ETHNOBIOLOGY AND CONSERVATION

RESEARCH ARTICLE

Ethnobiology and Conservation, 14:25 (1 July 2025)
doi:10.15451/ec2025-07-14.25-1-17
ISSN 2238-4782 ethnobioconservation.com

Worldwide patterns of wild mammal trade are driven by species ecology, evolutionary relatedness, and socio-political variables: inferences from the TRAFFIC bulletin

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ABSTRACT

Wildlife trade is one of the main drivers of species decline and extinction worldwide. Although many studies have investigated the magnitude and extent of the wildlife trade, little is known about the role that species traits play in the trade of species body parts and trade purposes. Here, we test how species traits, phylogenetic relationships, and socio-political variables determine the purpose of trade, number of body parts, species, and specimens traded. We compiled records of mammal trade from the TRAFFIC bulletin (n = 100 bulletins). We fitted Bayesian generalized linear models (GLMs) to test whether species traits influence the number of body parts, purpose of trade, and number of TRAFFIC bulletins per species. We fitted GLMs to test whether socio-political variables influence the number of trade records, species and specimens traded by country. Products of at least 16,279,031 specimens from 458 mammal species were traded, including 162 threatened species (65 vulnerable, 70 endangered, and 27 critically endangered) and two extinct species. Larger and "vulnerable" species are more likely to have more parts traded for more uses, and closely related species tend to be traded for similar purposes. In addition, 127 countries were associated with trade, with high-income countries (those with greater human development index) having a greater number of species traded. Our results highlight the importance of species traits and socio-political factors on mammal trades. We emphasize the need for multidisciplinary research to investigate the species loss due to trade based on species traits and socio-political factors.

Keywords: Ecological traits, wildlife trade, phylogenetic relationship, threat status, CITES.

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SIGNIFICANCE STATEMENT

In this paper, we have investigated the trait and phylogenetic correlates for 400+ wild mammal trade worldwide using modern phylogenetic comparative methods. We also tested if the patterns of trade between countries are related to socio-economical factors. We found that larger and more widespread species are more likely to have more parts traded for more uses. Closely-related species tend to be traded for the same purposes. In addition, 127 countries were associated with trade, with developed countries having more imports. While previous papers have already investigated correlates of trade patterns, ours is the first to consider a much wider range of trade purposes based on decade long public database considering shared ancestry. Therefore, we believe readers of Ethnobiology and Conservation will enjoy our manuscript because it addressed an applied question, providing results that can help not only understand causes of species loss due to trade, but also how to develop targeted conservation programs.

INTRODUCTION

Wildlife trade is a common practice around the globe (Andersson et al. 2021; Rosen and Smith 2010; Scheffers et al. 2019). Products and parts of wild vertebrates, in addition to whole specimens, supply demands from markets, such as pets, trophies, game meat, traditional medicine, and fur trade (Azeredo et al. 2024; Bush et al. 2014; Graham-Rowe 2011; Palazy et al. 2012). Mammals are among the most traded wild vertebrates on the planet (Bush et al. 2014; Harfoot et al. 2018; Scheffers et al. 2019), with estimates that at least 1 in 4 species is traded (Scheffers et al. 2019).

Although many studies have investigated wildlife trade and its effects on species (e.g., Hughes et al. 2022; Morton et al. 2021; Symes et al. 2018a), understanding the factors that determine the likelihood of a species be traded is complicated due to the diversity of species and products involved, the trade chain, cultural preferences, and the dynamics of trade itself (Challender et al. 2015; Phelps et al. 2016; Sas-rolfes et al. 2019). For example, wildlife trade may involve specific parts (e.g., bear bile; Feng et al. 2009), multiple parts of one individual/species (e.g., penis, bones, skins, claws, paws, and teeth; Saif et al. 2016; Valencia-Herverth et al. 2025), or even whole individuals, such as pangolins (Soewu and Ayodele 2009; Volpato et al. 2020). Furthermore, a single animal may be traded for various purposes e.g., traditional medicines and food (Alves et al. 2020; Soewu and Ayodele 2009; Volpato et al. 2020). This variety of factors (body parts traded and multiple trade purposes) can intensify the trade of versatile species and lead to their overexploitation to supply multiple wildlife markets. This may pose an extra threat to animal conservation (Hughes et al. 2022; Phelps et al. 2016; Sas-rolfes et al. 2019).

Previous studies suggest that the composition and volume of traded species are directly influenced by their intrinsic (e.g., body mass, evolutionary relationship) and extrinsic (e.g., threat status and CITES regulation) characteristics (Johnson et al. 2010; Palazy et al. 2012; Prescott et al. 2012; Su et al. 2015). These studies found that the choice of commercialized species is not random, but associated with species ecological traits (Palazy et al. 2012; Scheffers et al. 2019; Su et al. 2015). For example, larger, narrow-ranged, and threatened species are more likely to be commercialized than smaller, widespread, and non-threatened species (Palazy et al. 2012; Scheffers et al. 2019). In addition to the above traits, closely-related species are more likely to be traded than distantly-related ones (Scheffers et al. 2019; Tanalgo et al. 2023).

However, so far, most studies have focused on specific types of trade (e.g., trophies and pet trade; Johnson et al. 2010; Palazy et al. 2012; Su et al. 2015). Little is known about how species traits affect the species versatility (number of body parts and trade purposes). Furthermore, few studies have evaluated the influence of biases on trade reports (e.g., as in the recording of charismatic species) (Abellán et al. 2016; Margulies et al. 2019; Paudel et al. 2022). Therefore, identifying the drivers of species uses, inclusion in trade and biases related to the wildlife reports is critical for designing and/or improving interventions to mitigate the impacts of trade on target species populations and also prevent the loss of exploited species (Challender et al. 2015; Hughes et al. 2022; Paudel et al. 2022).

Socio-political aspects of countries and regions involved in trade can also play a key role in determining which species or parts are traded, as well as the volume of trade. Overall, high income countries (e.g., those with a higher *gross domestic product* - GDP and *human development index* – HDI) generally exert greater pressure on biodiversity (consumption of natural resources and commodities) than low to mid income countries (Andersson et al. 2021; Lenzen et al. 2012; Liew et al. 2021; Symes et al. 2018b). For example, countries with higher GDP tend to consume more wildlife products, because they have more money to spend on superfluous goods/items, such as trophies and pets (Andersson et al. 2021; Liew et al. 2021; Ribeiro et al. 2022). Therefore, to better understand the trade chain, both socio-political and biological traits need to be assessed together in an integrative framework.

Here, we compiled data on worldwide trade from the TRAFFIC bulletin to ask the following questions: 1) which species characteristics influence their trade in terms of body parts and trade purposes? 2) are trade and shared evolutionary history related? 3) how do socio-political factors influence mammal trade? We further explored taxonomic biases in wild mammal trade.

We hypothesize that: (1) larger, widespread, evolutionary distinct, and threatened species (vulnerable, endangered, or critically endangered) are more traded both in number of parts and trade purposes; (2) species with stronger trade restrictions (e.g., those included in the appendices of CITES I) have more parts used and are traded for multiple purposes; (3) closely related species are commercialized for the same purposes; and (4) high-income countries have higher number of records of trade and greater number of species and specimens traded.

MATERIAL AND METHODS

Data collection

The TRAFFIC bulletin (www.traffic.org) is the only journal that exclusively publishes information on the trade (legal and illegal) of animals and plants. In addition, the TRAFFIC organization operates another major database on illegal wildlife trade: the Wildlife Trade Portal (`https://www.wildlifetradeportal.org/dashboard`). However, in this study, we focused only on the TRAFFIC bulletin to address our hypothesis about biases in the wildlife trade report. The records came from news, government agencies, non-governmental organizations, case reports, and investigations led by the bulletin staff. We manually compiled data records on wild mammal trade (wild trade) from all 100 bulletins published between 1975 and 2019. Bulletins with special issues on specific trade in pangolins, ivory, rhino horns, and other specific taxa were not included. The dataset was compiled between January and April 2020. Only records related to the wild trade that allowed the identification of traded mammals to the species level were compiled. The following data were recorded for each transaction: species and parts traded, purpose, quantities (number of individuals, parts, and products), and year.

Our dataset was built using aspects that have been demonstrated to be important in recent research on wildlife trade (e.g., Challender et al. 2022). We did not treat each trade record as an independent shipment, as a single incident of trade report may contain multiple traded items (e.g., species or body parts). It is noteworthy that not all records contained standardized and complete information on the quantities and/or parts of animals sold (see Rosen and Smith 2010). For example, 77.2% and 36.4% ($n = 4,022$ and $1,895$) of the records had no information on importer and exporter countries, respectively. In addition, only 17.4% ($n = 905$) of the records had information about both exporters and importers. About 6.5% ($n = 340$) of records include temporal data, for example 1969-1979 or 1998-2008.

Species traits and phylogenetic data

Species body mass was obtained from the PanTHERIA and Phylacine databases (Faurby et al. 2018; Jones et al. 2009). Extent-of-occurrence data for each species were taken from the IUCN Red List (IUCN 2020) (Additional File 1). Evolutionary distinctiveness (ED) was calculated using the "fair proportion" approach (Redding et al. 2008) implemented in the R package picante (Kembel et al. 2010). This method divides the value of each branch length of a phylogeny by the number of species. This metric quantifies how isolated (distinct) a species is in a phylogeny. The higher the ED, the more distinct (few or no close living relatives) a given species is. To obtain a phylogeny for the species for which we had trait data, we pruned the fully-sampled tree of Upham et al. (2019), which includes 452 of the 458 species in our database (*Bubalus bubalis*, *Felis lybica*, *Leopardus pajeros*, *Otaria flavescens*, *Piliocolobus badius,* and *P. wladronae* were not present in the phylogeny). We used 1,000 dated trees from the posterior distribution, which were converted to a consensus tree using the R package phytools (Revell 2010). Species nomenclature followed The Mammal Diversity Database of the American Society of Mammalogists (Burgin et al. 2018).

CITES and IUCN data

Occurrence in the appendices of CITES was taken from CITES (CITES/UNEP-WCMC, 2020; `http://checklist.cites.org`). Species most threatened by trade are listed in Appendix I and are subject to stronger trade restrictions. In this case, they may only be traded for non-commercial purposes, such as scientific research or captive breeding programs. Species listed in appendices II and III have fewer restrictions and may be legally traded with export or import permits, if they comply with CITES requirements National Scientific Authorities and National Management Authorities. Threat status and population trend data for each species were taken from the IUCN Red List (IUCN 2020) (Additional File 1).

Socio-political variables

Human Development Index (HDI) – HDI was obtained from the UN Human Development Reports (HDR, UNDP, retrieved on 20.06.2020). This index shows the average performance of key dimensions of human development for a country or region based on income, health, and education indicators (Additional File 2). We used the mean index between the year range in which TRAFFIC bulletins were published (1975 – 2019).

Gross Domestic Product (GDP *per capita*) – GDP *per capita* was obtained from the World Bank database (databank.worldbank.org). This index represents the country's economic output divided by its population. This variable was used as a proxy for economic development (Additional File 2). We used the mean GDP *per capita* between the year range in which TRAFFIC bulletins were published (1975 – 2019).

Human Population Density (HPD) – HPD was obtained from the Open Spatial Demographic Data and Research database (https://hub.worldpop.org). This index represents the number of people per square kilometre (at a resolution of 30 arc-seconds – approximately 1 km^2 at the Equator) and was used as a proxy for natural resource consumption (Additional File 2). We used the mean HPD between 2000 – 2020.

Data standardization

Traded body parts are recorded using different terms (e.g., skulls, skins, skins bags, bones powder) through the TRAFFIC bulletins. Therefore, to reduce redundancy of parts and/or trade purpose and make the data comparable between item types and products sold, we grouped similar body parts into 24 categories, as follows: 1) fluids (ambergris, bile, blood, bone marrow, semen, tears, urine, musk); 2) organs (bladder, brain, eyes, gallbladder, genitals, glands, heart, intestines, liver, stomach, tongue, and penis); 3) arms, 4) claws, 5) ears, 6) feet, 7) hands and paws, 8) hooves, 9) jaws, 10) legs, 11) nose, 12) tail, 13) teeth, 14) whiskers, 15) unspecified parts, 16) ivory, including whole and/or cut tusks and ivory products; 17) bones/skeletons; 18) skin/leather; 19) specimens/whole organisms; 20) scales, 21) heads/trophies; 22) horns; 23) meat, and 24) spines. Therefore, if a given trade report includes 2 ears, 2 L of blood, 10 mL of urine, 4 paws, and 1 horn, we computed it as four body parts, as blood and urine were grouped as fluids, but ears, paws, and horns were considered independent body parts.

Trade purposes were divided into 10 categories: (1) manufactured goods (ivory carvings; jewelry made with teeth or claws); (2) circus/zoo animals; (3) food (human and animal); (4) leather; (5) religious-magical purposes; (6) pets; (7) scientific research; (8) commercial – when no specific purpose was given; (9) traditional medicine; and (10) hunting trophies and stuffed (taxidermies) animals (Additional File 3). We separated manufactured goods from religious-magical purposes as the latter can include organs, meat, whole organisms as well as some manufactured items (e.g., bone powder). However, analyses based on trade databases are knowingly subject to reporting errors and therefore need to be interpreted with caution (Morton et al. 2022).

The number of specimens per species was obtained by converting body parts (when available) into whole organism equivalents (henceforth WOE) (Challender et al. 2015; Harfoot et al. 2018). This metric uses body parts of species as parameters to estimate the number of individuals. For example, records that involve heads are considered as a single individual. Only records that provided numbers of whole tusks were used for the conversion of ivory tusks into numbers of specimens. Products made of ivory and records that gave the weight of tusks were not used. The body mass of captured or sold pangolins (individuals or scales) was converted into WOE based on metrics available in the literature (Challender et al. 2015; Ullmann et al. 2019) (Additional File 4 - Table S1). Not all products could be converted into WOEs (e.g., bones, teeth, meat, manufactured goods - ivory, leather, bones, etc.), and therefore only transactions that provided species-level identification for WOE were used (n= 3,287 records).

In view of geopolitical changes during the period assessed, Czechoslovakia, East Germany, the Union of Soviet Socialist Republics (USSR), South Yemen, and Zaire were renamed to Czech Republic, Germany, Russia, Yemen, and the Democratic Republic of Congo, respectively. Mainland China, Tibet, and Taiwan were renamed to China. The American territories of Samoa, Guam, and Rota were renamed to the United States. The Faroe Islands and Greenland were renamed to Denmark and New Caledonia was renamed to France. These changes were made based on UN Human Development Reports databases.

Statistical analyses

We fitted two phylogenetic mixed-effects generalized linear models with a Poisson distribution using the R package brms (Bürkner 2021) to test whether species traits (body mass, extent of occurrence, evolutionary distinctiveness, threat status, and presence in CITES appendices) affect the number of parts and uses. Threat status and presence in CITES appendices were treated as ordinal variables with five and four levels, respectively (LC $<$ NT $<$ VU $<$ EN $<$ CR; Absent $<$ III $<$ II $<$ I). We excluded species categorized as data deficient (DD) from the analyses because DD is not a threat status per se and is therefore not suitable for answering our hypotheses (Guedes et al. 2023). However, it is worth noting that many species categorized as DD are actually predicted to be prone to extinction (Borgelt et al. 2022; Morais et al. 2013). We included the IUCN and CITES status variables together in the full model because threat category (IUCN status) is perceived as a proxy for rarity and presence in CITES appendices (especially when associated with trade restrictions) can have the opposite effect and may stimulate trade by increasing demand for threatened species (Rivalan et al. 2007). Prior to analysis, all numerical variables were log10 – transformed, centered and scaled (z-transformation) to allow direct comparisons of effect sizes. Models were run with the set of species for which all trait data were available (n = 447 – the extinct species *Rucervus schomburgki* and *Pteropus pilosus* were excluded from this analysis) (Additional File 1). For all models (body parts, uses, and number of bulletins), we used the *get priors* function in the brms package to obtain model-specific priors. We used the inverse of the phylogenetic distance matrix to account for phylogenetic relationships between species. We used 4 chains with 5,000 iterations in all models, sampling every iteration and discarding the first 1,000 as burn-in. Model diagnosis was performed using density and trace plots of fixed effects. We used Rhat (potential scale reduction values) equal or below 1 as indicating good convergence. Moreover, we computed the probability of direction (pd) to assess the effect of each species traits on the number of parts, uses, and bulletins. Values indicate the certainty of the direction of an effect, therefore pd – values were considered as being significant when the likelihood of an effect in a certain direction was over 97.5%.

We further tested the phylogenetic signal for trade purposes using Fritz's D (Fritz and Purvis 2010) implemented in the R package caper (Orme et al. 2018). This is a measure of phylogenetic signal for binary traits and was applied here for each trade purpose individually (1 = traded for a given purpose; 0 = not traded). Fritz's D can be interpreted as follows: $D = 1$ corresponds to a random distribution of uses, $D = 0$ indicates that uses are clumped, $D > 1$ indicates phylogenetic overdispersion, and $D < 1$ indicates that purposes are more clustered than expected (strong phylogenetic signal) and suggests that humans tend to trade closely related species for the same purposes. For these analyses, the dataset containing all species sampled in the phylogeny (n = 452 species) was used (Additional File 3).

As a sensitivity analysis, we use the Fritz's D (Fritz and Purvis 2010) to test whether the trade reports are biased toward a given clade of the phylogeny considering all species included in phylogeny. Additionally, we calculated the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) to test whether trade reports are biased toward a given depth of the phylogeny considering only the species recorded in the TRAFFIC bulletins. For the null model, we randomized the community data matrix by drawing species from the pool of species occurring in the phylogenetic distance matrix with equal probability. NRI quantifies phylogenetic clustering/overdispersion of a community (here, each TRAFFIC bulletin), giving more weight to relationships closer to the root of the phylogeny, while NTI captures patterns closer to the tips. Positive values indicate that a community contains closely-related species (phylogenetic clustering) more than expected by chance, while negative values indicate phylogenetic overdispersion. For these analyses, we used all species sampled in the phylogeny (n = 452) (Additional File 5). Analyses were performed in the R package picante (Kembel et al. 2010). Clades contributing disproportionately to the pattern were identified using the NODESIG function in R (R Core Team 2021) adapted from Abellan et al. (2016).

To assess whether socio-political variables (IHD, GDP *per capita*, and HPD) affect the number of species, bulletins, and WOE per country, we fitted three generalized linear models with Poisson error distribution. Prior to the analysis, GDP *per capita* and human population density were log10 – transformed, and then centered and scaled (z-transformation) to allow direct comparisons of effect sizes. Analyses were performed in the R package glmmTMB (Brooks et al. 2017). Residual diagnostics were conducted in the R package DHARMa (Hartig 2022). Residuals had normal distribution and homogeneity of variance. Models did not show overdispersion. Finally, we used Spearman correlation to test whether the number of species was correlated with the number of bulletins per country.

RESULTS

Traded taxa and species traits

During the period-analyzed (1975-2019), at least 16,279,031 specimens (WOE) of wild mammals were traded, including manufactured goods (e.g., traditional medicines or carving/sculptures, jewellery) and body parts of at least 458 species from 79 families and 19 orders (Figure 1). Of the species involved, 424 (92.6%) are terrestrial and 34 (7.4%) are marine. The population trends of 246 species (53.71%) are "decreasing", while 92 (20.1%) are "stable", 81 (17.7%) are "unknown", and 39 (8.51%) are "increasing" (Additional File 1).

Species body mass and threat status positively in-

Table 1. Results of the Bayesian GLMM models to test the effect of species traits on the number of parts, uses, and bulletins of mammal species traded. c = conditional, m = marginal.

	Incidence rate ratios	Standard Error	CI (95%)	Rhat	P direction
Model Parts – $R^2 = 0.141^m/0.397^c$					
Intercept	1.79	0.76	0.73 – 4.23	1.00	90.39%
Body mass (g)	1.31	0.08	1.16 – 1.49	1.00	**100,00%**
Geographical occurrence (km^2)	1.03	0.05	0.93 – 1.13	1.00	70.16%
Evolutionary distinctiveness	1.04	0.04	0.96 – 1.12	1.00	84.29%
CITES III	1.15	0.11	0.96 – 1.38	1.00	93.77%
CITES II	1.02	0.10	0.84 – 1.23	1.00	57.02%
CITES I	1.30	0.15	1.03 – 1.64	1.00	**98.53%**
IUCN - LC	0.91	0.13	0.69 – 1.19	1.00	74.70%
IUCN - NT	0.95	0.10	0.78 – 1.16	1.00	68.74%
IUCN - VU	1.12	0.12	0.91 – 1.38	1.00	**97.92%**
IUCN - EN	1.21	0.11	1.01 – 1.45	1.00	89.49%
Model Uses - $R^2 = 0.148^m/0.260^c$					
Intercept	1.76	0.45	1.01 – 2.98	1.00	97.60%
Body mass (g)	1.20	0.07	1.08 – 1.35	1.00	**99.96%**
Geographical occurrence (km^2)	1.02	0.05	0.93 – 1.13	1.00	67.71%
Evolutionary distinctiveness	1.02	0.04	0.95 – 1.11	1.00	74.11%
CITES III	1.12	0.10	0.93 – 1.33	1.00	88.83%
CITES II	1.06	0.11	0.87 – 1.29	1.00	70.82%
CITES I	1.04	0.13	0.81 – 1.32	1.00	61.72%
IUCN - LC	1.08	0.15	0.83 – 1.41	1.00	71.71%
IUCN - NT	0.94	0.10	0.77 – 1.15	1.00	71.87%
IUCN - VU	0.97	0.11	0.78 – 1.20	1.00	**99.81%**
IUCN - EN	1.31	0.12	1.09 – 1.58	1.00	59.83%
Model Bulletins - $R^2 = 0.032^m/0.891^c$					
Intercept	1.76	1.85	0.13 – 21.25	1.00	67.46%
Body mass (g)	1.38	0.16	1.10 – 1.72	1.00	**99.74%**
Geographical occurrence (km^2)	1.16	0.07	1.03 – 1.31	1.00	**99.46%**
Evolutionary distinctiveness	1.02	0.05	0.94 – 1.12	1.00	69.86%
CITES III	1.16	0.14	0.91 – 1.48	1.00	88.68%
CITES II	1.09	0.13	0.86 – 1.39	1.00	77.02%
CITES I	1.50	0.22	1.12 – 2.01	1.00	**99.74%**
IUCN - LC	0.85	0.15	0.60 – 1.19	1.00	**99.60%**
IUCN - NT	1.16	0.15	0.90 – 1.49	1.00	75.92%
IUCN - VU	0.91	0.11	0.71 – 1.17	1.00	88.24%
IUCN - EN	1.34	0.15	1.08 – 1.66	1.00	82.46%

fluenced the number of parts and the uses for species traded (Table 1; Figure 2a – b; Figure 3a – c). In addition, species listed in the CITES appendix I have more parts traded (Table 1). We found no effect of evolutionary distinctiveness and geographical range on the number of body parts and uses. Closely related species were traded for the same purposes in all 10 categories (Table 2; Figure 4). In addition, our results show that 26 threatened species (13 vulnerable, 12 endangered, and 1 critically endangered) have parts and/or products traded and were not included in any CITES appendices (Additional File 1).

Species body mass, geographical range size, presence in the CITES appendix I, and species classified as "Least concern" positively influenced the number of entries in the TRAFFIC bulletin (Table 1; Figure 5). This means that larger, widespread species, and species with trade regulations, and those not experiencing any strong threat were more represented in the TRAFFIC bulletins (Figure 5). There is a phylogenetic signal for the species included in the bulletins (considering all species included in the phylogeny) (D = 0.4555; $P < 0.0001$). Furthermore, species included in the bulletins were phylogenetic clustered at both root and tip level (NRI = 2.5915, NTI = 2.6234; $P < 0.05$), indicating that trade is biased towards a few representative clades. Specifically, some clades have contributed disproportionately to the reports, es-

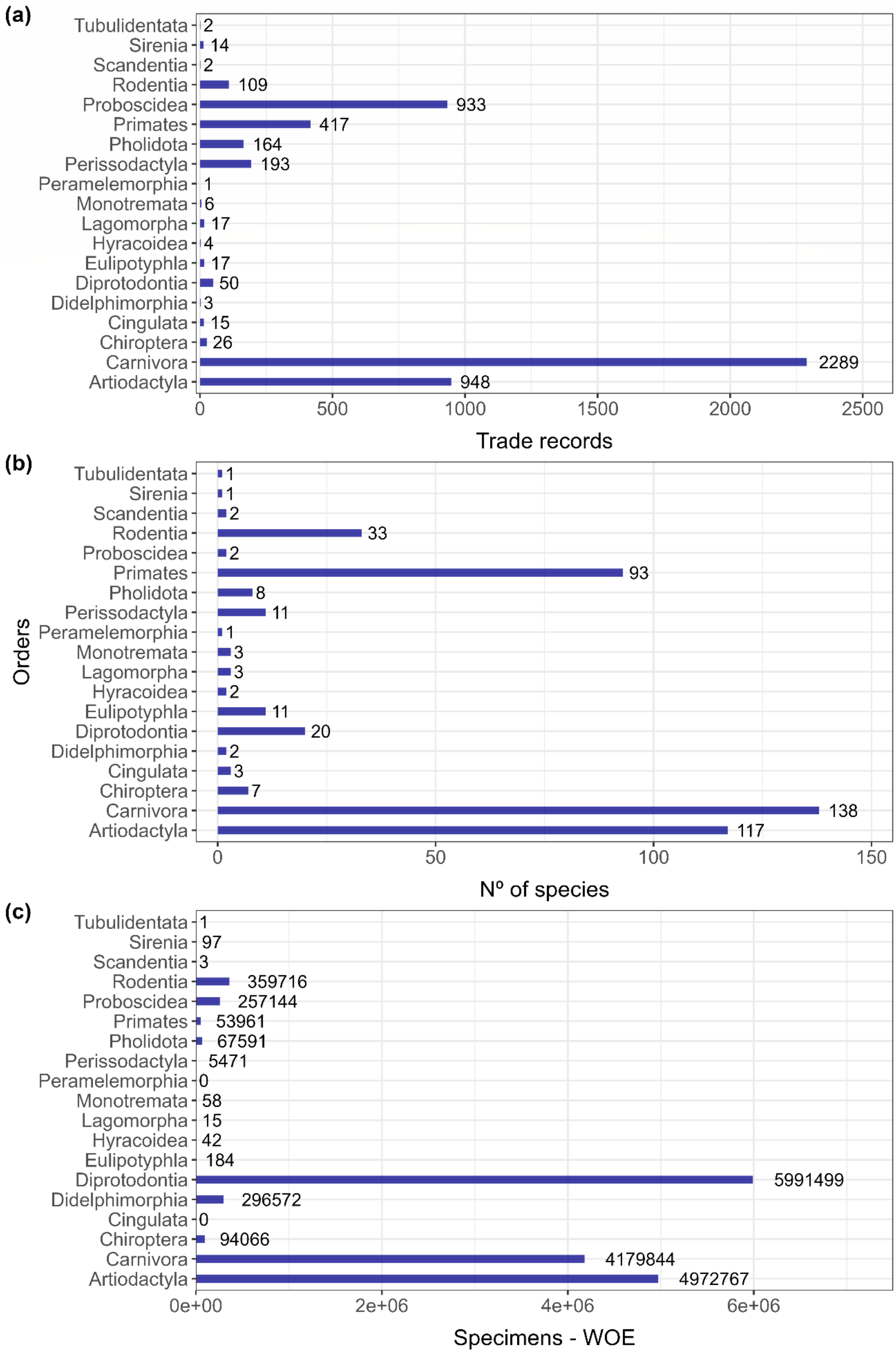

Figure 1. (a) Number of trade records, (b) species, and (c) specimens of mammals traded per order. (Additional File 4 - Table S2 for values per family).

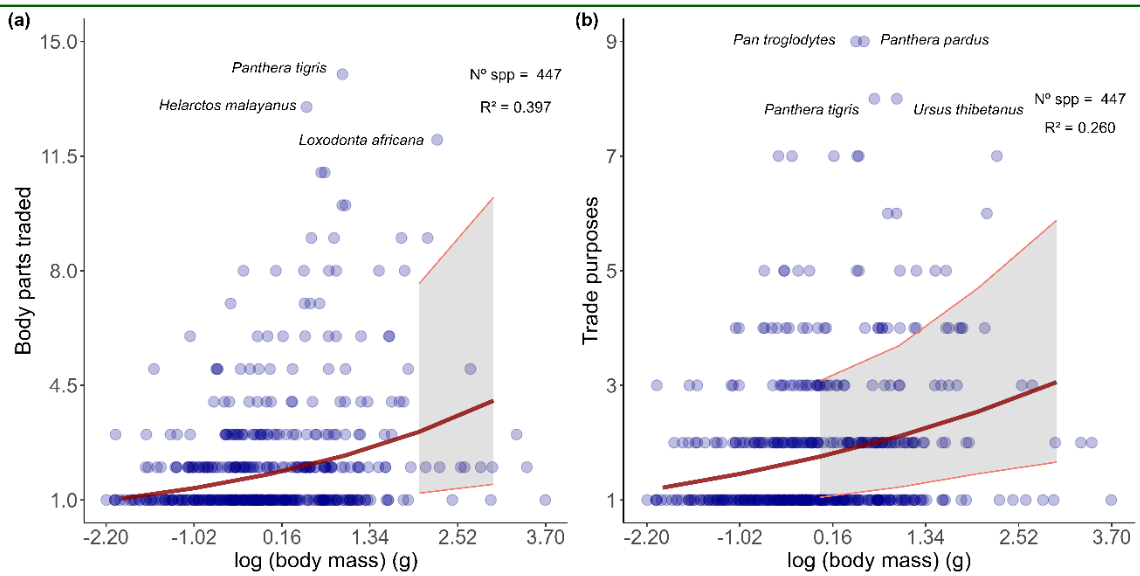

Figure 2. Plot showing the positive relationship between body mass on the number of body parts (a) and uses (b) of traded mammals as predicted by the Bayesian model.

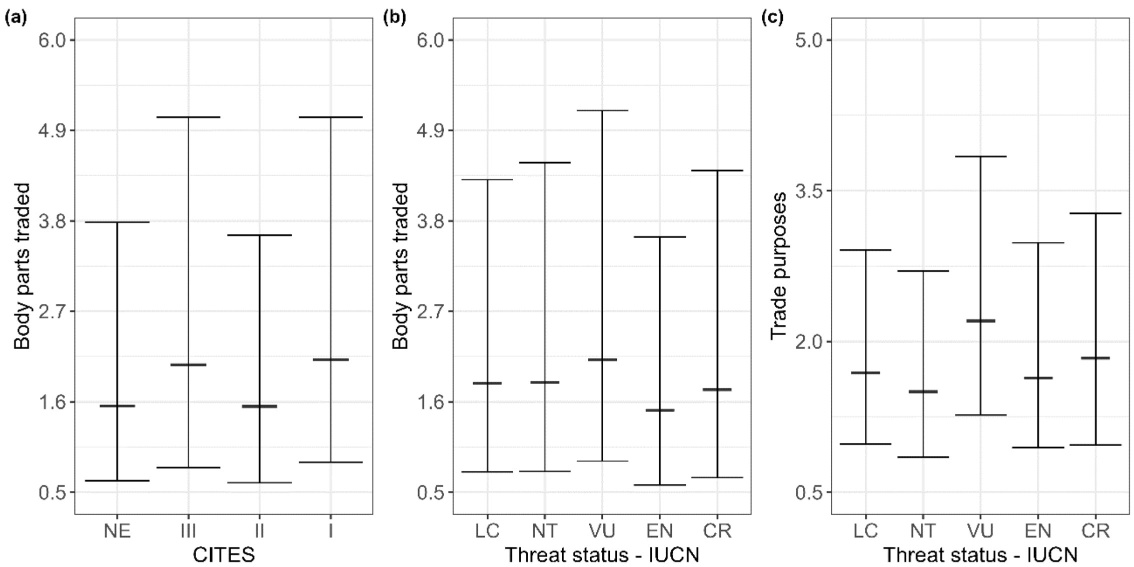

Figure 3. Plot showing the differences between the number of body parts and trade purposes of mammals for CITES appendices (body parts) and threat category (parts and uses) as predicted by the Bayesian model.

pecially Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea (Additional File 4 - Figure S1).

Socio-political variables

At least 127 countries are involved in wild mammal trade (Figure 6), of which 125 are Parties to the CITES Convention (Additional File 2). In terms of socio-political variables, only HDI influenced the number of traded species per country (Table 3). In general, countries with higher HDI scores tended to trade more species (Figure 7). The number of species was strongly correlated with the number of bulletins per country (rho = 0.82; $P < 0.0001$).

DISCUSSION

We found that at least 7.15% of mammal species (458 out of 6,399 known species; Burgin et al. 2018) have been traded in the last 40 years. Our results confirm partially our first hypothesis that larger species have more parts traded and are used for more purposes than smaller species. Prior studies that have examined

Table 2. Phylogenetic signal (Fritz's D) of the 10 trade purposes.

Trade purposes	Number of species	D	P-value (Brownian)	P-value (Random)
1 – Manufactured	64	0.5291368	**0.0001**	**0.0001**
2 – Circus/Zoo	30	0.9325216	**0.013**	**0.0001**
3 – Food	128	0.5596142	**0.0001**	**0.0001**
4 – Leather	27	0.6069808	**0.0001**	**0.002**
5 – Magic-Religious	35	0.6607803	**0.0001**	**0.0001**
6 – Pet	46	0.7728501	**0.0001**	**0.0001**
7 – Scientific research	11	0.7759848	**0.031**	**0.004**
8 – Commercial	357	0.7654602	**0.0001**	**0.0001**
9 – Traditional medicine	97	0.7812306	**0.0001**	**0.0001**
10 – Trophies	59	0.4237164	**0.0001**	**0.004**

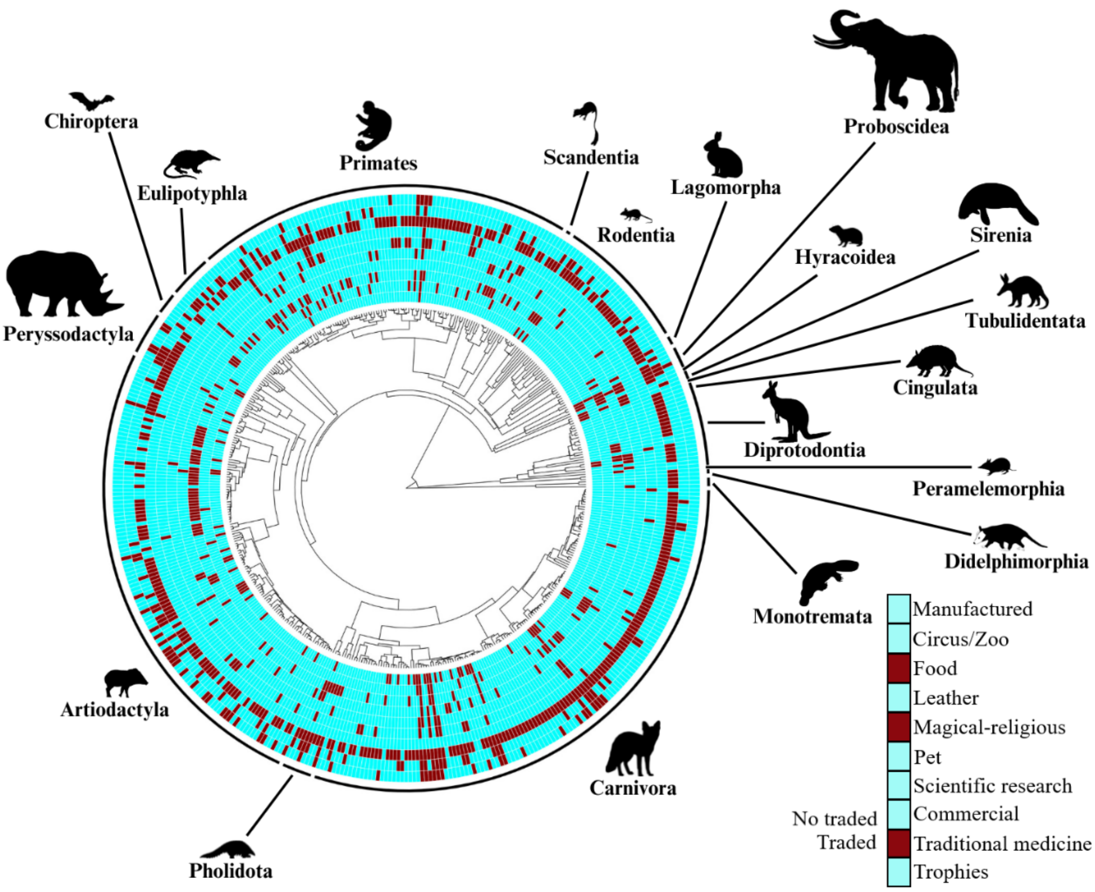

Figure 4. Phylogenetic tree of mammal species included in the analyses showing their use in each of the 11 trade purposes. Each species used for a particular trade purpose is indicated (in purple): each line represents a use category, from 1 (inner ring) to 11 (outer ring). Trade purposes follow the same sequence as in Table 2.

the use (e.g., for food and traditional medicine) and trade of wild mammals also showed that body mass is a key trait for species selection and use (Alves et al. 2020; Hughes et al. 2022; Scheffers et al. 2019).

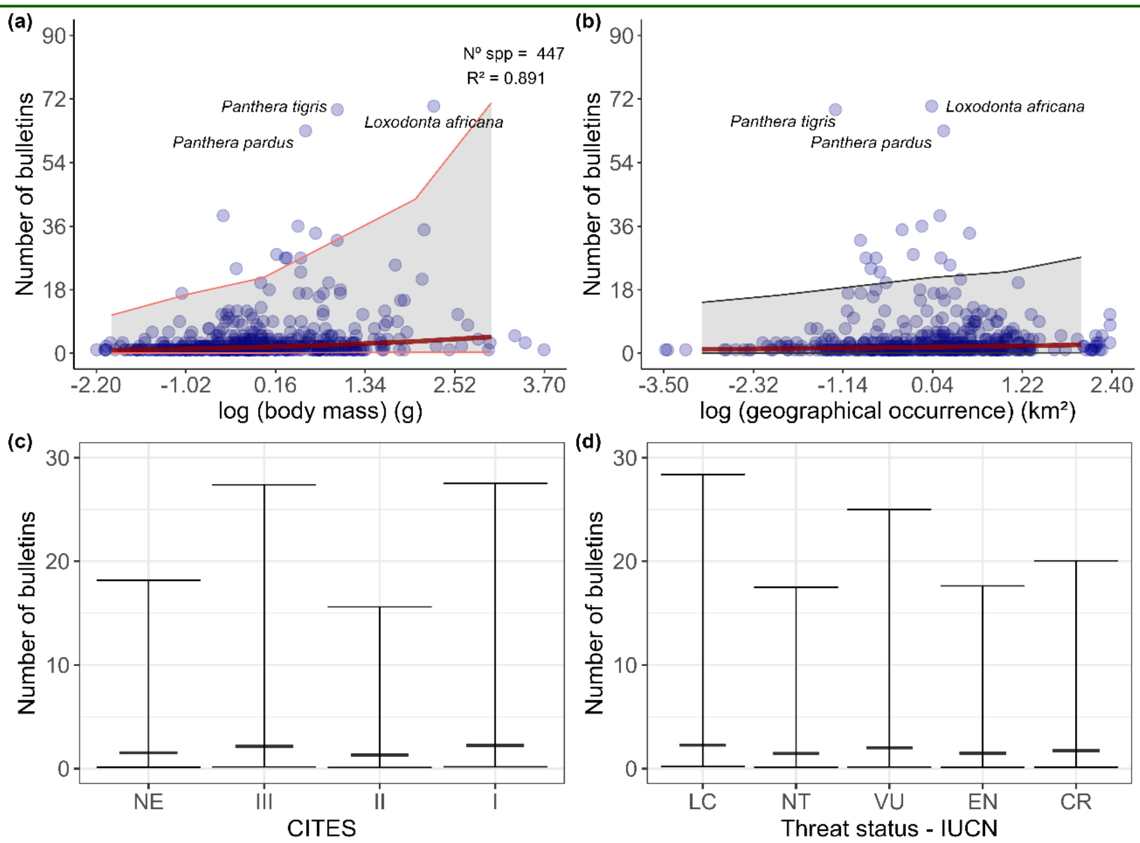

Figure 5. Plot showing the effect of species traits on the number of bulletins as predicted by the Bayesian model.

Large-bodied species provide more products used in traditional medicine (Alves et al. 2020), are also more valued in the trophy trade (Johnson et al. 2010; Palazy et al. 2012), and as pets (Su et al. 2015). For example, the price and list of species traded as trophies are directly influenced by their size, which results in a higher demand and a higher market value for them (Johnson et al. 2010; Palazy et al. 2012). Thus, our results not only provide independent evidence to support those results, using a different dataset (although limited in the number of species), but also reveal the influence of body mass, threat status, and presence in CITES appendix on two aspects not previously investigated: the number of body parts and trade purposes.

We found that threatened species and those listed in CITES appendix I have more body parts and trade uses, supporting our second hypothesis. Threat status and presence in CITES is perceived as a proxy for rarity and may increase the demand for or the value/price of a given species (Chen 2016; Johnson et al. 2010; Palazy et al. 2012; Rivalan et al. 2007; Su et al. 2015). For example, threatened birds from the Taiwan pet market are more expensive than non-threatened species (Su et al. 2015). The threat status also influences the price of wild mammals traded as trophies in African countries (Johnson et al. 2010).

Interestingly, we found no effect of geographic range size and evolutionary distinctiveness on the number of traded body parts. Nevertheless, recent studies have shown that a great number of evolutionarily distinct species, which are also the most ancient species that play a crucial role in global ecosystems, are exploited for wildlife trade (Hughes et al. 2023; Scheffers et al. 2019). Similarly, species with narrow geographic ranges (Johnson et al. 2010) are traded more heavily in the trophy trade. However, these studies have used a different analytical approach to assess wildlife trade, such as presence/absence in trade (Scheffers et al. 2019; Hughes et al. 2023) and the price/value of trophies (Johnson et al. 2010).

Our results support the claim that taxa with greater number of parts and uses may have a higher incidence of trade and of threat by wildlife trade (Additional File 1). For example, *Panthera tigris*, *Helarctos malayanus, Loxodonta africana, Capricornis sumatraensis,* and *Ursus thibetanus* that had the largest numbers of body parts and *Pan troglodytes*, *P. tigris*, *P. pardus*, and *U. thibetanus* that had the highest number of uses are all considered "threatened" species by the IUCN. In addition, these species also

Table 3. Results of linear generalised models to test the effect of socio-political indices on the number of trade records, species and specimens –WOE traded by country. c = conditional, m = marginal.

	Incidence Rate Ratios	**Std. Error**	**CI (95%)**	**P value**
Species – $R^2 = 0.0949^m/0.9443^c$				
(Intercept)	6.59	0.72	5.33 – 8.15	<**0.001**
GDP per capita	0.56	0.18	0.30 – 1.04	0.065
HDI	2.25	0.71	1.22 – 4.18	**0.010**
HPD	1.09	0.12	0.88 – 1.34	0.438
Bulletins – $R^2 = 0.0178^m/0.9398^c$				
(Intercept)	6.13	0.69	4.91 – 7.64	<**0.001**
GDP per capita	0.72	0.23	0.38 – 1.37	0.319
HDI	1.46	0.47	0.78 – 2.76	0.239
HPD	1.06	0.12	0.85 – 1.32	0.624
WOE – $R^2 = 0.1237^m/0.9999^c$				
(Intercept)	1571.14	506.16	835.58 – 2954.20	<**0.001**
GDP per capita	1.89	1.79	0.30 – 12.11	0.500
HDI	1.77	1.66	0.28 – 11.15	0.544
HPD	0.53	0.17	0.28 – 1.00	0.051

had the greatest number of records. Furthermore, due to the greater cultural value (Volpato et al. 2020) and risks (law enforcement) associated with poaching and trade of threatened species, there may be a maximization of uses of these species (they may be used for various purposes, e.g., in traditional medicines and culinary products, wet markets), directly increasing the number of body parts traded per species. As some authors point out (Alves and Rosa 2006; Alves et al. 2020), the diversity of uses of a species can be a factor that increases demand for products derived from it and increases commercial pressure on it.

Another important finding is that closely-related taxa were traded for similar purposes, which supports our third hypothesis. This result shows that the choice of a species for a particular use is not random, but directed toward taxa that share similar characteristics. Common ancestry also determined trade in other terrestrial vertebrates (Scheffers et al. 2019). This fact can be observed in the trade of certain groups, such as rhinos, felids, and pangolins. When populations of these species are depleted, trade is directed toward another phylogenetically closer species (Scheffers et al. 2019). For example, there has been an increasing demand for lion bones as a substitute for tiger bone in traditional medicines and the production of wine in Asian markets (Coals et al. 2020).

Our results show that larger and widespread taxa, species listed in CITES appendix I, and non-threatened ones are overrepresented in TRAFFIC bulletin records. In addition, species recorded in the bulletins are phylogenetically clustered at different phylogenetic scales. For example, Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea had species recorded in at least 20 TRAFFIC bulletins. This pattern points out to a taxonomic bias in our dataset. Therefore, our results only apply to these specific clades within mammals. Studies on wildlife trade may be affected by the uncertainty and bias related to the data used (Challender et al. 2022; Paudel et al. 2022). Although the scope of the TRAFFIC bulletin is on publishing information on wildlife trade, it might not capture the full variety of species, countries, and types of trade. Much of its published information came from non-governmental institutions, seizures by law enforcement, and newspaper reports, which may lead to inaccurate taxonomic identification, and bias on the parts or items traded as well as the reported countries (Berec et al. 2018; Smith et al. 2009). This same problem may be observed in other datasets used for wildlife trade investigations. For example, based on the United States Fish and Wildlife Service (USFWS)

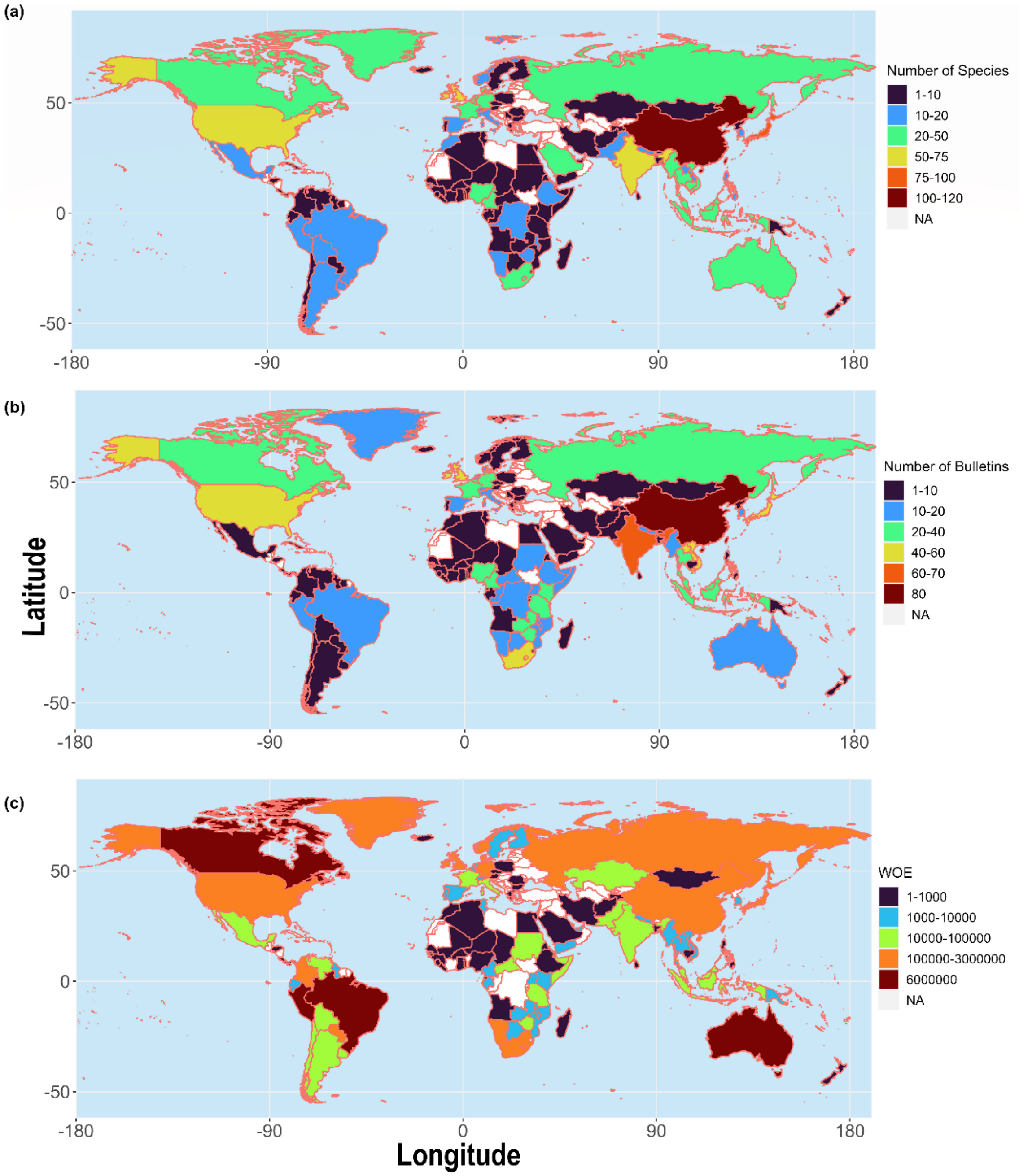

Figure 6. World map showing the main countries involved in wild mammal trade in terms of number of species, trade records, and specimens (WOE) traded.

– Law Enforcement Management Information System (LEMIS), only 13% of wildlife specimens imported into the USA were identified to the species level (Smith et al. 2009). For the CITES database, considering only the trade of *Ursus americanus*, 96% of entries in the CITES database were not complete and 75% of entries did not include the quantities or type of items listed (Berec et al. 2018). Additionally, larger, charismatic, and threatened species are reported more often on seizure records and media (Paudel et al. 2022). This may justify for example, the high number of bulletins records that include Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea, which have many larger, threatened, and charismatic species, such as "big cats", rhinos, apes, and elephants. Some factors can influence this over-reporting. For example, larger and charismatic species are more easily recognised by customs officials, therefore they tend to be more reported in the media (Paudel et al. 2022). Alternatively, those species could be recorded more regularly

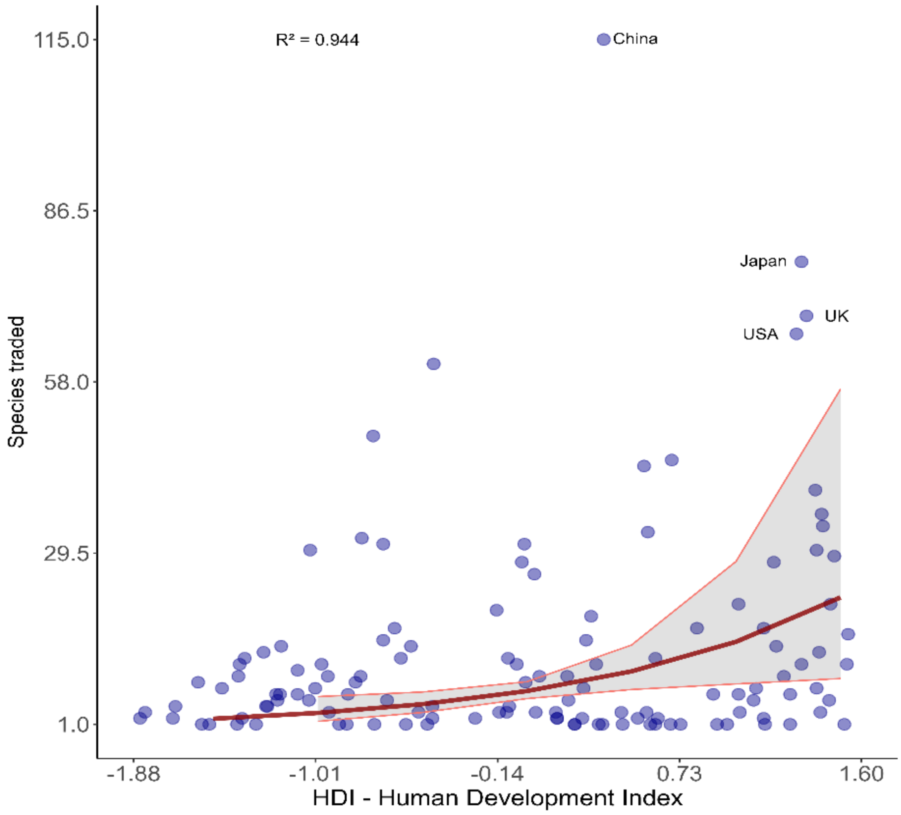

Figure 7. Plot showing the effect of HDI on the number of species traded *per* country, as predicted by the glmm.

because of their high demands (Scheffers et al. 2019). Despite its limitations, TRAFFIC can be a valuable resource to identify trends in wildlife reports, since it includes records of species listed and non-listed in CITES, and can serve as a baseline to investigate underlying sources of biases and reporting preference on wildlife trade reports.

Trade in wild mammals is widespread worldwide. Our results show that there is a difference in the number of traded species and WOE per country. For example, countries with the largest number of traded species are in Asia (> 50 species), except for the USA and the UK, while the countries with the largest number of traded WOE are in Oceania (> 5,000,000 specimens) and South America (> 2,000,000 specimens). Conversely, the most frequently reported countries in TRAFFIC bulletins are India and China (both with n = 61 and n = 115 bulletins, respectively). These results show that analyses to understand the spatial patterns in the wild mammal trade need to consider the different nuances in wildlife trade. For example, Japan and China had the greater number of species (> 70 species), while Brazil, Peru, and Australia had the greater number of WOE (> 2,000,000 specimens). Many factors can contribute to these differences. For instance, trade chains can encompass countries that play different roles (Liew et al. 2021; Ribeiro et al. 2022; Van Vliet et al. 2014; Van Vliet et al. 2022; Wu et al. 2025); some may act as suppliers of wildlife products, while others may drive the flow of traded species, acting as consumers (Wu et al. 2025). China is considered the most important centre for wildlife consumption and trade in Asia (Jackson et al. 2023; Wu et al. 2025). At least 90 species of wild mammals are used in traditional Chinese medicine (Alves et al. 2020), and all pangolins, rhino, and felids species are traded in the numerous wildlife markets (fur/skins, trophies, restaurants, traditional medicine/culinary) in the country (Hughes 2021; Volpato et al. 2020; Zhu and Zhu 2020). The greater number of WOE traded by Australia is due to the high harvest rates of *Trichosurus vulpecula* (> 450,000 WOE) and *Pseudocheirus peregrinus* (> 5,000,000 WOE) for fur/skin and meat trading programmes as a measure for reducing crop and grazing damage (TRAFFIC bulletin Volume 12 Issue 3). In the past decades, Australia has been the main exporter of pelts and hides of Diprotodontia species (TRAFFIC bulletin Volume 12 Issue 3). Brazil and Peru were also among the main exporters of fur/skins in South America (Antunes et al. 2016; Redford 1992). At least 23.3 million (between 21.6 – 26.8 million) wild mammals have been hunted for the fur/skin trade in the Amazon basin over the past century (Antunes et al. 2016).

Our study further shows that more species of wild mammals were traded in countries with higher Human Development Index. These results partially support our fourth hypothesis, showing that high-income countries tend to consume more wildlife products than low-and middle-income countries. However, developed countries, such as Japan and China appear to be the main consumers of wildlife products and are among the largest economies in the world, confirming previous findings (Liew et al. 2021; Symes et al. 2018b). Overall, the demand for wildlife products are higher in high-income countries of the northern hemisphere, while low-middle income countries in the south hemisphere act as suppliers of wildlife products (Liew et al. 2021). Although most countries have laws and are signatory of international commitments, such as CITES, that restrict and regulate wildlife trade, the wide diversity of species and regional influence make problem solving difficult (Phelps et al. 2016; Sas-rolfes et al. 2019). This fact highlights the need for ongoing assessment and reformulation of measures to regulate and monitor trade in wild mammals, as well as measures to mitigate the impacts caused by trade and prevent over-exploitation of species.

In conclusion, our study highlights the importance and contribution of species traits (body mass, threat status, and presence in CITES-listing) and socio-political factors to the dynamics of wild mammal trade. Our results show that (1) larger and vulnerable species are more traded and versatile in terms of body parts and trade purposes, (2) closely related species tend to be traded for similar purposes, and (3) the mammal trade record is biased towards specific lineages. Although there are numerous studies on wildlife trade, the extent of the impact of trade on many species is unclear because most traded species (including threatened species) remain unprotected at local and international scales. Furthermore, current conservation and management measures for traded species are ineffective and fail to protect species. Given that a single species may be traded for more than one purpose, understanding the factors involved in wildlife trade is important for developing strategies to mitigate its impacts. For example, including or changing the status of species listed in CITES appendix, or providing financial assistance for the conservation of target species based on trade purposes or body parts traded. Moreover, a single body part can be used and traded for many purposes (e.g., rhino horn and pangolin scales are both used for traditional medicines and handcrafts). Thus, understanding species and their body parts uses are key to improve conservation practices of overexploited species, which can be a challenge for national and international law enforcement agencies worldwide.

DATA AVAILABILITY

All data supporting the findings of this study are provided in the additional files accompanying the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

CONTRIBUTION STATEMENT

HKLS, RRDB, and RRNA designed the project; HKLS built the dataset; HKLS, AF, and DBP performed the analyses; HKLS and RRNA led the writing of the article with contributions from all authors.

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Received: 01 January 2025
Accepted: 01 February 2025
Published: 01 July 2025

Editor: Anna Karolina Martins Borges

Additional Files

Add File 1. Spreadsheet containing trade data (number of records, specimens, body parts and uses) and species attributes (body mass, geographic range, Evolutionary distinctiveness, threat status and CITES appendices).

https://ethnobioconservation.com/index.php/ebc/article/view/1067/493

Add File 2. Spreadsheet containing number of trade records, species and specimens traded, and socio-political variables by country.

Countries	Species	Bulletins	WOE	CITES	hdi	gdp_per_capita	density	poverty
Afghanistan	9	2	223	YES	0.478	400	46.32	NA
Algeria	1	1	1	YES	0.745	2800.17	15.9	36.6
Andorra	1	1	NA	YES	0.858	26114.05	170.22	NA
Angola	1	5	159	YES	0.586	1702.01	19.2	78
Argentina	17	10	93169	YES	0.842	6749.76	14.94	10.6
Australia	29	15	5980114	YES	0.951	29011.9	2.88	1
Austria	6	5	410	YES	0.916	28972.13	102.2	1
Bahrain	6	1	52	YES	0.875	15020.29	1711.18	NA
Bangladesh	2	1	2	YES	0.632	1855.7	1240	14.3
Belgium	30	37	9967	YES	0.937	27413.68	358.94	0.3
Benin	10	1	NA	YES	0.525	618.87	80.9	83.6
Bhutan	2	2	22	YES	0.666	1283.2	17.12	8.4
Bolivia	12	9	22073	YES	0.692	1388.78	9.34	15.2
Botswana	4	11	3265	YES	0.693	3542.47	3.42	63.5
Brazil	15	12	2231809	YES	0.754	5042.14	23.12	28.4
Brunei	1	1	NA	YES	0.829	21891.78	67.14	NA
Bulgaria	2	2	83	YES	0.795	4166.85	67.26	4.5
Burkina Faso	1	1	23	YES	0.449	402.6	57.9	87.2
Burundi	2	10	24295	YES	0.426	190.01	354.9	96.5
Cambodia	31	9	913	YES	0.593	722.38	80.54	NA
Cameroon	32	27	4080	YES	0.576	1044.23	44.44	74.8
Canada	40	23	1620796	YES	0.936	27743.05	3.7	0.7
Central African Republic	3	11	25086	YES	0.404	350.49	6.9	96.2

to be continued...

Countries	Species	Bulletins	WOE	CITES	hdi	gdp_per_capita	density	poverty
Chad	1	7	305	YES	0.394	437	9.58	89.4
Chile	6	4	18505	YES	0.855	6655.89	22.94	8
China	115	76	102169	YES	0.768	2556.22	147.92	24
Colombia	7	6	472385	YES	0.752	3288.16	39.9	7
Republic of Congo	8	20	2806	YES	0.571	1503.59	12.6	83.5
Costa Rica	1	1	10	YES	0.809	4885.53	88.68	14.1
Cuba	1	1	NA	YES	0.764	3871.61	101.98	NA
Cyprus	1	1	NA	YES	0.896	16193.2	118.18	0.2
Czech Republic	7	6	54	YES	0.889	13568.16	134.42	0.4
Ivory Coast	3	7	NA	YES	0.55	1256.49	65.42	75.6
Democratic Republic of the Congo	11	19	11018	YES	0.479	331.5	28.94	97.4
Denmark	21	12	510689	YES	0.948	35701.11	129.7	0.4
Djibouti	5	5	18	YES	0.509	1278.35	39.26	78.5
Ecuador	5	2	2880	YES	0.74	3040.36	58.86	29.9
Egypt	2	2	46	YES	0.731	1420.56	84.88	68.8
Equatorial Guinea	5	5	42	YES	0.596	5237.13	36.02	NA
Eritrea	1	1	11	YES	0.492	365.86	25.22	NA
Ethiopia	13	13	789	YES	0.498	311.94	79.08	90.9
Finland	3	2	1801	YES	0.94	28899.1	17.42	0.1
France	28	24	28001	YES	0.903	25932.08	114.64	0.4
Gabon	8	10	2882	YES	0.706	5615.58	6.42	31.2
Gambia	4	3	27	YES	0.5	504.94	173.16	80.6
Germany	34	26	172542	YES	0.942	27691.5	231.92	0.2
Ghana	4	4	415	YES	0.632	784.6	106.9	78.5
Greece	5	4	12	YES	0.887	14131.93	82.08	3.9

to be continued...

Countries	Species	Bulletins	WOE	CITES	hdi	gdp_per_capita	density	poverty
Guinea	7	7	265	YES	0.465	567.75	42.52	86.8
Guinea-Bissau	12	1	1	YES	0.483	352.37	46.22	87.2
Guyana	3	3	1794	YES	0.714	2231.39	3.64	56.6
Honduras	3	2	18	YES	0.621	1351.3	73.84	49.5
Iceland	1	1	500	YES	0.959	34501.7	3.12	0
India	61	61	34836	YES	0.633	730.52	391.88	83
Indonesia	31	33	54197	YES	0.705	1506.44	128.48	60.4
Iran	1	1	1	YES	0.783	3114.6	50	0.6
Italy	17	19	15525	YES	0.895	22257.17	198.14	2.2
Japan	78	44	166518	YES	0.925	29658.66	344.2	1.4
Kazakhstan	2	3	23483	YES	0.811	5641.52	6.24	14.3
Kenya	9	29	7081	YES	0.575	701.25	72.48	91.3
Laos	12	43	1295	YES	0.607	905.68	27.4	70.5
Liberia	2	2	3	YES	0.481	503.72	40.54	88.9
Luxemburg	1	1	50	YES	0.916	113218.7	250	0.1
Madagascar	4	3	1	YES	0.501	385.09	36.38	98.2
Malawi	14	13	2085	YES	0.512	383.47	157.36	97.3
Malaysia	33	34	49061	YES	0.803	5091.81	84.7	3.4
Mali	4	4	267	YES	0.428	414.38	12.2	81
Malta	2	1	NA	YES	0.895	30186.2	1514	0.3
Mexico	19	8	20089	YES	0.758	6003.11	58.72	32.5
Micronesia	1	1	8250	NO	0.628	2307.84	126.12	74.8
Mongolia	9	5	70	YES	0.739	1842.76	1.78	38.3
Morocco	20	5	577	YES	0.683	1856.07	78.94	42.1
Mozambique	8	16	9745	YES	0.446	411.98	30.94	96.1

to be continued...

Countries	Species	Bulletins	WOE	CITES	hdi	gdp_per_capita	density	poverty
Myanmar	49	14	3610	YES	0.585	380.05	76	68.2
Namibia	14	16	181037	YES	0.615	3291.61	2.62	57.3
Nepal	17	18	3404	YES	0.602	380.57	179.98	80.4
Netherlands	36	14	4053	YES	0.941	30699.31	481.1	0.2
New Zealand	7	6	147	YES	0.937	20954.82	15.98	NA
Niger	2	2	20	YES	0.4	344.17	14.42	95
Nigeria	30	22	352	YES	0.535	1252.36	178.18	90.8
North Korea	2	2	NA	NO	NA	NA	201.34	NA
Norway	11	8	437034	YES	0.961	46785.49	15.72	0.5
Pakistan	11	10	19649	YES	0.544	645.53	207.22	84.5
Palau	1	1	78750	YES	0.767	11539.11	35.12	NA
Panama	1	1	445	YES	0.805	5826.6	48.3	12.9
Papua New Guinea	1	1	1900	YES	0.558	1257.4	15.92	90.2
Paraguay	9	8	358674	YES	0.717	2705.81	15.72	19.9
Peru	11	12	2345552	YES	0.762	2895.6	22.84	33.7
Philippines	11	9	115	YES	0.699	1448.09	317.3	55.3
Poland	3	2	1	YES	0.876	8822.11	124.6	0.8
Portugal	1	4	1407	YES	0.866	12640.01	113.66	2.6
Romania	1	2	2	YES	0.821	5511.42	87.86	10
Russia	45	34	372570	YES	0.822	6803.26	8.82	4.1
Rwanda	5	3	10	YES	0.534	380.84	428.26	92.2
Saudi Arabia	21	2	73	YES	0.875	12844.69	14.46	NA
Senegal	6	6	28	YES	0.511	938.81	66.6	74.4
Serbia	3	1	NA	YES	0.802	4777.53	119.42	10.1
Sierra Leone	1	4	253	YES	0.477	317.46	87.52	89.9

to be continued...

Countries	Species	Bulletins	WOE	CITES	hdi	gdp_per_capita	density	poverty
Singapore	13	23	42495	YES	0.939	27070.62	7221.4	NA
Solomon Islands	1	1	28	YES	0.564	1192.98	18.6	88.5
Somalia	3	12	11212	YES	NA	221.02	19.22	68.6
South Africa	26	50	254150	YES	0.713	4322.53	42.56	61.6
South Korea	11	14	1731	YES	0.925	13741.17	496.32	1.2
Spain	14	16	5697	YES	0.905	17470.01	89.42	3.1
Sri Lanka	3	4	337	YES	0.782	1461.99	308.76	49.3
Saint Vincent	2	1	5	YES	0.751	3897.49	262.46	NA
Sudan	6	14	16280	YES	0.508	890.77	18.88	86.2
Suriname	3	2	2333	YES	0.73	3702.05	3.6	44.5
Swaziland	1	1	NA	YES	0.611	3915.6	66	29.2
Sweden	5	4	7952	YES	0.947	33981.97	22.42	0.9
Switzerland	16	11	5188	YES	0.962	52393.52	197.62	0.2
Tajikistan	3	1	25	YES	0.685	526.62	54.76	66.4
Tanzania	9	30	29433	YES	0.549	553.86	51.36	92.3
Thailand	44	35	4125	YES	0.8	2874.91	130.9	12.2
Togo	7	3	306	YES	0.539	544.53	114.14	84
Tonga	1	1	5000	YES	0.745	2135.93	129.8	47.9
Tunisia	2	3	1181	YES	0.731	2400.13	69.12	17.9
USA	66	49	710679	YES	0.921	34145.09	33.54	1
Uganda	6	13	2265	YES	0.525	401.93	162.88	91.1
United Arab Emirates	9	9	1535	YES	0.911	34415.08	89.02	0.4
UK	69	48	167441	YES	0.929	26668.51	261	0.7
Uruguay	12	5	33456	YES	0.809	7413.48	19.26	6.7
Venezuela	3	3	10985	YES	0.691	5328.58	30.38	38.8

to be continued...

Countries	Species	Bulletins	WOE	CITES	hdi	gdp_per_capita	density	poverty
Vietnam	28	41	4085	YES	0.703	1160.66	271.16	18.7
Yemen	1	2	1383	YES	0.455	776.77	51.56	85.4
Zambia	6	25	7961	YES	0.565	778.19	18.96	91
Zimbabwe	15	22	31884	YES	0.593	852.53	33.76	85

Add File 3. Spreadsheet containing trade categories for mammal species.

https://ethnobioconservation.com/index.php/ebc/article/view/1067/494

Add File 4. Supplementary information.

https://ethnobioconservation.com/index.php/ebc/article/view/1067/499

Add File 5. Spreadsheet containing mammal species in each TRAFFIC bulletin.

https://ethnobioconservation.com/index.php/ebc/article/view/1067/495