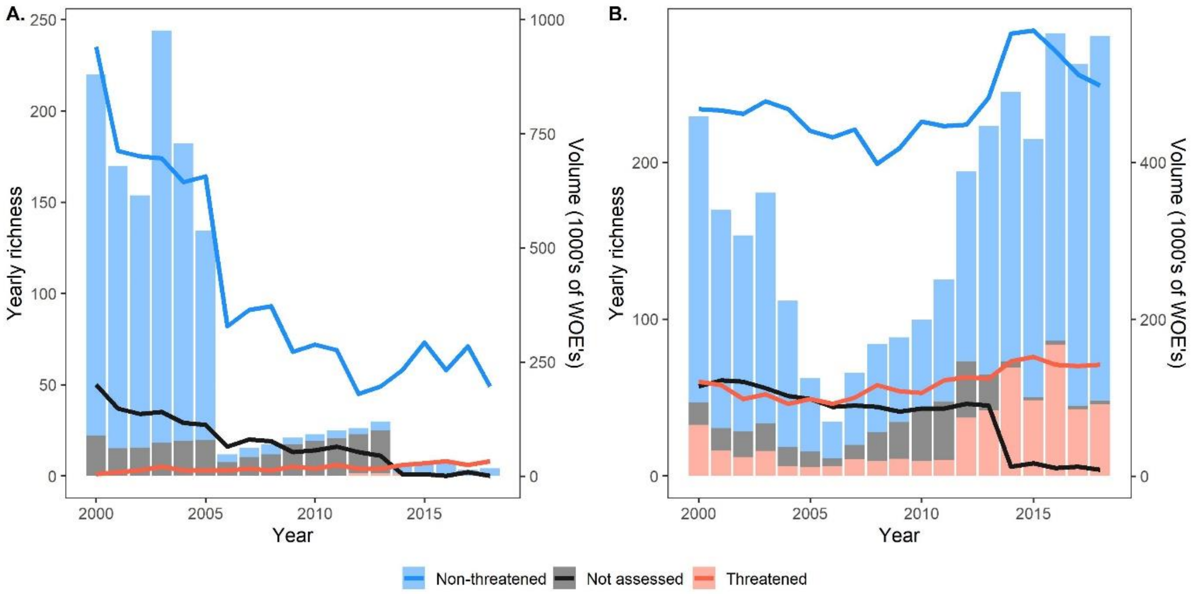

Figure 3. Captive- and wild-sourced volumes and richness 2000 – 2018. A. Species richness (lines) from wild sources overlaid on total traded volume (bars) from wild sources. B. Species richness (lines) from captive sources overlaid on total traded volume (bars) from captive sources. Note the different scales between plots.

Estimated volumes of trade for the average not assessed species were low and uncertain from captive sources (Figure 4A), while wild-sourced volumes declined rapidly in 2000. Similarly, wild-sourced trade for the average non-threatened species fell rapidly from 2000 (median yearly change = -0.41 WOEs, 90% HDCI: -1.42 to 0.01, *pd* = 100.00%, Figure 3D), whereas the captive-sourced trade increased ever faster (Figure 4B and E). Volumes for the average threatened species were low and uncertain from captive sources, while the wild-sourced trend showed a gradual increase (Figures 3C and F, and Table S11). These trends were reflected in both species presence and volumes when traded when both parts of the model are examined individually (Figure S5 and Table S10).

As non-threatened species represent the majority of traded species, this is indicative of a clear shift in species-level trade from wild-sourced species in 2000 to the dominance of captive-bred trade by 2018 (Figure 4B). While the trade in not assessed and threatened species shows less clear change, they reveal the consistent dominance of captive- over wild-sourced trade, with this becoming clearer in more recent years for threatened species (Figure 4A and C). Even accounting for yearly fluctuations (long-dashed lines Figure 4A, B and C), these patterns hold (Figure S3).

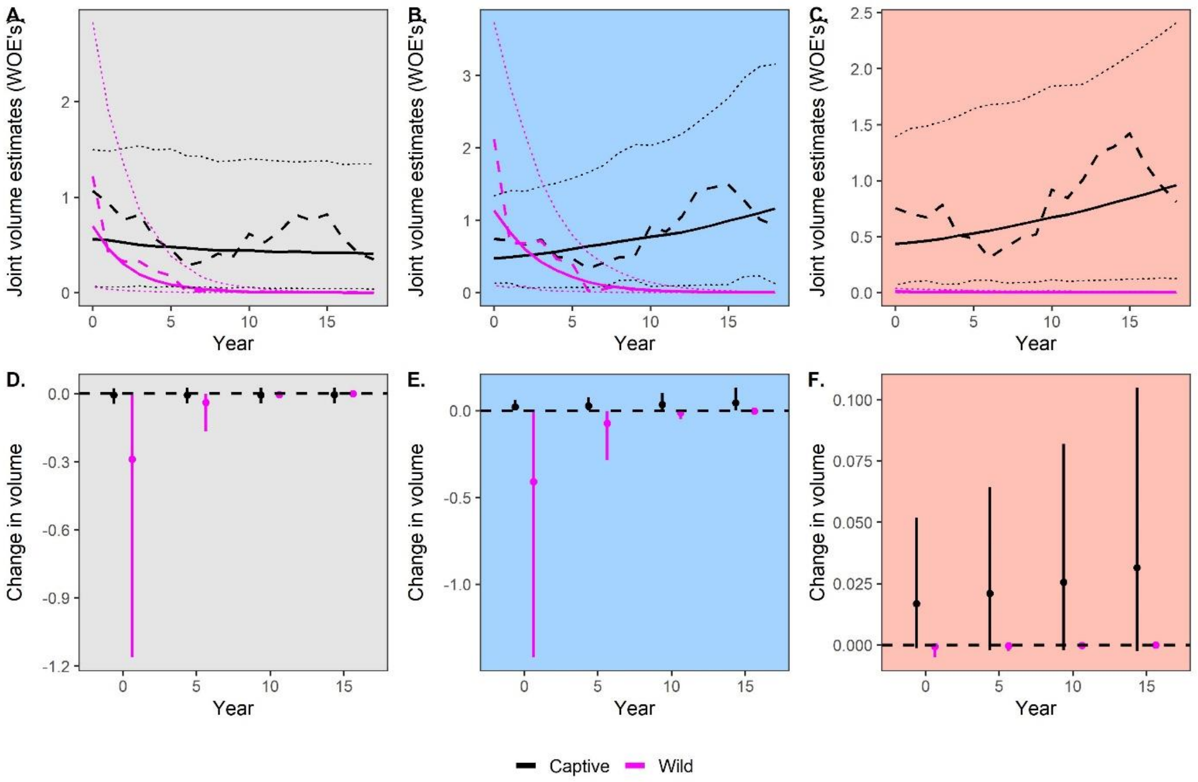

Figure 4. Contrasting captive and wild-sourced trends through time. A-C. Joint marginal estimates of traded volume for the average Not evaluated (A), Non-threatened (B) and Threatened (C) species (all traits set to their mean). The long-dash lines denote the posterior medians when the modelled source-varying yearly fluctuations are included, uncertainty not shown for clarity. D-F. The change in volumes per increase in 1-year at reference values (2000, 2005, 2010 and 2015) for Not assessed (D), Non-threatened (E) and Threatened (F). Lines and points are posterior medians, and error bars and dotted error ribbons are 90% highest density continuous intervals (HDCI). See Figure S5 and Tables S10-11 for a further breakdown of this.

Species trends in the captive- and wild-sourced trade

While traits can co-vary subtly with average trade volumes and presence, species-level variation dominates legal trade. Even among demographically similar species (or within a species across multiple years) traded volumes span magnitudes. A variance decomposition analysis of the joint posterior predictive distribution yielded a median variance ratio of 0.99… (90% CI: 0.99… - 1.00), indicating almost all the variance in yearly traded volumes is recovered by the hierarchical temporal and species-level effects.

While many species are drawn from both captive and wild sources, few do so consistently through time. Our conceptual basis for how species-level captive- and wild-source trends and volumes vary results in four distinct scenarios (Figure 5A). In 2000, the highest proportion of species (*n* = 236/503, 46.9%) fell into the upper left panel scenario, where wild traded volumes exceed captive traded volumes, but median captive volumes are increasing at a faster yearly rate (Figure 5B). However, by 2010, most species fell into the upper right panel scenario (*n* = 238/346, 68.8% with a positive median slope and volume difference), indicating greater species-level volumes from captive than wild- sources, and that these captive-sourced volumes are increasing relative to the wild-sourced trade.

By 2018, this remained true for 69.6% of species in trade (n = 236/339). For 20.0% of these species (n = 68/339), the 90% HDCI was all > 0 indicating greater certainty in the difference. Out of the 75 threatened species traded in 2018, only 8 are traded from wild sources, with 4 traded exclusively from wild sources (less than 20 individuals per species in 2018). Of threatened species, 11 had greater captive volumes and increasing slope differences (upper right panel), and all were not traded from wild sources. This includes the heavily traded, Endangered Sun Parakeet (*Aratinga solstitialis*), with captive trade rising steadily since 2009 to annual volumes greater than 20,000 WOEs.

Only two species fell fully (including the difference in slope 90% HDCI) into the potentially concerning lower left “red” panel. This was the Least-concern Monk Parakeet (*Myiopsitta monachus*) in 2000 (then not evaluated). In 2000, the Monk Parakeet was traded in 11633 WOE’s more from wild sources than captive and that wild trade was rapidly increasing. Trade in the Monk Parakeet has since sharply flipped with the captive trade now dominating and the wild-sourced trade nearly absent. The other species was the Papuan hornbill (Rhyticeros plicatus) in 2010, which was rarely present in captive trade but traded intermittently in low and increasing volumes from wild sources.

At the species level, there is evidence in the upper left panel (Figure 5D) of species recently (2018) being traded predominantly from wild sources but where captive-sourced volumes are increasing faster through time. This is the case for 12 species (where the slope 90% HDCI does not cross 0), an example being the Least Concern Orange-winged Amazon (*Amazona amazonica*), which has historically been traded in volumes magnitudes greater from wild than captive sources. However, in recent years wild-sourced trade has dramatically declined, with captive trade consistently increasing. From our results, it seems possible that the captive trade will soon dominate trade for this and other species. The opposite pattern, when captive species are traded in higher volumes but have decreasing trends relative to wild sources occurs in only ten species. In all cases wild-sourced trade was absent, while captive-sourced trade declined rapidly, thus indicating overall trade declines in these species (E.g. Pale-headed Rosella, *Platycercus adscitus*).

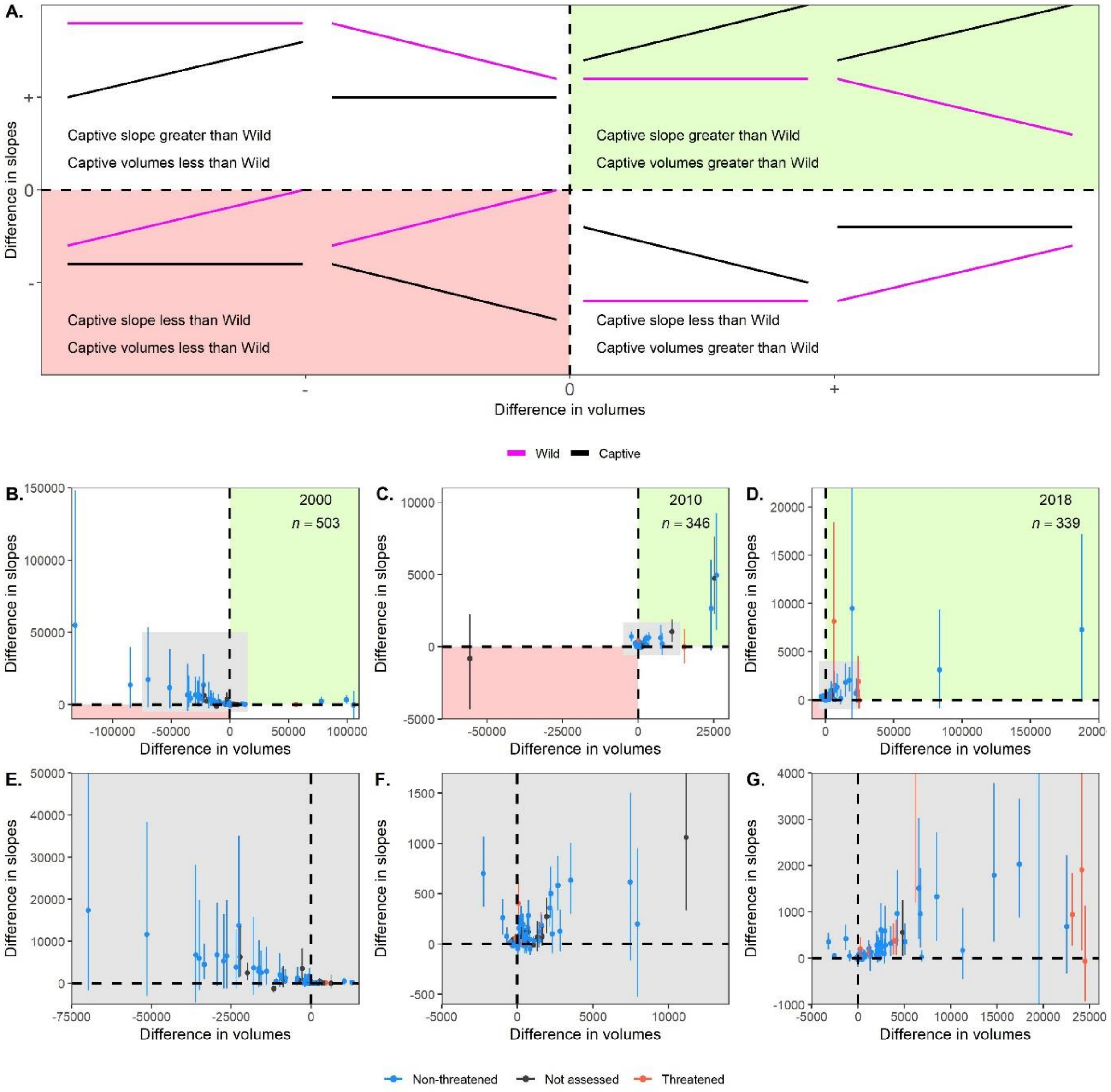

Figure 5. Species-level comparisons of differences in captive and wild-sourced trade volumes and trends through time. A. Conceptual interpretation of +/- slopes and volume differences. Red (wild-sourced) and black (captive-sourced) lines show volumes through time for a figurative species, the illustrative scenarios are examples of volumes and trends that would fall into that quarter they are not the only possible scenarios. The lower left panel in red highlights a potentially concerning scenario where for a given time wild-sourced volumes are greater than captive and the wild-sourced

trend is more positive than the captive trend. The upper right green panel denotes the opposite where for a given time both captive volumes and trends are greater than wild-sourced. B, C and D, show species-level differences in traded volume on the x-axis and median yearly trend differences (slope, see methods) on the y-axis for a given year (2000, 2010 and 2018). Inset *n* gives the number of species traded from either source in the given year, species that were not traded from any source in the selected years were not included here. E, F, and G show the zoomed-in central density of points highlighted in B, C and D. Point colour denotes species threat status in that year. Vertical error bars show the 90% HDCI for differences in species slope, differences in volume have no quantifiable uncertainty as they were calculated directly from the processed CITES trade data.

4.5 Discussion

This study emphasises the large and widening discrepancy between the expanding captive- and shrinking wild-sourced legal trade in wildlife at the species level. Furthermore, we highlight certain traits have clear associations with either captive- or wild-sourced trade. While certain traits have been examined in the context of species desirability in trade (Hinsley et al., 2015), we highlight key less-considered traits that may be crucial in mediating species availability in different types of trade.

Traits in trade

As in previous studies (Scheffers et al., 2019; Yin et al., 2020), we find body mass correlates with species probability of trade and add adult survival and maximum longevity as further demographic traits associated with species presence in both general trade and specifically CITES trade. Larger-bodied individuals have been historically targeted to maximize hunter cost per unit effort (Jerozolimski and Peres, 2003) and globally such species have increased extinction risk (Ripple et al., 2017). While body mass had a clear association with presence in trade, the lack of association between body mass and volumes likely stems from the abundance of small and medium-sized species (e.g. lovebirds, *Agapornis* species) in trade. The increasing volumes of captive-sourced trade from proportionately longer-lived species is likely due to the popularity of large, long-lived Psittacidae in trade (Sanchez-Mercado et al., 2020), a group commonly traded in large volumes and amenable to captive breeding.

The increasing volume of trade with decreasing adult survival in the captive-bred trade, suggests a complementary association with relatively faster-reproducing species for their size or longevity. The prevalence of 1000's (of WOEs) of both characteristically faster breeding (Yellow-fronted Parakeet, *Cyanoramphus auriceps*, annual adult survival of <48%) and slower breeding (Yellow-crowned Amazon, *Amazona ochrocephala*, maximum longevity of 56-years) species in captive trade suggest captive breeding can supply species across the demographic spectrum, rather than focusing only on small, faster reproducing species. Further research could examine whether breeding facilities bird choice is consciously mediated by the ease of breeding or whether the perceived demand for species outweighs this.

The general lack of consistent trait associations within wild-sourced trade suggests that broadly life-history traits may have less influence on this trade. This could be because wild-sourced trade is more opportunistic, dependent on habitat and range features determining how accessible species are, or other less-quantifiable traits could be mediating demand and therefore their volumes. These traits could include song beauty or complexity, plumage pattern or colour, or specific utility (e.g. raptors for sport hunting (Panter et al., 2019)). As captive-sourced trade eclipses wild-sourced trade in both volume and diversity, attention must now be on ensuring the captive-sourced trade is well regulated and does no detriment to wild populations, and where possible benefits them.

Captive breeding opportunities and pitfalls

Evidence of the success of managed captive breeding or ranching for trade exists for a variety of reptilian species, most notably American alligators (*Alligator mississippiensis*) (J. Nickum et al., 2018), and Morelet's, Australian freshwater, Nile, and Saltwater crocodiles (*Crocodylus moreletii, C. johnstoni, C. nilocticus and C. porosus*) (Thorbjarnarson, 1999). In Australia, historical commercial hunting of saltwater crocodiles decimated wild populations (Webb, 2002), but subsequent captive and ranching programs have seen the industry blossom in the Northern Territory, with populations recovering more than 5% annually (Daltry et al., 2016). This further stimulated other businesses, with tourism ventures growing in tandem with the recovered populations, and both commercial facilities and indigenous landowners deriving income from harvested eggs and hatchlings (Daltry et al., 2016). However, the benefits are not always consistent. Vietnam is estimated to have >1100 crocodile farms, predominantly stocked with Siamese crocodiles (*Crocodylus siamensis*), but native wild populations and those in neighbouring Laos have been decimated to stock these farms (Daltry et al., 2016). A 2008 Wildlife Conservation Society report concluded "it is universally accepted that it was wildlife farms that have caused the near extirpation of this species in Vietnam and continue to deplete populations in other range countries".

Captive trade is often discussed as inherently beneficial (Burivalova et al., 2017), but due to absent regulation and oversight there is a high risk of laundering. A study in Kalimantan found all permitted captive breeding businesses had no active breeding programs, thus appearing as little more than a front for wild-caught species (Rentschlar et al., 2018). There are thus considerable implicit risks in expanding captive-bred trade without sufficient regulatory rigour. Nijman and Shepherd (Nijman and Shepherd, 2015) report on the trade of the Papuan hornbill (*Rhyticeros plicatus*), where between 1995 and 2011 over a thousand captive-bred individuals were imported from the Solomon Islands (>70% of the hornbill trade in that period). The lack of any known commercial breeding facilities on the Solomon Islands and hornbills' highly specialised breeding strategy sheds doubt on the veracity of these truly being captive-bred (Nijman and Shepherd, 2015).

For species heavily persecuted by trade such as the Endangered Black-winged Myna (*Acridotheres melanopterus*), which has a wild population estimated at 150 – 190 (BirdLife International, 2021), captive breeding has supplied Indonesian markets for over 20 years, resulting in up to 40,000 individuals in private ownership (Nijman et al., 2018). This vast demand puts pressure on wild populations if even a tiny portion of it is sourced from wild populations, which current research suggests is the case (Nijman et al., 2018). To avoid further scenarios where species are extinct in the wild but have robust private populations, captive breeding programs must be interwoven with conservation outcomes (e.g., reintroduction) and have transparent traceability to guard against laundering.

CITES legislation has supported the expansion and maintenance of captive breeding to supply the trade in listed species, urging Parties to provide "*incentives to captive-breeding operations… such as faster processing of permit applications … or possible reduced export fees*" (specifically regarding Appendix I species) (CITES, 2010). However, even for Appendix I species only relatively sparse biological information and a legal acquisition finding for the parental stock is submitted to the Secretariat, with the main responsibility falling on the Scientific and Management Authorities of the exporting Party. For instance, the

Indonesian captive-breeding production plan used inaccurate or unrealistic biological parameters for 76.7% ($n = 99/129$) of species, 88 species had lower reproductive outputs when corrected parameters were used, and 38 species had quotas set that even exceeded the maximum possible output when the inaccurate parameters were used (Janssen and Chng, 2018). The flawed parameter values and unrealistic quotas further questions whether this was an unintentional mistake or another example of operations utilising wild individuals under a captive label. This type of overt error is why oversight, sense-checking or review must be a prerequisite to trade.

Policy recommendations and conclusions

The literature is comparatively sparse on the success of captive breeding displacing wild trade in bird species. For example, in Java successful efforts to increase captive bird popularity have been largely nullified by a complementary expansion of the wild-caught trade in native birds (H. Marshall et al., 2020b). Reasons for this could include a lack of access to captive-bred birds in areas of high demand and their comparatively high price or the perception that captive individuals are worse singers than their wild counterparts (Burivalova et al., 2017).

We echo our previous call for more public and accessible data (Morton et al., 2022) regarding how CITES Parties and facilities determine captive breeding parameters and the evidence to ensure wild populations are not adversely affected (e.g. being used to stock facilities). This data should at least include the publication of breeding facilities' stock, its origins, and the expected annual production (supported by life-history parameters). There are currently more than 500 CITES registered captive breeding facilities for Appendix I species alone (Appendix II facilities are not recorded). Implementing any form of review or checking of facilities records would be a monumental undertaking, but we can see two possible mechanisms. Firstly, it could be centralised from the CITES Committees and funded directly by the CITES Trust Fund, however this would be unwieldy to implement, time-consuming and stretch existing funding. Secondly, if breeders were mandated to submit such data to an openly accessible platform the data would be easily accessed by researchers, non-governmental organisations and other Parties' Scientific authorities. This approach avoids necessarily checking the records for every facility but makes the data available in the case of suspicious or unlikely seeming trade records. How this would feed into CITES regulations and policy is uncertain. At a minimum, frameworks could be implemented to embed this data collection in the existing Review of Significant Trade process, ensuring for species of potential concern it is available.

In conclusion, the declining wild-sourced trade and compensatory rise in captive-bred trade have great conservation potential to maintain livelihoods and income based on utilisation while sparing species unable to sustain extraction from the wild. However, without improved transparency and either greater Party-level scrutiny or the introduction of a form of independent oversight, declaring captive breeding a wide-scale success would seem naïve.

4.6 Author Contributions

O.M., B.R.S., T.H., and D.P.E. conceived the study idea; O.M. collated the data; O.M. analysed the data and produced the figures with input from B.R.S., T.H., and D.P.E.; and O.M. wrote the first draft of the manuscript with all co-authors substantially contributing to revisions.

4.7 Data Availability

Data and code will be freely available from an institutional repository upon publication.

4.8 Acknowledgements

I would like to thank Emma C. Hughes for providing guidance when reconciling avian taxonomies and phylogenies.

4.10 Supplementary materials

Data preparation (Part 1)

We focused our analysis on traded bird species and then removed all re-exports to avoid double counting (keeping only original exports, where the exporter matches the recorded origin or no origin is given). Where trades ultimately pass through multiple countries, they may be reported multiple times artificially inflating their presence in the data. All trade records listed as pre-convention specimens or seizure events were similarly excluded. All listed trades from any source were kept (subsequent analyses work with subsets classified as either wild-sourced or captive-bred). We further removed all records where the species was indeterminate (e.g. where the species was listed as "*Aves*", "… *spp*" or "… *hybrid*") or where the species was not listed in a CITES appendix (Appendix code "N"). We focused only on exporter-reported values for the main text. However, using only exports could be an overestimation if some records reflect granted permits, not realised trade, so we also present a supplementary analysis using importer-reported values..

Data preparation (Part 2)

After focusing only on trade in birds ("Aves"), all re-exports were removed to avoid double-counting, only original export records were retained, and only exporter-reported values were used to avoid duplicating records. We further removed all species not clearly traded under a CITES Appendix, specified in the data as Appendix "N". Subsequently, we classified the source of trade as either captive, wild, or removed. Using the CITES `Source` variable, we class wild-sourced trades as the codes W, X, or R, captive-sourced trades as codes A, C, D, or F, and removed records where the code was U, *NA*, I, and O (unknown, not recorded, denoting seizures, and pre-Convention specimens, respectively). Commercial trade was defined as all trades with a `Purpose` code T or P, the code P was included following previous studies to capture aspects of the pet trade (Bush et al., 2014). All other codes and NA values were excluded; while some commercial trade may be done under codes such as M (medical) or Q (circus), such codes could also represent non-commercial trades and in light of this uncertainty were excluded.

Volumes in CITES trade are reported as an array of `Terms` (live, skulls, skin fragments, teeth, etc.), which make direct use of the reported `Quantity` misleading. We standardised all records to whole organism equivalents (WOEs) as proposed by (Harfoot et al., 2018a). This allows direct comparison as 1 WOE denotes 1 individual. Building on the existing conversion protocol, we add three additional terms each denoting 1 WOE (eggs, eggs (live), and specimen). We applied this conversion protocol only to records where the `Unit` was given as *NA* denoting the number of specimens. This is necessary as sometimes records are reported in a diverse range of units (Bags, cubic metres, boxes, etc.), which cannot be accurately converted to meaningful WOEs. In total, only 2.9% of avian records could not be converted to WOEs and were discarded. We focused our timeframe on the years 2000 – 2018; while the current CITES data release has records up to 2021, the reporting for recent years is still being collected so we conservatively only include data to 2018.

Using the historic CITES listings, we constructed time series for each species source (captive or wild) combination corresponding to when it was listed (and/or removed or re-listed). For example, a species may have been traded consistently from 2005, but not recorded in the database before that. This could be because the species was simply not traded for those years, or that the species was not listed in Appendices until 2005 so its trade was not recorded. In the former, those years the species was not traded (2000 - 2004) would be recorded as zeroes, whereas in the second case those years would be absent with the species time series only starting in 2005. Species that were only traded from one source were given a complete zero series for the other source (e.g., a species listed from 2000 to 2018 only traded from wild sources has that wild source series and a captive source series of all zeroes). Similarly, we maintained only wild-sourced trade records where the exporter for each record was recorded as a range country for the species as per the IUCN geographic range (accessed via the Red List API using the "*rredlist*" R package).

Model Interpretation (Part 2) – First derivative approach

This first derivative can be interpreted as the slope or instantaneous rate of change at specific values of a variable when others are fixed. A difference value (ε) of 0.0001 was used, values of 0.01 and 0.001 were also tested and results remained consistent. To calculate the model estimated change in volume per increase in year in this way, we selected representative year values (2000, 2005, 2010, and 2015), held all traits fixed (at their mean) and calculated the expectation of the entire posterior distribution for the average species. This was then repeated with the year shifted by the small difference value and the change (slope) between the two points calculated (*Eq. 3*).

$$First\ derivative = \frac{Posterior_{\varepsilon} - Posterior}{\varepsilon} \qquad Eq.\ 3$$

Supplementary reanalysis

As both importing and exporting parties report data to CITES, trades are often reported more than once, although for a number of valid reasons these importer and exporter reported records rarely match up. While we present the main text results using the exporter reported values, it is important to acknowledge that the importer reported data may not reflect the same patterns. Therefore, we present a full reanalysis of all data using the importer reported values. The data cleaning and modelling process used was identical in every other way to the main methods.

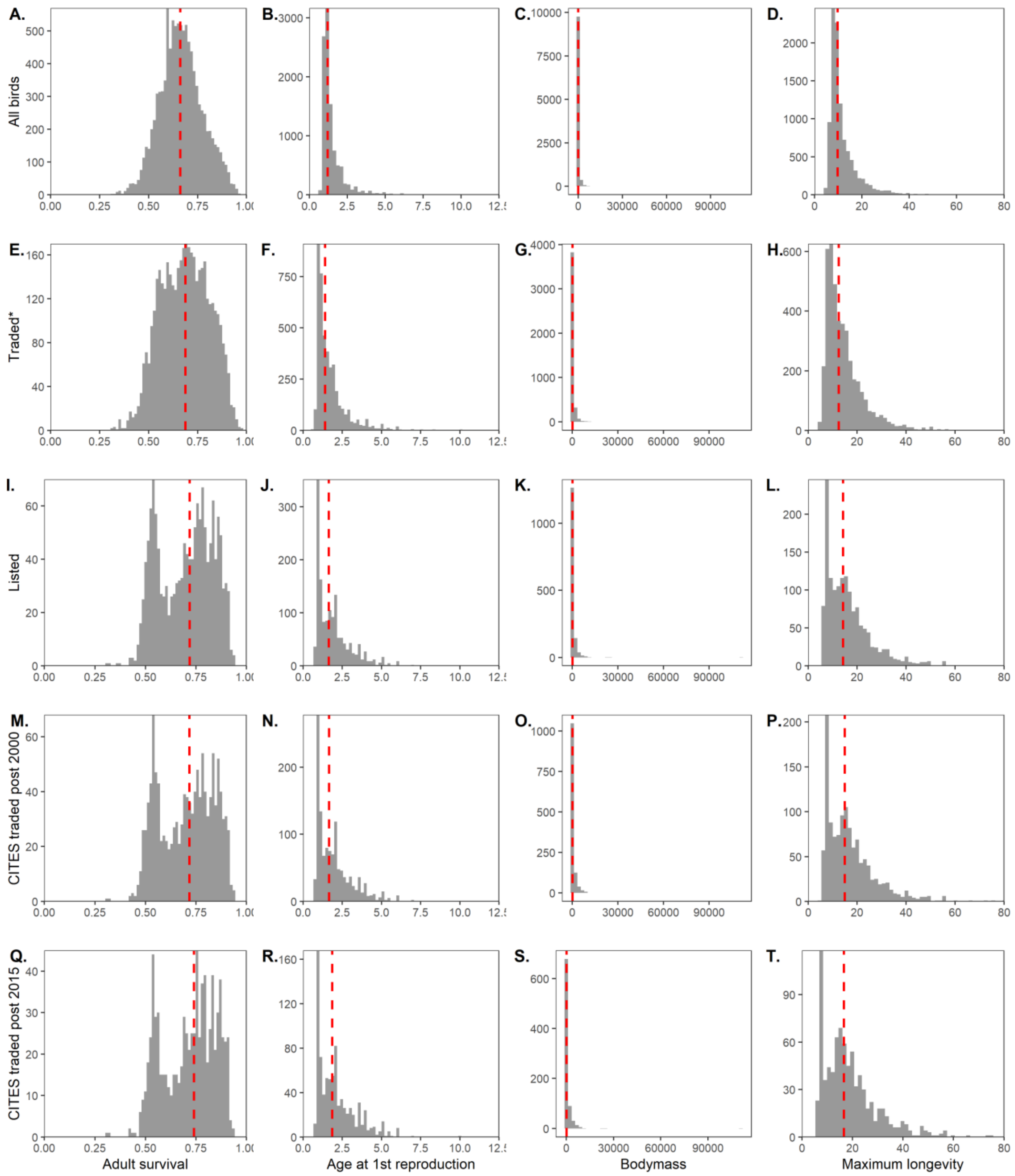

Figure S1. Raw trait distributions. Columns of figures show the distribution of values for each trait (adult survival, age at first reproduction, bodymass and maximum longevity). Rows show the distribution for each trait for all species, all traded species, all CITES listed species, all historically CITES traded species and all recently CITES traded species. Red dashed lines show the median values in each panel.

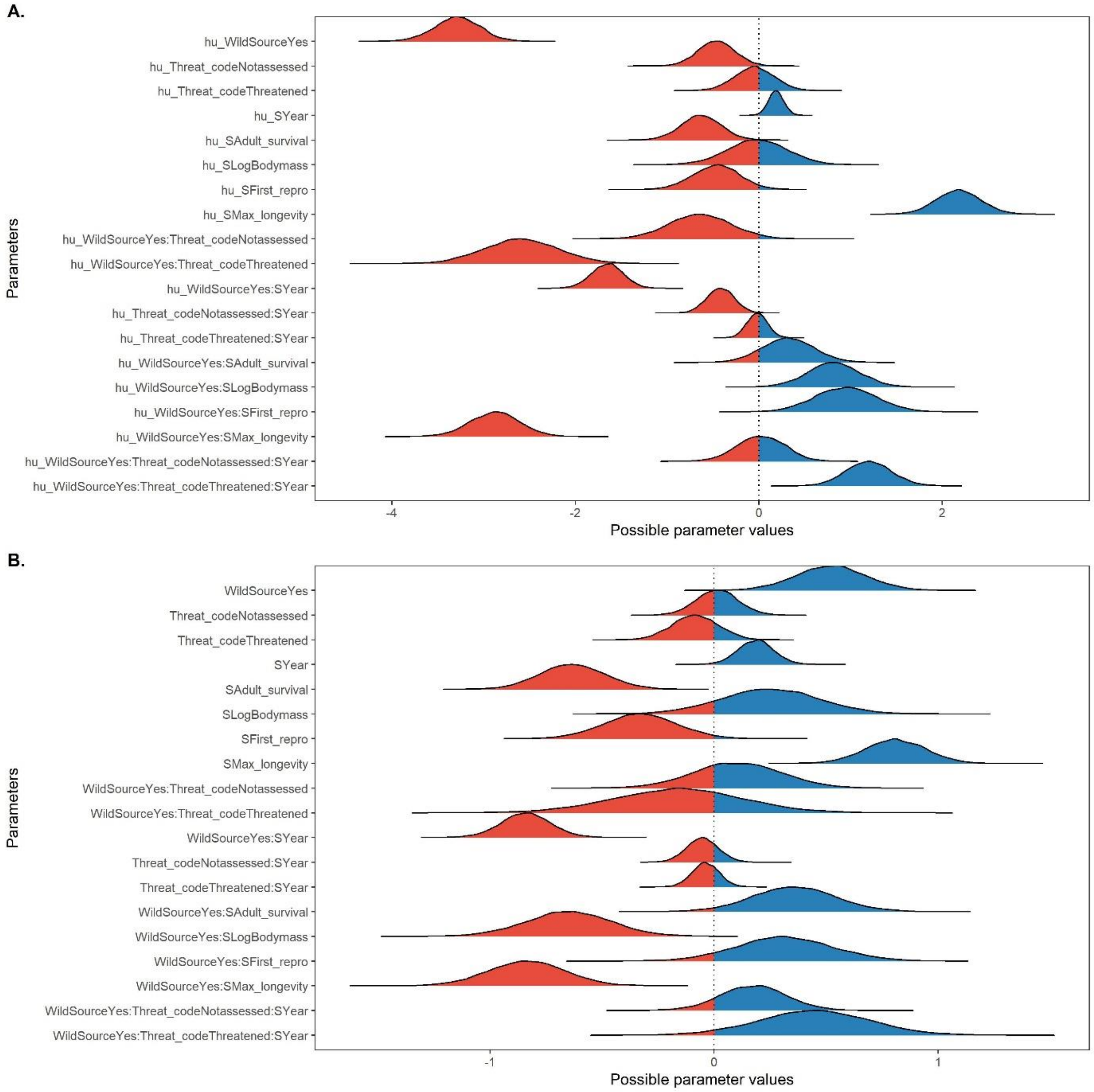

Figure S2. Summary plot of possible modelled parameter values. A. hurdle (pre-fixed by hu) parameter values. B. Negative binomial parameter values. Ridge plots show the entire posterior distribution of each parameter. We caution against the interpretation of any one effect in isolation due to the hierarchy of interactions, e.g. examining *WildSourceYes:SYear* to understand the difference in effect (slopes) between captive (reference level, *SYear*) and wild-sourced trade is specifically only relevant to the reference threat-level (non-threatened) due the higher order three-way interaction of source, threat and time. To contrast temporal trends across sources for other threat levels one must further incorporate the interactions of threat and time, and threat, source and time. See Tables S1 – 6 for such results and summed parameters showing more clearly the estimated association of year for all combinations of source and threat.

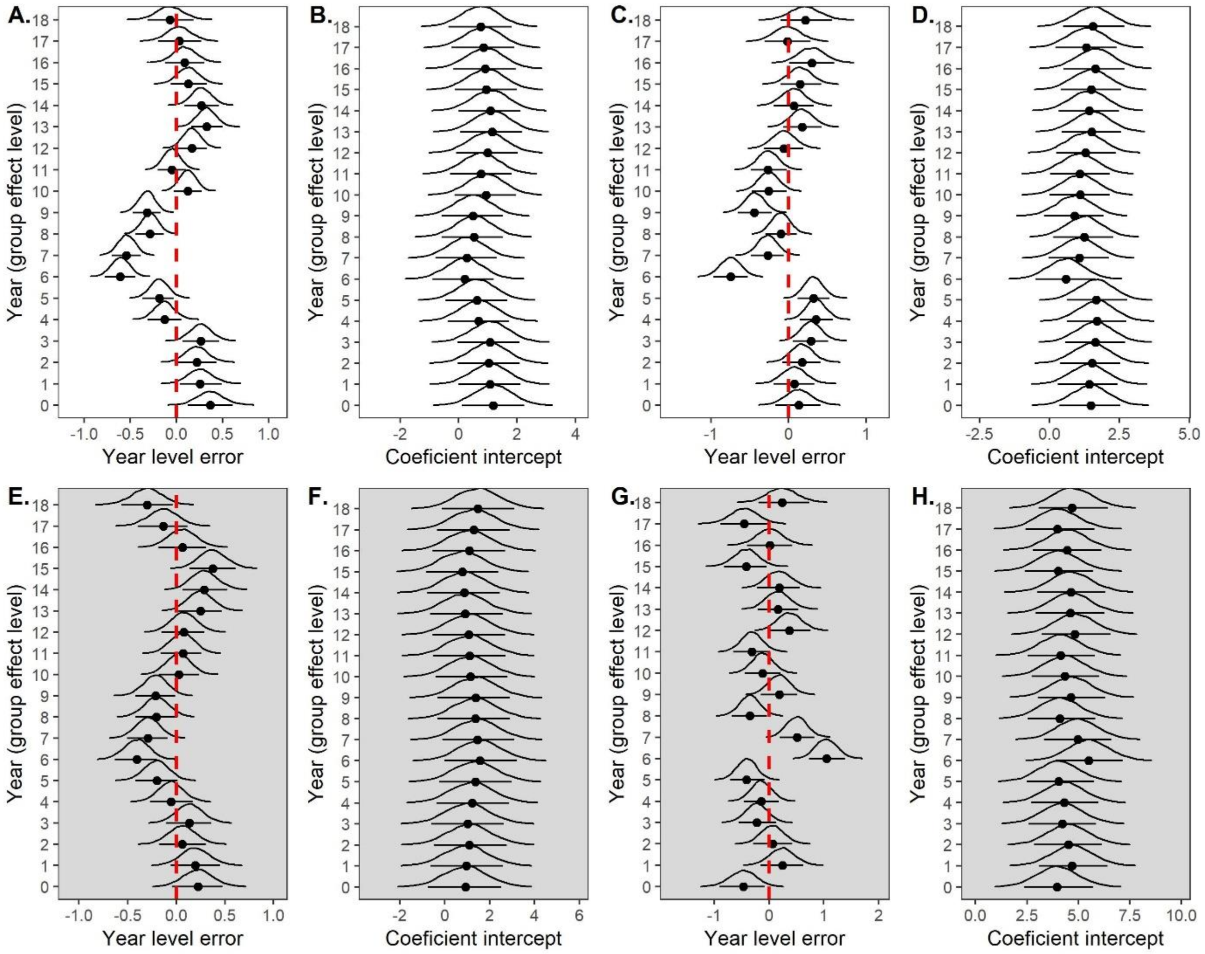

Figure S3. Modelled yearly fluctuations in trade reoccurrence and volume. First row refers to *mu* (log scale) parameter and the second row to *hu* (logit scale). The first column (A, E) shows the deviations from the grand mean for captive sourced trades at the Non-threatened reference level. The second column (B, F) shows the same group coefficient intercept estimates. The subsequent columns refer to wild-sourced trades in non-threatened species as opposed to captive sourced. Points are posterior medians, lines are 90% HDI's and the ridge plots show the full parameter distribution.

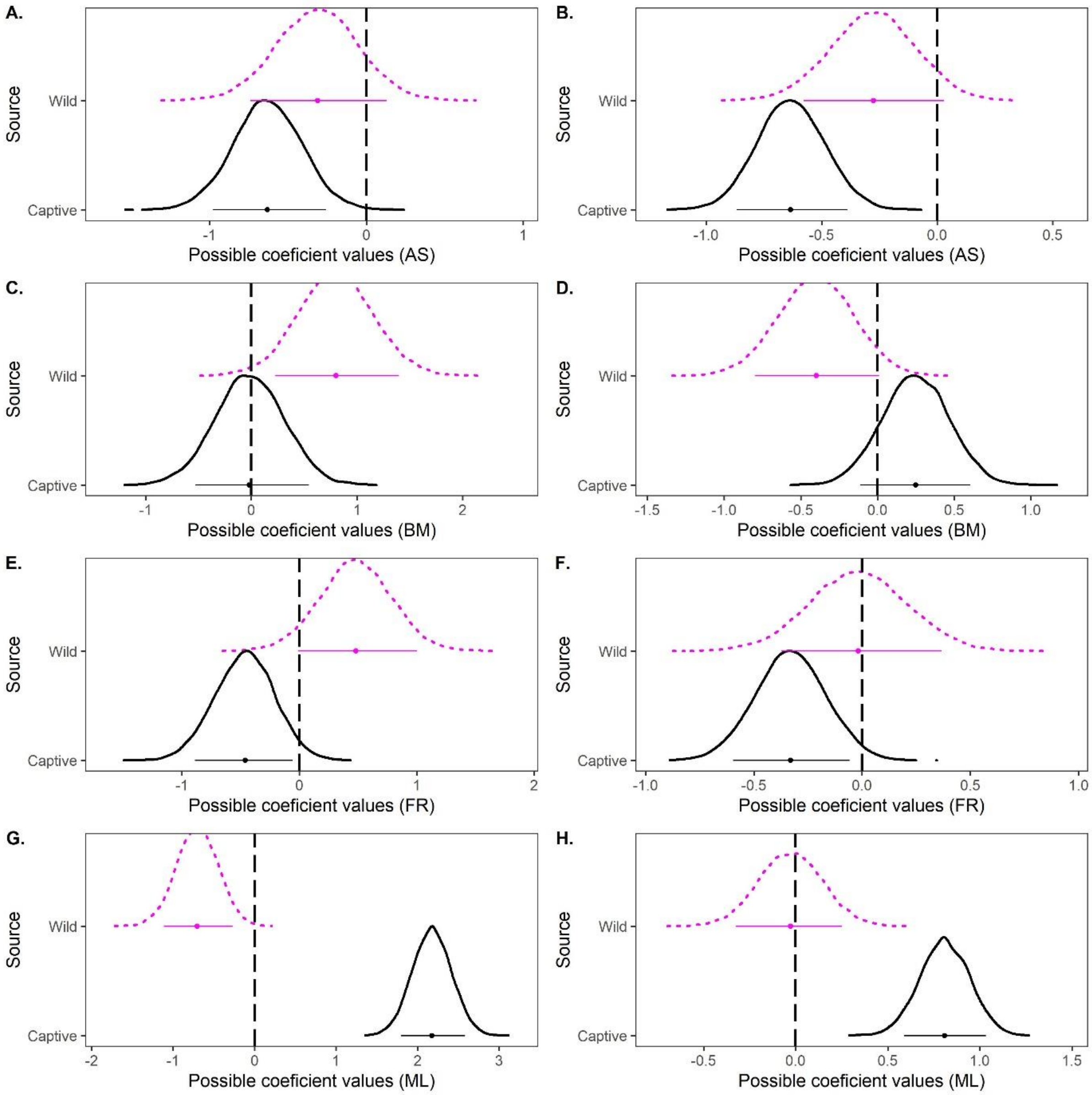

Figure S4. Contrast captive and wild-sourced trait relationships. The left side column examines the *hu* (reoccurrence) parameter and the right the *mu* (volume when traded) parameters. Rows reflect each trait, adult survival, bodymass, age at first reproduction and maximum longevity respectively A, B, C and D. Point and line colours denote wild (magenta) or captive (black) source. A positive value denotes increasing volumes when traded (*mu*) or occurrence in trade (*hu*) is associated with increasing trait values. Lines and points are posterior medians, and error bars and error ribbons are 90% highest density continuous intervals (HDCI). Dashed reference lines at zero. The further marginal interaction of year with traits is set to 0 for interpretation.

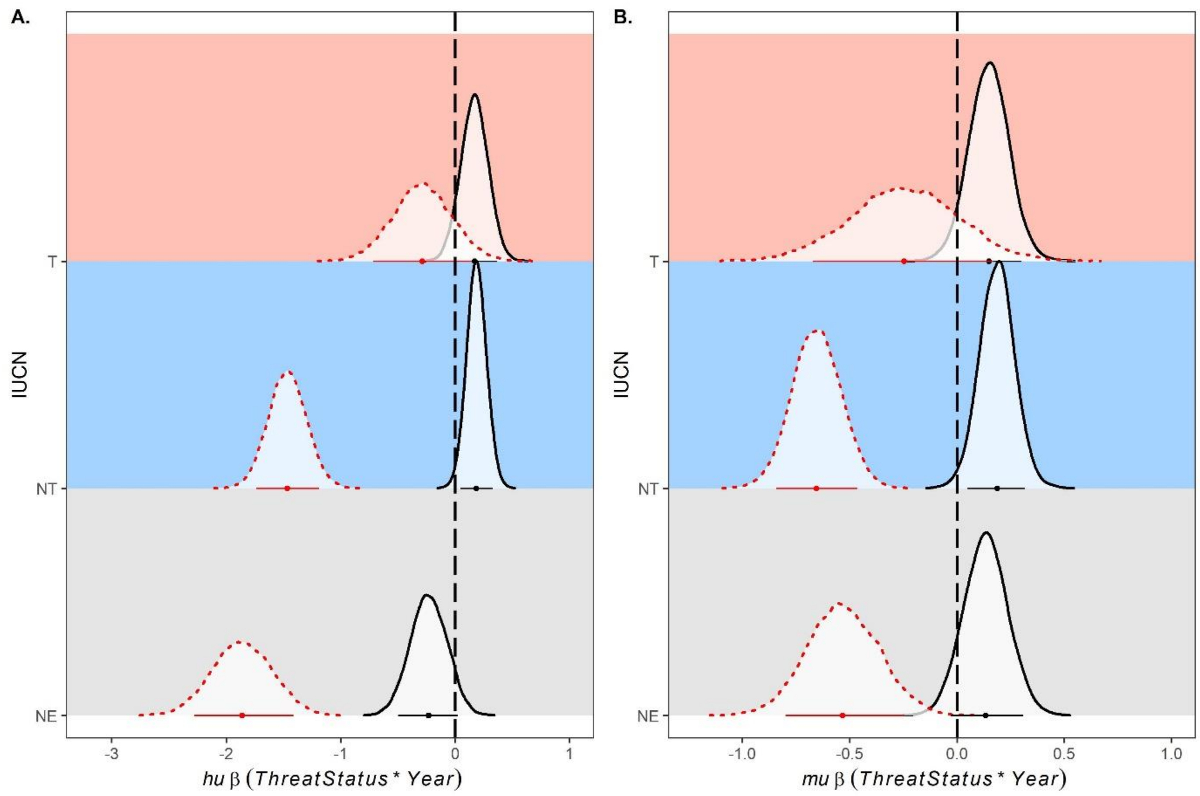

Figure S5. Contrasting captive and wild-sourced trends through time. Coefficients for year by source and threat status (slope) for *hu* (A) and *mu* (B). The marginal interaction of year with traits is set to 0 here for interpretation. Background colours denote threat status (Not evaluated - NE, Non-threatened - NT and Threatened – T, respectively grey, blue and light red) and point and line colours denote wild or captive source (respectively red and black). Dashed reference line at zero. Points are posterior medians and error bars are 90% highest density continuous intervals (HDCI).

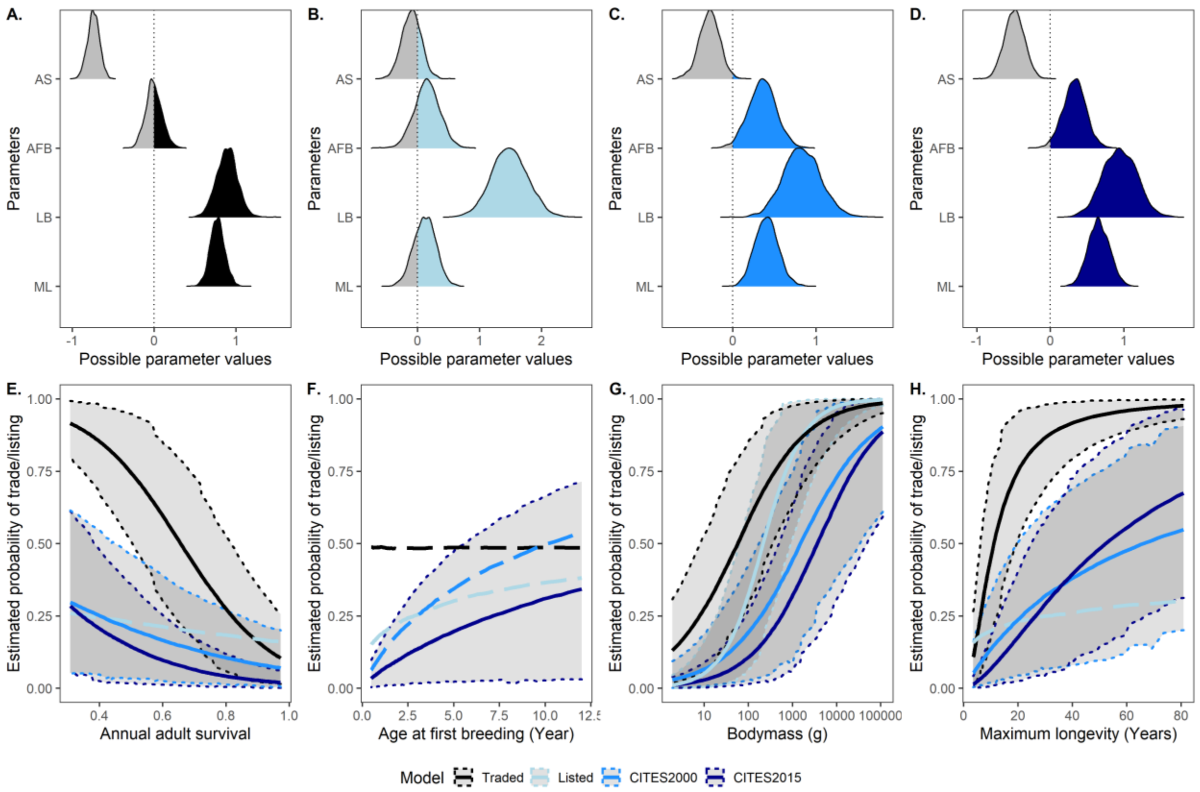

Figure S6. Relationship of life-history traits and species probability of trade and listing in the Appendices using importer reported data. A – D. Life history parameter estimates from traded (A), listed (B), CITES-traded historically (since 2000) (C) and CITES-traded recently (since 2015) (D) models. All estimates are the direct effect assuming other traits are held constant. E – H. Conditional posterior probability estimates for each life-history trait: adult survival (E), age at first breeding (F), body mass (the axis is on a log10 scale for clarity, G), and maximum longevity (H). Colours denote the model, lines denote medians, long-dash lines are used when there is no directional effect (trend direction uncertain), and grey shading shows the 90% highest density interval (interval not shown for parameters with uncertain direction). Conditional estimates are estimated across the full range of that trait (e.g., adult survival) with the remaining traits (e.g., age at first breeding, body mass, and longevity) held at their respective mean.

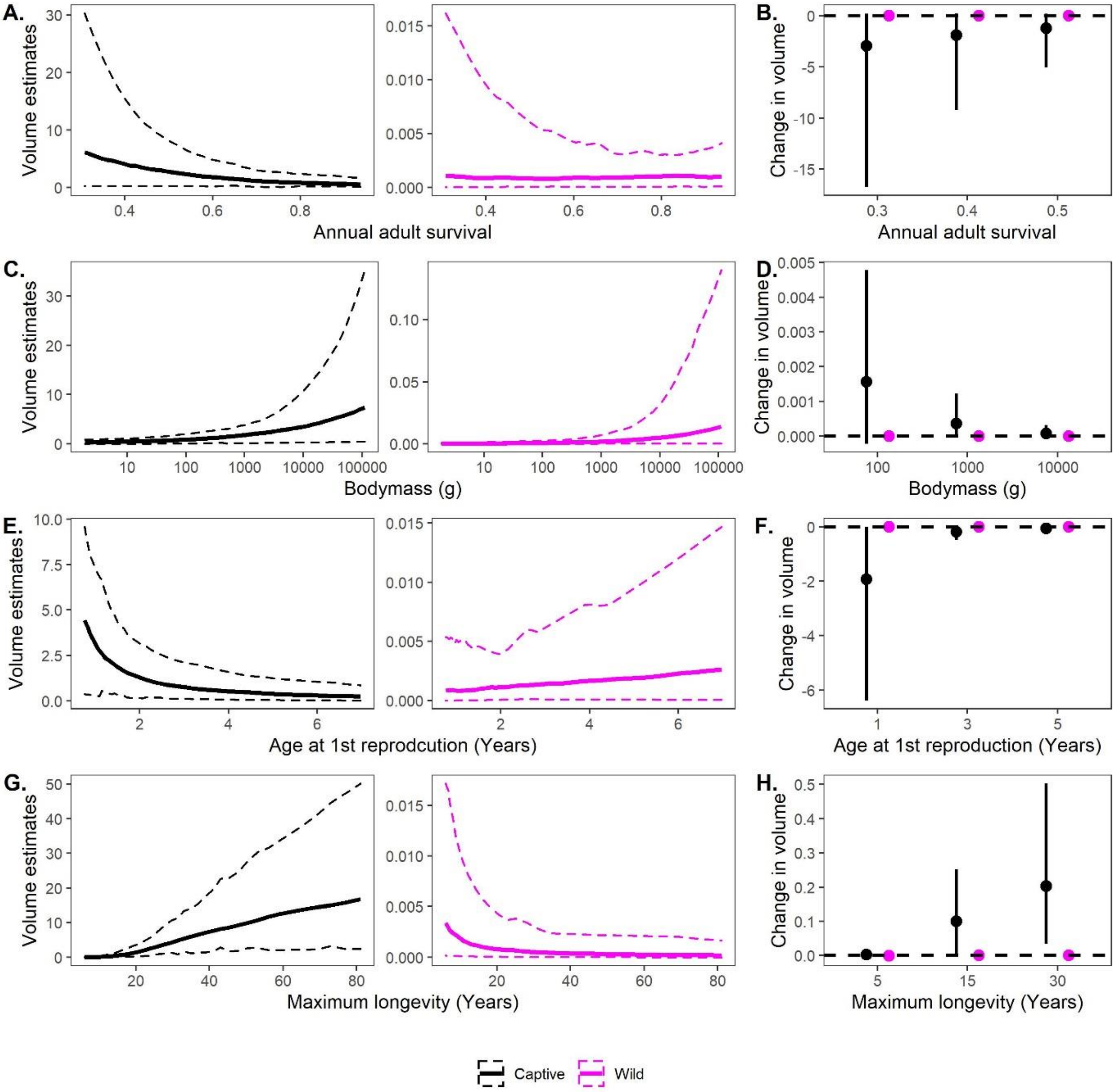

Figure S7. Joint volume estimates across trait values using importer reported data. The first column shows marginal effect plots for the posterior of the full model for the average species with the year fixed at 2018, with all traits bar the focal trait held at their mean. Panels show the marginal plots for adult survival (A), body mass (C), age at first reproduction (E), and maximum longevity (G). Estimates for wild-sourced trade have a grey background (right) and captive-sourced trade a white background (left), these are shown in separate sub-panels for clarity due to magnitudes of difference. Traits were transformed back to their original scale with only body mass presented on a log10 scale for clarity. Lines differ in length as each threat category was not extrapolated beyond the highest observed value of the focal trait. The second column (B, D, F H) shows the first derivative, the change in volume per 1 unit (gram or year) change in trait at reference values. For adult survival, the change is per 0.1 increase in survival. Solid points and lines are posterior medians and dashed intervals the posterior 90% HDCI. See Figure S4 and Tables S2 – S9 for a further breakdown of this.

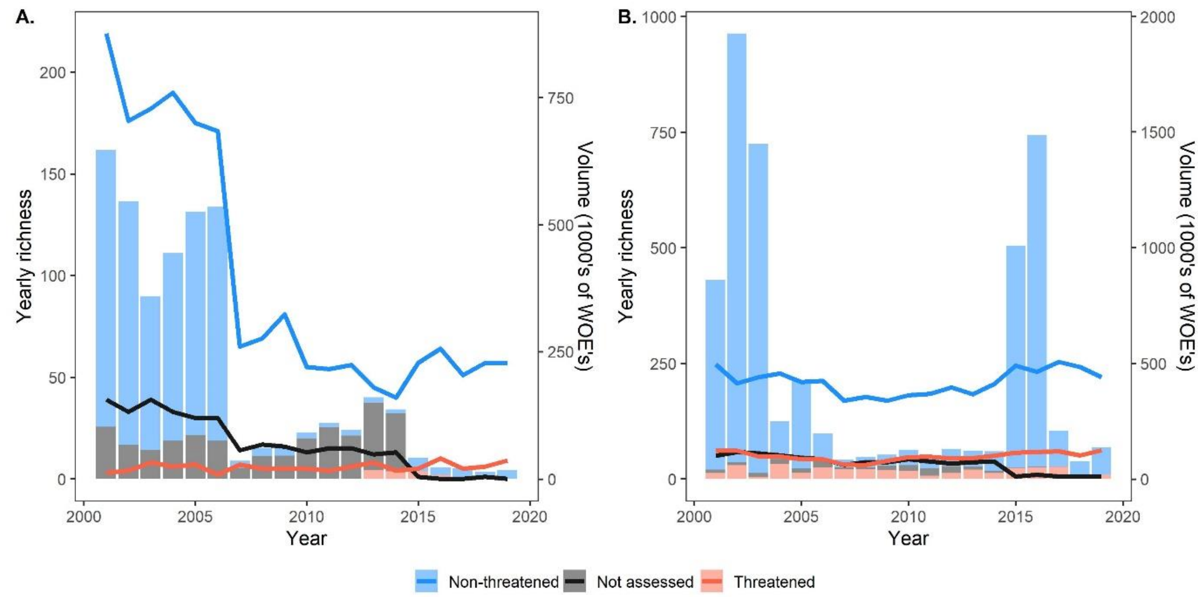

Figure S8. Species captive- and wild-sourced volumes 2000 – 2018 using importer reported data. A. Species richness (line) from wild sources overlaid on total traded volume (bars) from wild sources. B. Species richness (line) from captive sources overlaid on total traded volume (bars) from captive sources. Colours denote threat status blue (Non-threatened), grey (Not assessed) and red (threatened). Note the different scales between plots.

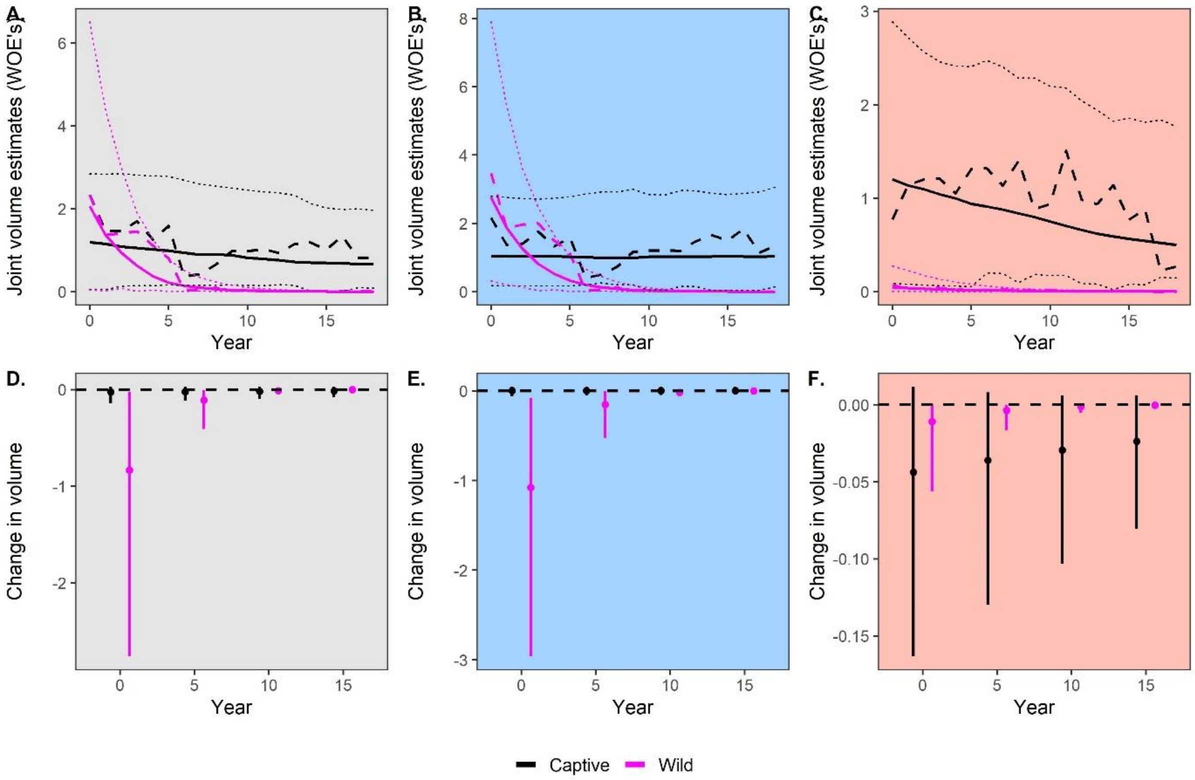

Figure S9. Contrasting captive and wild-sourced trends through time using importer reported values. A-C. Joint marginal estimates of traded volume for the average Not evaluated (A), Non-threatened (B) and Threatened (C) species (all traits set to their mean). The long-dash lines denote the posterior medians when the modelled source-varying yearly fluctuations are included, the uncertainty for these lines is not shown for clarity. D-F. The change in volumes per increase in 1-year at reference values (2000, 2005, 2010 and 2015) for Not assessed (D), Non-threatened (E) and Threatened (F). Lines and points are posterior medians, error bars and dotted error ribbons are 90% highest density continuous intervals (HDCI). See Figure S5 and Tables S10-11 for a further breakdown of this.

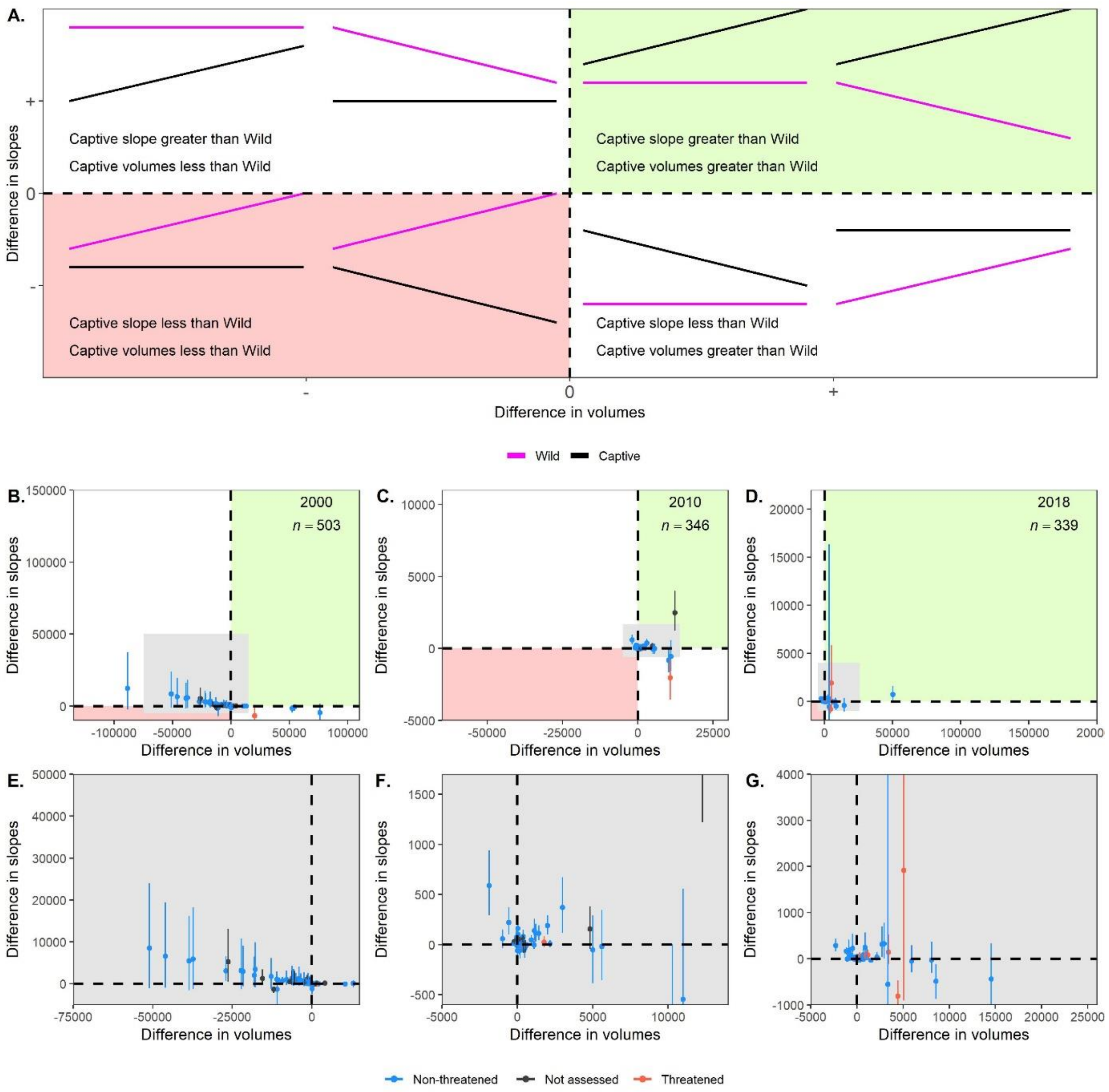

Figure S10. Species-level comparisons of differences in captive and wild-sourced trade volumes and trends through time using importer reported data. A. Conceptual interpretation of +/- slopes and volume differences. Red (wild-sourced) and black (captive-sourced) lines show volumes through time for a figurative species, the illustrative scenarios are examples of volumes and trends that would fall into that quarter they are not the only possible scenarios. The lower left panel in red highlights a potentially concerning scenario where for a given time wild-sourced volumes are greater than captive and the wild-sourced trend is more positive than the captive trend. The upper right green panel denotes the opposite where for a given time both captive volumes and trends are greater than wild-sourced. B, C and D, show species-level differences in traded volume on the x-axis and median yearly trend differences (slope, see methods) on the y-axis for a given year (2000, 2010 and 2018). Inset *n* gives the number of species traded from either source in the given year, species that were not traded from any source in the selected years were not included here. E, F, and G show the zoomed-in central density of points highlighted in B, C and D. Point colour denotes species threat status in that year (red = threatened, blue = non-threatened and black

= not assessed). Vertical error bars show the 90% HDCI for differences in species slope, differences in volume have no quantified uncertainty as they were calculated directly from the processed CITES trade data. Scales used for the main text figure retained here for comparisons.

Table S1. Estimated marginal coefficients shown in Figure 1. Medians and 90% HDCI calculated from the full posterior distribution. The *pd* provides evidence of the direction of effect (positive or negative), parameters with a high certainty of direction (*pd* > 97.50%) are shaded grey.

Model	**Trait**	**Coefficient median**	**90% HDCI**	***Pd* (%)**
Traded as per Scheffers et al 2019.	Adult survival	-0.74	-0.86 to -0.62	100.00
	Age at first breeding	0.00	-0.18 to 0.16	50.35
	Bodymass	0.89	0.67 to 1.08	100.00
	Max longevity	0.77	0.62 to 0.91	100.00
Listed as per CITES	Adult survival	-0.10	-0.35 to 0.17	72.95
	Age at first breeding	0.15	-0.21 to 0.47	76.00
	Bodymass	1.49	1.04 to 1.97	100.00
	Max longevity	0.12	-0.17 to 0.4	75.40
CITES traded since 2000 (historic trade)	Adult survival	-0.25	-0.45 to -0.05	98.05
	Age at first breeding	0.30	0.03 to 0.55	96.85
	Bodymass	0.78	0.43 to 1.16	99.95
	Max longevity	0.43	0.20 to 0.66	99.90
CITES traded since 2015 (recent trade)	Adult survival	-0.48	-0.72 to -0.26	100.00
	Age at first breeding	0.34	0.06 to 0.59	98.05
	Bodymass	1.03	0.66 to 1.43	100.00
	Max longevity	0.58	0.34 to 0.85	100.00

Table S2. Estimated marginal coefficients for probability of being traded (hu) shown in Figure 2. All estimates are the direct effect assuming other traits and the year are held constant. Medians and 90% HDCI calculated from the full posterior distribution. The *pd* provides evidence of the direction of effect (positive or negative), parameters with a high certainty of direction (*pd* > 97.50%) are shaded grey. Marginal coefficients assume year remains at the mean and threat is non-threatened.

Trait	**Source**	**Par**	**Coefficient median**	**Interval**	***Pd* (%)**
AS	Captive	*hu*	-0.63	-0.98 to -0.26	99.77
AS	Wild	*hu*	-0.31	-0.74 to 0.13	88.36
BM	Captive	*hu*	-0.02	-0.53 to 0.55	51.98
BM	Wild	*hu*	0.8	0.23 to 1.4	98.54
FR	Captive	*hu*	-0.46	-0.89 to -0.06	96.88
FR	Wild	*hu*	0.48	-0.01 to 1	93.88
ML	Captive	*hu*	2.18	1.8 to 2.58	100
ML	Wild	*hu*	-0.7	-1.11 to -0.27	99.72

Table S3. Estimated marginal coefficients for volume when traded (mu) shown in Figure 2. All estimates are the direct effect assuming other traits and the year are held constant. Medians and 90% HDCI calculated from the full posterior distribution. The *pd* provides evidence of the direction of effect (positive or negative), parameters with a high certainty of direction (*pd* > 97.50%) are shaded grey. Marginal coefficients assume year remains at the mean and threat is non-threatened.

Trait	**Source**	**Par**	**Coefficient median**	**Interval**	***Pd* (%)**
AS	Captive	*mu*	-0.63	-0.87 to -0.39	100
AS	Wild	*mu*	-0.27	-0.58 to 0.03	93.24
BM	Captive	*mu*	0.25	-0.11 to 0.61	87.1
BM	Wild	*mu*	-0.4	-0.8 to 0.01	94.96
FR	Captive	*mu*	-0.33	-0.59 to -0.06	97.94
FR	Wild	*mu*	-0.02	-0.37 to 0.37	52.97
ML	Captive	*mu*	0.81	0.59 to 1.03	100
ML	Wild	*mu*	-0.03	-0.32 to 0.25	56.02

Table S4. Contrasting the direct effects of each trait between captive and wild-sourced for probability of being traded (hu). Medians and 90% HDCI calculated from the full posterior distribution. The *pd* provides evidence of the direction of effect (positive or negative), parameters with a high certainty of direction (*pd* > 97.50%) indicating a substantial difference are shaded grey. Marginal coefficients assume year remains at the mean and threat is non-threatened.

Trait	Par	Median	Interval	Pd (%)
AS	*hu*	-0.32	-0.81 to 0.12	86.86
BM	*hu*	-0.81	-1.29 to -0.34	99.78
FR	*hu*	-0.95	-1.49 to -0.4	99.77
ML	*hu*	2.88	2.43 to 3.32	100

Table S5. Contrasting the direct effects of each trait between captive and wild-sourced for volumes when traded (mu). Medians and 90% HDCI calculated from the full posterior distribution. The *pd* provides evidence of the direction of effect (positive or negative), parameters with a high certainty of direction (*pd* > 97.50%) indicating a substantial difference are shaded grey. Marginal coefficients assume year remains at the mean and threat is non-threatened.

Trait	Par	Median	Interval	Pd (%)
AS	*mu*	0.36	0.06 to 0.66	97.25
BM	*mu*	-0.65	-0.97 to -0.34	99.97
FR	*mu*	0.31	-0.05 to 0.65	92.89
ML	*mu*	-0.84	-1.11 to -0.55	100

Table S6. First derivatives (slopes) at specified values of adult survival. All other traits were held at their mean, the year fixed at 2018 and non-threatened set as the threat reference level. The median value is interpreted as the change in WOEs per 0.1 unit increase in adult survival at the specified value. This method has utility, as the joint distribution is a non-linear combination of both the Bernoulli and negative binomial sub models, so the separate coefficients don't individually reflect estimated changes in volumes, whereas this approach does. The interval is the 90% HDCI, and the *pd* is the direct probability of direction, slopes with a clear +/- direction (*pd* > 97.5%) are highlighted in grey.

Adult survival	Source	Median	Interval	Pd (%)
0.3	Captive	-14.94	-50.54 to -0.54	100.00
	Wild	-0.01	-0.07 to 0	95.83
0.4	Captive	-8.16	-25.15 to -0.4	100.00
	Wild	0.00	-0.03 to 0	95.63
0.5	Captive	-4.35	-12.39 to -0.24	100.00
	Wild	0.00	-0.02 to 0	95.35

Table S7. First derivatives (slopes) at specified values of body mass. All other traits were held at their mean, the year fixed at 2018 and non-threatened set as the threat reference level. The median value is interpreted as the change in WOEs per 1 gram increase in body mass at the specified value. This method has utility, as the joint distribution is a non-linear combination of both the Bernoulli and negative binomial sub models, so the separate coefficients don’t individually reflect estimated changes in volumes, whereas this approach does. The interval is the 90% HDCI, and the *pd* is the direct probability of direction, slopes with a clear +/- direction (*pd* > 97.5%) are highlighted in grey.

Body mass (g)	**Source**	**Median**	**Interval**	**Pd (%)**
100	Captive	0.00051	-0.00158 to 0.00325	75.08
	Wild	0	0 to 0.00002	91.04
1000	Captive	0.00007	-0.0002 to 0.00054	74.28
	Wild	0	0 to 0	94.54
10000	Captive	0.00001	-0.00002 to 0.00009	73.79
	Wild	0	0 to 0	96.63

Table S8. First derivatives (slopes) at specified values of age at first reproduction. All other traits were held at their mean, the year fixed at 2018 and non-threatened set as the threat reference level. The median value is interpreted as the change in WOEs per 1-year increase in age at first reproduction at the specified value. This method has utility, as the joint distribution is a non-linear combination of both the Bernoulli and negative binomial sub models, so the separate coefficients don't individually reflect estimated changes in volumes, whereas this approach does. The interval is the 90% HDCI, and the *pd* is the direct probability of direction, slopes with a clear +/- direction (*pd* > 97.5%) are highlighted in grey.

Body mass (g)	**Source**	**Median**	**Interval**	**Pd (%)**
1	Captive	-1.57	-5.07 to 0.06	99.58
	Wild	0.00	0 to 0	90.97
3	Captive	-0.17	-0.48 to -0.01	99.63
	Wild	0.00	0 to 0	92.52
5	Captive	-0.06	-0.17 to 0	99.60
	Wild	0.00	0 to 0.01	92.95

Table S9. First derivatives (slopes) at specified values of maximum longevity. All other traits were held at their mean, the year fixed at 2018 and non-threatened set as the threat reference level. The median value is interpreted as the change in WOEs per 1-year increase in maximum longevity at the specified value. This method has utility, as the joint distribution is a non-linear combination of both the Bernoulli and negative binomial sub models, so the separate coefficients don't individually reflect estimated changes in volumes, whereas this approach does. The interval is the 90% HDCI, and the *pd* is the direct probability of direction, slopes with a clear +/- direction (*pd* > 97.5%) are highlighted in grey.

Body mass (g)	**Source**	**Median**	**Interval**	**Pd (%)**
5	Captive	0.00123	0.00003 to 0.00517	100.00
	Wild	-0.00306	-0.02013 to 0.00015	99.67
15	Captive	0.10447	0.00579 to 0.27616	100.00
	Wild	-0.00019	-0.0009 to 0.00001	99.58
30	Captive	0.32008	0.05274 to 0.79215	100.00
	Wild	-0.00003	-0.00014 to 0	99.48

Table S10. Estimated marginal coefficients for year shown in Figure 4. All estimates are the direct effect assuming all traits are held constant at their mean. Medians and 90% HDCI calculated from the full posterior distribution. The *pd* provides evidence of the direction of effect (positive or negative), parameters with a high certainty of direction (*pd* > 97.50%) are shaded grey. Threat terms NE, NT and T denote not evaluated not threatened and threatened categories of threat respectively.

Par	**Source**	**Threat**	**Median**	**90% HDCI**	***Pd* (%)**
Hu	Captive	NE	-0.23	-0.5 to 0.02	92.75
		NT	0.19	0.05 to 0.33	98.62
		T	0.17	-0.02 to 0.37	92.28
	Wild	NE	-1.86	-2.28 to -1.41	100
		NT	-1.47	-1.74 to -1.19	100
		T	-0.29	-0.71 to 0.14	86.25
Mu	Captive	NE	0.13	-0.03 to 0.31	90.72
		NT	0.19	0.05 to 0.32	98.71
		T	0.15	-0.01 to 0.3	94.52
	Wild	NE	-0.53	-0.8 to -0.25	99.88
		NT	-0.65	-0.84 to -0.46	100
		T	-0.25	-0.67 to 0.17	83.26

Table S11. First derivatives (slopes) at specified values of year. All traits were held at their mean. The median value is interpreted as the change in WOEs per 1-year increase in time at the specified value. This method has utility, as the joint distribution is a non-linear combination of both the Bernoulli and negative binomial sub models, so the separate coefficients don't individually reflect estimated changes in volumes, whereas this approach does. The interval is the 90% HDCI, and the *pd* is the direct probability of direction, slopes with a clear +/- direction (*pd* > 97.5%) are highlighted in grey.

Year	Source	Threat	Median	Interval	***Pd*** **(%)**
0	Captive	Threatened	0.01685	-0.00135 to 0.05179	97.97
		Non-threatened	0.02151	0.00116 to 0.05984	99.86
		Not assessed	-0.00702	-0.04458 to 0.02413	72.73
	Wild	Threatened	-0.00057	-0.0051 to 0.00028	93.42
		Non-threatened	-0.40947	-1.42224 to -0.0095	100.00
		Not assessed	-0.28923	-1.16305 to -0.00425	100.00
5	Captive	Threatened	0.02094	-0.00216 to 0.06437	98.07
		Non-threatened	0.02754	0.00102 to 0.07713	99.88
		Not assessed	-0.00656	-0.04305 to 0.02668	72.55
	Wild	Threatened	-0.00034	-0.00246 to 0.00029	93.00
		Non-threatened	-0.07359	-0.28528 to -0.00169	100.00
		Not assessed	-0.0389	-0.16695 to -0.00061	100.00
10	Captive	Threatened	0.02562	-0.00211 to 0.08184	98.07
		Non-threatened	0.03512	0.00112 to 0.10113	99.88
		Not assessed	-0.00598	-0.04446 to 0.02525	72.14
	Wild	Threatened	-0.0002	-0.00132 to 0.00018	92.60
		Non-threatened	-0.01213	-0.04901 to -0.00032	100.00
		Not assessed	-0.00487	-0.02061 to -0.00009	100.00
15	Captive	Threatened	0.03149	-0.0025 to 0.10488	98.08
		Non-threatened	0.04467	0.00148 to 0.13286	99.87
		Not assessed	-0.00534	-0.04159 to 0.02668	71.85
	Wild	Threatened	-0.00012	-0.00076 to 0.00012	92.19
		Non-threatened	-0.00205	-0.00834 to -0.00004	100.00
		Not assessed	-0.00062	-0.00271 to -0.00001	100.00

Chapter 5

General discussion

5.1 Summary

Overexploitation is a key driver of the current biodiversity crisis, reconciling this with sustainable use and conservation outcomes is imperative. The scale of human reliance on wildlife trade products (Nielsen et al., 2018) and the number of species potentially affected by trade (Fukushima et al., 2020; Marsh et al., 2021; Scheffers et al., 2019) make this a substantial challenge. Sustainable use will be part of the solution to achieve both conservation and socioeconomic outcomes (Hutton and Leader-Williams, 2003). Yet there is continuing need to provide evidence that such practices do not become unsustainable and where they do that this is remedied swiftly. Poorly regulated or illegal trade has the potential for great harm to species, globally pangolin species are heavily threatened due to trade (Heinrich et al., 2016). High global demand for their scales and meat for traditional medicines has led to global trade bans (the Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES] Appendix I listings) and a growing illicit trade (Xu et al., 2016). However, where coherent and enforceable management plans are in place trade has the potential to provide a sustainable food source, income and conservation benefits (Daltry et al., 2016). Examples of this include community-orientated trophy hunting operations (e.g. Uriel and Suleiman Markhor in Pakistan (Frisina and Tareen, 2008)) and large-scale farms ranching crocodilians for leather and meat (e.g. Australian Freshwater crocodiles, *Crocodylus johnsoni*, and Saltwater crocodiles, *Crocodylus porosus,* in Australia (Corey et al., 2018; Daltry et al., 2016)).

However, trade does not only concern a handful of charismatic species, but instead a litany of species, with some traded globally in huge numbers and others only opportunistically and in certain regions. A global phenomenon like trade requires a global response, and since 1975 and the signing of the Convention, Parties to CITES have sought to enable the international legal trade in wildlife while preventing unsustainable and harmful trade. How well it is achieving this aim and how best to continue to approach trade management and policy remain at the heart of discourse surrounding CITES (Challender et al., 2015a). However, across the spectrum of opinion, a call for greater evidence and transparency is prevalent in both policy and academic reviews of CITES (Challender et al., 2015a; Cooney et al., 2021; Phelps et al., 2011). The main aims of this thesis were to contribute to this debate by (1) drawing together and synthesizing data on the impacts of trade on species populations, (2) develop methods to better use the comprehensive CITES trade database and examine the effectiveness of trade regulation in protecting threatened species and (3) further unpick the divergence in the captive and wild-sourced trade of CITES-listed species and probe for life-history traits correlated with these sources.

In Chapter two I conducted a meta-analysis of the abundance impacts of trade. Research efforts were focused across the tropics with studies from South America and Sub-Saharan Africa dominating. Taxonomically, research was also heavily skewed to mammals, with a large number of studies concerning only the impacts of the bushmeat trade. Overall, where trade occurred species abundances declined by 62% on average (Morton et al., 2021). Studies looking more broadly at hunting in the tropics align with these findings, showcasing mean declines of 58 and 83% for birds and mammals respectively (Benítez-López et al., 2017). Declines were more strongly correlated with larger-scale national and international trade (rather than local) and proximity to human settlement. This is evident in Northern Sumatra, the expansion of road networks into the forests has facilitated trappers to deplete bird populations within 5km of road (Harris et al., 2017). However, nuance dominates species responses, with many species-site abundance responses showing uncertain impacts of trade. Chapter 1 does not advocate an end to trade, nor that trade is inherently incompatible with conservation, but it does quantify a baseline and highlights how poorly the impacts of trade have been quantified.

The remaining Chapters focused on the comprehensive CITES trade database which holds over 22 million trade records between CITES parties. Previous studies have largely focused on individual species trade trends through time, e.g. grey and Timneh parrots (*Psittacus erithacus* and *Psittacus timneh*) (R O Martin, 2018), which provide a detailed discussion of exact yearly volumes between importer-exporter pairs. A potential shortcoming of this approach is that it assumes we are *a priori* aware of species that need studying (e.g. are threatened by unsustainable trade), so such an approach is unlikely to uncover newly threatened species but rather confirms existing expectations that trade occurs in high levels. Such research is crucial as it provides valuable evidence and discourse for some of the most threatened species in trade. However, attempts must be made to look further across multiple species and taxonomic groups. Much of the work currently on multiple species looks across the broad total volumes of trade across a given group, e.g. the total trade in birds to and from China (Li and Jiang, 2014). Focused studies of individual species risk missing less well-known species that are also of concern, similarly broad totals summing over many species obfuscate individual species trends thus losing nuance.

Chapters 3 and 4 focused on applying methods able to model the hundreds of CITES-listed species in international trade at the species-level, not summed across taxa. Crucial to this was incorporating the many species infrequently traded, i.e. only traded for 5 years in a 20-year period. To do this I applied hierarchical Bayesian hurdle models able to handle the diversity of traded species and their frequent appearance and disappearance from trade. In Chapter 3, I explored how wild-sourced trade volumes varied across species extinction risk for 1025 bird, mammal, amphibian, and reptile species. Trade richness, volume and reoccurrence were dominated by Red List Least Concern species, and across threat statuses trade volumes are either falling or uncertain for the average species across taxa. The only exception was Least Concern reptiles where volumes for the average species have increased steadily through time. Of the diversity of species traded between 2000 and 2018, it should be noted that few are consistently traded throughout this time, and most are estimated not to reoccur in recent trade. I further examined how responsive trade is to an assessment of threat or extinction in two ways. Firstly, some CITES species are split-listed between Appendix I and II, with more threatened populations in Appendix I and less threatened species in Appendix II. Trade from the Appendix II populations was higher for nearly all species, with trade from the Appendix I populations nearly always absent. This indicates that for a select pool of species CITES is protecting vulnerable populations from international demand while meeting international demand from more robust, less threatened populations. Secondly, a broader analysis of whether trade volumes and reoccurrence correlate with updated IUCN Red List assessments revealed a general lack of association between the two. In many cases, this was because by the reassessment year the species was already absent from trade. For other species, it highlights a potentially concerning disconnect between species' increasing rarity and trade volumes. This develops on previous work that suggested the CITES listing process lags behind the IUCN’s assessments of threats attributed to trade (Frank and Wilcove, 2019).

The decline of the wild-sourced trade, in CITES-listed species, and the rise of captive-bred volumes have been well documented in the summed total volumes traded for many major taxonomic classes (Harfoot et al., 2018a). Chapter 3 built on this and provides evidence of species-level declines in the wild-sourced trade. Chapter 4 develops this further to contrast the species-level international captive and wild-sourced trade in 779 listed bird species and examine whether these distinct sources associate with different spectra of species life history. Captive sourced trade volumes correlated with species longevity, adult survival and maximum survival while wild-sourced trade only had weak associations with longevity.

Despite this, independent species-level variation dominates the trade in CITES-listed species, with some closely related and demographically alike species differing greatly in their reoccurrence and volume in trade. The analysis further highlighted extensive switches from wild-sourced trade to captive-sourced trade for many species, with the wild-sourced trade declining through time and the captive trade increasing or uncertain. The switching of species and the emergence of new species from captive sources puts a great onus on the effectiveness of CITES and the Parties to prevent laundering and detrimental leakage to wild populations (Janssen and Chng, 2018; Lyons and Natusch, 2011; Nijman and Shepherd, 2015). This Chapter built on previous studies, finding strong associations between species presence in trade and body mass (Scheffers et al., 2019) and the number of individuals in the Australian pet trade associated with body mass and annual fecundity (Toomes et al., 2022). In contrast, the international trade in captive-bred listed species focused on a broad range of demographic values, not specifically just those that are typically faster or slower reproducing (Chapter 4).

5.1.1 Wider applicability of findings

The generalisability of the findings of this thesis should be approached cautiously, particularly regarding Chapter 1. The relatively small number of studies, limited taxonomic and geographic range, and lack of trade purposes quantified mean that the abundance declines found should not be extrapolated to other parts of the world or specific instances of trade. In reality, there is a sore need for population and context-specific data on species to truly ask whether trade is harmful or sustainable, a task compounded by the number of species traded. Chapter 3 is more widely applicable to global trade and does offer the fullest possible picture of the wild-sourced vertebrate trade in listed species. It highlights a number of threatened species subject to relatively high trade levels that may be sustainable but require evidence to support that. However, the models were parametrised to examine temporal trends and their association with species threat, not predict future trends. Predictive modelling of CITES trade remains a research frontier, hampered partly by the high species-level variability and more notably by the varying pool of listed species able to appear in the CITES trade database (subject to a formal listing at the CITES Conference of the Parties). Chapter 4 provides life history traits that correlate with captive avian trade that require further study as to whether these traits are prevalent due to their inherent attractiveness or rather just indicative of their suitability for captive breeding. It does however have relevance in highlighting a growing number of captive-bred species traded in high volumes whose provenance (e.g., the feasibility of actually being captive-bred) requires investigating. The CITES trade database is the largest and most coherent record of international trade at the species level available. However, there is growing evidence of substantial international trade from other sources including the dark web (Harrison et al., 2016) and various legal selling sites (Hughes et al., 2021; B. M. Marshall et al., 2020; Marshall et al., 2022).Future work should aim to standardise and incorporate multiple data sources to build a truly full picture of global trade.

The remainder of this Chapter focuses on placing the implications of these findings in the wider global context and looks in greater depth at CITES policy mechanisms underpinning sustainable trade. Specifically, this focuses on the need for transparent, data-driven, and evidenced assessments of species' sustainable use in international trade.

5.2 Evidence-based policy

Trade has the potential to both greatly benefit and greatly harm species (Joanen et al., 2021; Mambeya et al., 2018). Even where species are subject to vast international demand, well-managed offtake in large enough volumes to meet supply needs is still possible. More than 300,000 reticulated pythons (*Python reticulatus*) are harvested from Indonesia and Malaysia annually to supply both skins and meat, yet repeat surveys show no discernible impacts on populations (Natusch et al., 2016). However, generalising sustainability beyond a single focal species is challenging. Demographic surveys of the closely related blood python (*Python brongersmai*) in Indonesia do show a detrimental response to collection pressure, with smaller individuals and fewer juveniles passing through processing facilities in 2015-2016 compared to 1996-1997 (Natusch et al., 2019). The contrast in responses of the two species can be attributed to their varying ecologies with blood pythons potentially being easier to access due to their presence in human-altered landscapes (e.g. oil palm plantations), lack of dispersal between patches and their reduced clutch size compared to reticulated pythons. This nuance is reflected across thousands of traded species and between populations of a single species, underscoring that sustainability can rarely be assumed without explicitly being evidenced.

5.2.1 Evidence in practice

International policy instruments have embraced attempting to evidence sustainability in international trade. For Parties to CITES (The Convention on International Trade in Endangered Species of Wild Fauna and Flora) to trade a CITES Appendix I or II listed species sourced from wild populations they must evidence both that the specimen was legally obtained and that its trade will not be to the detriment of the species (for Appendix I listed species trade must also not be primarily for commercial purposes). From a sustainable use perspective evidencing that trade will not be detrimental to a species via a Non-detriment Finding (NDF) is crucial.

Over the years CITES and the Parties have tried to establish global standards, guidelines and requirements for NDFs to include. The most recently published example emphasises making scientifically informed NDFs and guides making NDFs for Appendix II timber/tree species (Wolf et al., 2018). The outlined process explicitly covers overcoming initial issues including taxonomic uncertainty and the early application of any mitigating factors or exclusions (e.g. only certain derivative products are covered by the Appendix listing). An extensive process is then suggested to evaluate the potential risk of trade including considering the species conservation concern (e.g. recent IUCN Red List Assessments), biological risks (e.g. distribution, habitat specificity, resilience etc.) and the impacts of harvest (e.g. areas affected, annual offtake, growth and mortality rates etc.). Further steps then consider the impacts relative to the numbers being traded, e.g., are volumes much lower than the agreed quota, are volumes much higher than the expected annual production and how large and certain is any illegal trade in the species. The final suggested step considers what mitigation action is underway and how harvested areas are managed to protect species populations. A pivotal component of this process is collecting relevant information from all appropriate sources, which can include expert opinion, local knowledge, various databases (e.g. The IUCN Red List, The CITES UNEP-WCMC trade database etc.) and field surveys. This exhaustive and robust evidence can then be used to support a positive or negative NDF (and a quota).

There is great concern that despite clear and robust advice, the NDF process is often reduced to a cursory appraisal that cannot be said to protect species. In 2003 the Solomon Islands (at this time not a Party to the Convention), captured 94 Indo-Pacific bottlenose dolphins (CITES Appendix II listed) and later traded a number of these with Mexico, the United Arab Emirates and the Philippines (Parsons et al., 2010). Despite the Solomon Islands non-Party status, Parties to the Convention should not accept exports from non-Parties without certification of non-detriment and evidence that the specimens were acquired legally. The IUCN Cetacean Specialist group indicated great concern over allowing the trades to occur, pointing to the complete lack of studies on the species in the vicinity and therefore the impossibility of a rigorous evidence-based NDF (CITES, 2008). Despite this, the evidence of non-detriment was accepted by the Importing Parties and the CITES Secretary-General (Wijnstekers, 2007). Concerningly, as part of the Secretariats statement emphasis was placed on other interested groups presenting evidence of unsustainably “[the Secretariat] *has received no evidence to demonstrate that trade which is now taking place, or is intended to take place, will have a detrimental impact upon wild dolphin populations*”. This sharply flips the Convention's written position on NDFs, which highlights evidence that trade will *not* be detrimental is required, not that others must provide evidence that trade *is* detrimental. The former being a much more precautionary stance than the latter.

5.2.2 Barriers to improving evidence use

An impediment to digging deeper into the evidence used to ratify sustainable use is that NDFs are not required to be submitted, reviewed or archived anywhere centrally. The lack of centrality has two key repercussions, (1) potentially detailed population assessments of great conservation relevance to wider groups (e.g. researchers) are kept out of the public domain and (2) it is impossible for the evidence of non-detriment to be reviewed openly in cases where sustainability is questioned. In Chapter 3, I explicitly examine whether CITES trade is able to respond to changing evidence of species extinction risk (changes in Red List status), the general lack of association between volumes and presence with new assessments suggests a disconnect. I further highlight a number of species that despite being assessed into more threatened statuses, (often with trade given as a key reason for this) resulted in no change in trade volumes. Given that intentional use contributes to elevated extinction risk for at least 2752 species (out of 9753 assessed species) (Marsh et al., 2021), evidencing the sustainability of trade is crucial.

In 1994 CITES explicitly adopted the precautionary principle that where a lack of scientific certainty exists around the outcome (whether trade will cause detriment to the species), action should be taken to avert potential (and implicitly unknown) harm (Dickson, 1999). The principle is simple to understand yet hard to implement effectively. Trade never affects only the species traded and all trade has wider links to a diverse array of livelihoods and thus financial and socioeconomic effects on those involved in the trade. Thus, in the face of scientific uncertainty on the detrimental impact on a species, yet the certainty of financial harm to harvesters, how then should the principle be applied? Also, it is likely to be impossible (especially on meaningful timescales) for Parties Scientific Authorities to gather and collate population-specific data on harvest impacts for all traded species and thus be certain of no detriment for some species. The NDF process is therefore inherently laden with judgement calls where data is absent, the risk of detriment is uncertain, and sources conflict (Aylesworth et al., 2020). However, the available evidence should still support the final judgement. In Brazil NDFs for *Arapaima spp*. have been criticized for over-reliance on '*technical opinion reports'* that do not require evidence, leading to largely unregulated fishing offtakes and estimated population declines (Castello and Stewart, 2010).

There are clear knowledge gaps in the preparation of NDFs. A review of available NDFs highlighted the following areas are not always considered (or included): species identification, source, ecosystem roles, population trends, threats, inherent vulnerability (e.g. reproductive strategy), ongoing management and/or monitoring, the likelihood of illegal trade, inclusive knowledge (e.g. academic research, grey literature, surveys, expert opinion, local knowledge etc.), transparent sources (and analysis), inclusivity (joint decision making and/or stakeholder involvement), multiple sources of evidence, and how the precautionary principle applies (CITES, 2020b). Developing the robust inclusion of all these areas is a necessity that requires both the development of monitoring schemes and formalised processes to consistently make judgements based on missing data. Some of these required areas remain largely open biological questions, for example, the wider impacts of harvesting for trade on ecosystems as a whole are largely unknown. Insights from the wider hunting literature suggest in some cases persistent removal can result in dramatic effects including direct effects on forest structure and function (Abernethy et al., 2013), and the potential proliferation of smaller non-target species (Barychka et al., 2021). Similarly, where harvesting and other threats co-occur consideration of the potential synergistic impacts (Symes et al., 2018) and the cumulative impact of multiple threats potentially destabilising populations (Capdevila et al., 2022) is crucial and yet currently absent for many NDFs.

5.2.3 Bans

It would be remiss to not briefly discuss trade bans (or more commonly listing in CITES Appendix I), given the results presented in this thesis detail potential negative impacts of trade (Chapter 2) and highlight a number of trade-threatened species traded in high volumes (Chapter 3). Trade bans are frequently advocated and large-scale or global bans have been called for by several groups (D’cruze et al., 2020; Xiao et al., 2021; Yang et al., 2020) and charities (including World Animal Protection and End The Trade) in recent years. Proponents of a ban suggest that wildlife consumption isn’t an essential part of people's diets (e.g. China (Xiao et al., 2021)), harbours too greater risk of zoonotic disease, and isn’t necessary to meet conservation goals (D’cruze et al., 2020).

The apparent simplicity of bans can be attractive. However, there is compelling evidence that trade bans do more harm than good. Primarily, they have the potential to stimulate trade while bans are implemented (Rivalan et al., 2007) or simply shift trade from legal to illegal mediums (Challender et al., 2019c; Challender and MacMillan, 2014). Similarly, there is limited evidence that blanket trade or consumption bans would significantly reduce zoonotic disease risk (E and J, 2020) with some recent outbreaks originating from commercial meat farms (e.g. H1N1 influenza likely originated from commercial North American swine farms (Mena et al., 2016)). Further consideration must be given to the nutritional, cultural and societal factors driving trade and consumption, as without engaging fully with these issues any interventions and bans will be doomed to fail in the face of unchanged market demand (Thomas-Walters et al., 2021, 2020). The only equitable way to reconcile conservation, development and society is through a reformed and transparent sustainable use infrastructure, not a short-sighted ban (as outlined here, detailed in Chapter 3 and similarly echoed in the wider literature (Aylesworth et al., 2020; Challender et al., 2015b; Foster and Vincent, 2021; Frank and Wilcove, 2019; Smith et al., 2011)).

5.3 Conclusions and recommendations

This thesis attempts to tackle key questions on the impacts, management and patterns of the wildlife trade, using both published data and the trade records from the CITES trade database.

There are four main findings stemming from this work. Firstly, we have a generally poor knowledge of the species-level impacts of trade from rigorous field studies. The studies that exist are both geographically and taxonomically clustered and at the species-level display a range of positive and negative responses to trade. Secondly, at the species-level wild-sourced trade in CITES-listed species is broadly declining with few notable exceptions. Thirdly, trade volumes in listed species are largely disconnected from changes in species extinction risk. Often this is because trade has declined and disappeared prior to change occurring, but in a few cases highlights persistent trade as species become more threatened. And finally, at the species-level captive-sourced trade is replacing the wild-sourced trade and expanding the pool of traded species. The expansion of the captive trade does broadly associate with species reproductive traits but spans a range of faster and slower trait values indicating the flexibility of supply. A key takeaway from this, in my opinion, is the importance of species-level variability in both trade volumes and trade impacts. Scaling up or extrapolating data from one species to inform us of another carries great risk without context-specific data encompassing both the target species biology and the wider economic, market, socioeconomic forces governing the species trade.

Future research should focus on (1) attempting to quantify the abundance impacts of trade for a wider range of species including those less charismatic and often ignored taxonomic groups (e.g. amphibians, invertebrates etc.), (2) developing the use of large species-level models of trade presence and volume beyond vertebrate taxa, and (3) unpicking key biological questions regarding the wider impacts of trade, including ecosystem-level effects of harvesting for heavily traded species, and whether species traits mediate species response to trade. Beyond research, global policy must also respond to best ensure the sustainable trade in CITES-listed species. To further this aim, the Parties should begin a transition process to open and accessible NDFs, highlighting what available evidence was used and where there was uncertainty how was this resolved to a judgement. The inclusion of such information is crucial and could be used to support conditional NDFs, where trade is permitted but agreements are made to put in place additional measures (e.g. implementing community offtake records or enforcement upskilling) (Aylesworth et al., 2020).

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