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Trends in the global trade of live CITES-listed raptors: Trade volumes, spatiotemporal dynamics and conservation implications

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ABSTRACT

The global legal wildlife trade is worth US$4–20 billion to the world's economy every year. Raptors frequently enter the wildlife trade for use as display animals, by falconers or hobbyists for sport and recreation. Using data from the Convention on International Trade in Endangered Species of Wild Fauna and Flora's (CITES) Trade Database, we examined trends in the global, legal commercial trade of CITES-listed raptors between 1975 and 2020. Overall 272 species were traded, totalling 188,149 traded individuals, which increased over time. Hybrid Falcons (N = 50,366) were most commonly traded, comprising more than a third of the global diurnal CITES-listed raptor trade, followed by Gyrfalcons (*Falco rusticolus*; N = 30,510), Saker Falcons (*F. cherrug*; N = 21,679), Peregrine Falcons (*F. peregrinus*; N = 13,390) and Northern White-faced Owls (*Ptilopsis leucotis*; N = 6725). More than half of wild-caught diurnal raptors were classified as globally threatened. The United Kingdom was the largest exporter of live raptors and the United Arab Emirates was the largest importer. Countries with higher GDPs (US$) imported more raptors than those with smaller GDPs. Larger-bodied diurnal species were traded more relative to smaller-bodied conspecifics. Following the introduction of the European Union's Wild Bird Trade Ban in 2005, the number of traded wild-caught raptors declined. Despite its limitations, the CITES Trade Database provides an important baseline of the global legal trade of live raptors. However, better understanding of illegal wildlife trade networks and smuggling routes, both on-the-ground and online, are essential for future conservation efforts.

1. Introduction

The legal global wildlife trade is worth US$4–20 billion dollars to the world's economy (Morton et al., 2021), with millions of species and their derivative parts traded globally every year (Barber-Meyer, 2010; Rosen and Smith, 2010; Harfoot et al., 2018; Scheffers et al., 2019). Demand for animals used as food, luxury and commodity goods, entertainment and for traditional medicines drives the global legal trade in wildlife (Baker et al., 2013). Approximately one-fifth of legal wildlife trade transactions originate from the demand for pets and for animals used for entertainment purposes (Bush et al., 2014).

In contrast, overexploitation of wildlife as a result of the illegal global wildlife trade has been identified as a leading threat for many wild plant and animal populations (Auliya et al., 2016; Scheffers et al., 2019; Fukushima et al., 2020; Hughes et al., 2021). However, there is a paucity of illegal trade data due to the majority of it taking place "underground" and therefore being extremely difficult to monitor (Hansen et al., 2012). Subsequent attempts to quantify the illegal wildlife trade often only provide limited insights into the full extent of illegal wildlife trade networks (t' Sas-Rolfes et al., 2019). As a result, conservation scientists often rely on inferences made from the legal wildlife trade when assessing the impacts of human activities on plant and animal populations.

Overarching studies and reviews of scientific and grey literature, focused on the legal wildlife trade, have found that birds account for most traded species within the global trade of terrestrial vertebrates (Bush et al., 2014; Scheffers et al., 2019), with approximately half a million birds exported globally, per year, between 2010 and 2020 (CITES 2020). Raptors (defined here as the orders Falconiformes, Accipitriformes and Strigiformes) were identified as one of the most traded

Abbreviations: CITES, Convention on International Trade in Endangered Species of Wild Fauna and Flora; GDP, Gross Domestic Product (US$).

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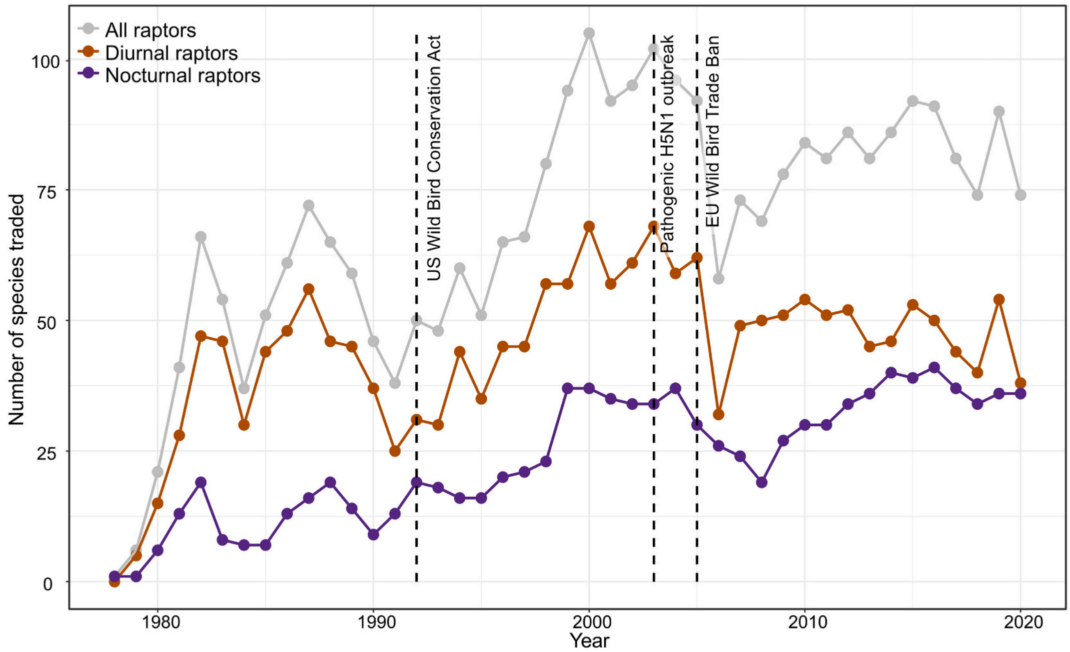

Fig. 1. Number of CITES-listed raptor species traded globally for commercial purposes between 1975 and 2020. Important world events that may impact the international trade of live raptors presented as dashed lines.

groups, third only to parrots (Psittaciformes) and songbirds (Passeriformes) (Bush et al., 2014). Approximately half of the 557 described raptor species are experiencing global population declines, with 18 % of described species classified as “globally threatened” (vulnerable, endangered or critically endangered) on the IUCN Red List of Threatened Species (McClure et al., 2018; O'Bryan et al., 2022). Threats to wild raptor populations include collisions with energy infrastructure (Péron et al., 2017; Murgatroyd et al., 2021), vehicle collisions (Panter et al., 2022), direct and indirect persecution (Whitfield et al., 2004; Madden et al., 2019), agricultural intensification (McClure et al., 2018), bioaccumulation of contaminants (Garvin et al., 2020; Padayachee et al., 2023), climate change (Martínez-Ruiz et al., 2023) and overexploitation by the illegal wildlife trade (Wyatt, 2011; Panter and White, 2020).

Drivers of the legal and illegal raptor trade include the use of birds as display animals or they are sought after by falconers and hobbyists for sport and recreation, particularly in Asia, Europe and The Middle East (Upton, 2002; Ostrowski et al., 2008; Wyatt, 2009; Al-Sheikhly, 2011; Dixon, 2012; Soma, 2012; Wakefield, 2012; Koch, 2015; Kolnegari et al., 2021). Diurnal raptors, i.e., hawks, eagles, kites and vultures, are often used in industry in attempts to control pests (Erickson et al., 1990), to reduce bird strikes at airports (Dolbeer, 1998), or to remove unsolicited un-manned aerial vehicles (UAVs) (Slavimir, 2017). Additionally, raptors are also used for entertainment and educational purposes including historical re-enactments. In Japan nocturnal raptors, i.e., owls, and to a lesser extent diurnal raptors, are frequently used as display animals in bird cafés, enticing tourists to enter and to spend money, and are also traded as pets (Vall-llosera and Su, 2018).

The demand for owls for consumption is occurring throughout East Asia, with two trade consignments totalling 1000 plucked owls destined for Chinese restaurants being intercepted by Malaysian authorities in 2008 (Shepherd and Shepherd, 2009). In every major Indonesian city, owls are frequently offered for sale in bird markets (Shepherd, 2012), and surveys of Thailand's Chatuchak weekend market found several raptor species being offered for sale despite trade of native species being prohibited by law (Chng and Eaton, 2016). However, little is known about the ecology of many species, especially in south-east Asia (Buechley et al., 2019), and whether the illegal wildlife trade is negatively impacting their conservation status (Symes et al., 2018). Recent evidence suggests that the illegal raptor trade, as well as the trade of other taxonomic groups, is moving online (Phassaraudomsak and Krishnasamy, 2018; Siriwat and Nijman, 2020) and is accelerated by social media which remains largely unmonitored (Iqbal, 2016; Gunawan and Noske, 2017; Panter and White, 2020).

Since 1975, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (hereafter ‘CITES’; https://cites.org/) has been instrumental in monitoring and regulating the global trade in wild species (Smith et al., 2011; Challender et al., 2015; Harfoot et al., 2018; Andersson et al., 2021). Open-access trade data are available from the CITES Trade Database (CITES 2021; www.trade.cites.org) which is managed by the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) on behalf of the CITES Secretariat. To date, the Database holds approximately 23 million records of the trade in wildlife for >38,700 “scientific names of taxa” (CITES Secretariat and UNEP-WCMC, 2022). Data are collected for species that cross international borders only and do not represent trade within a country. Previous research has utilised these data to explore aspects of the global wildlife trade across various taxonomic scales, including for individual species (Sayektiningsih and Broto, 2021), genera (Pernetta, 2009; Foster et al., 2014) and larger taxonomic groups (Jiang et al., 2013; Li and Jiang, 2014; Heinrich et al., 2016; Wang et al., 2021), and also to inform conservation and law enforcement policies (Muller et al., 2022). However, the CITES Trade Database only provides trade records for legal wildlife transactions for CITES-listed species yet extensive criminal networks persist and facilitate the smuggling of wildlife and derivative parts which remains difficult to monitor (Rosen and Smith, 2010; Phelps et al., 2016). To date, there has been no global-level synthesis of the legal trade in live CITES-listed raptors traded for commercial purposes. It remains unclear which species are most traded, how trade volumes have changed over time, and the impacts of the wildlife trade on raptors of conservation concern.

Here, we use data from the CITES Trade Database to examine trends in the legal, global commercial trade of live CITES-listed raptors between 1975 and 2020 (i.e., from the inception of the CITES convention until recently). Specifically, we explore 1) trends over time and the most traded species globally, 2) the countries comprising the largest exporters and importers of live raptors, 3) the effects of species morphological

Table 1
Top 10 globally traded CITES-listed diurnal and nocturnal raptor species, live birds traded for commercial purposes, between 1975 and 2020. Global IUCN Red List Categories: LC = 'least concern', VU = 'vulnerable', EN = 'endangered' and CR = 'critically endangered'.

Species	IUCN Red List Category	CITES Appendix	Number of traded individuals	Proportion of global trade
Diurnal raptors				
Hybrid Falcons	–	I - II	50,366	26.8
Gyrfalcon (*Falco rusticolus*)	LC	I	30,510	16.2
Saker Falcon (*Falco cherrug*)	EN	II	21,679	11.5
Peregrine Falcon (*Falco peregrinus*)	LC	I	13,390	7.1
Northern Goshawk (*Accipiter gentilis*)	LC	II	4613	2.5
Unidentified *Falco* spp.	–		3132	1.7
Harris' Hawk (*Parabuteo unicinctus*)	LC	II	2511	1.3
American Kestrel (*Falco sparverius*)	LC	II	1653	0.9
Common Kestrel (*Falco tinnunculus*)	LC	II	1410	0.7
White-backed Vulture (*Gyps africanus*)	CR	II	1393	0.7
Total (diurnal raptors)			130,657	69.4
Nocturnal raptors				
Northern White-faced Owl (*Ptilopsis leucotis*)	LC	II	6725	3.6
Eurasian Scops-owl (*Otus scops*)	LC	II	4683	2.5
Little Owl (*Athene noctua*)	LC	II	3567	1.9
Western Barn Owl (*Tyto alba*)	LC	II	2513	1.3
Burrowing Owl (*Athene cunicularia*)	LC	II	1817	1.0
Pallid Scops-owl (*Otus brucei*)	LC	II	1672	0.9
Eurasian Eagle-owl (*Bubo bubo*)	LC	II	1665	0.9
Snowy Owl (*Bubo scandiacus*)	VU	II	1605	0.9
Ferruginous Pygmy-owl (*Glaucidium brasilianum*)	LC	II	1596	0.8
Northern Long-eared Owl (*Asio otus*)	LC	II	952	0.5
Total (nocturnal raptors)			26,795	14.2
Total (top traded diurnal and nocturnal raptors)			157,452	83.7

traits on trade volumes (i.e., body mass (g), beak, wing and tarsus length (cm), and the ratio between body mass and tarsus length), 4) the proportions of threatened species traded, 5) the effect of species range size on trade volumes.

In line with previous research on Psittaciformes (Chan et al., 2021), we predict that more affluent countries will act as larger importers whereas those less affluent will act as larger exporters of live raptors globally. Due to diurnal raptors being sought-after mainly by falconers and hobbyists (Wyatt, 2009), we expect to find a body size effect whereby larger diurnal species, and those with larger tarsi relating to strength and power, will be more prominent in the global trade relative to smaller species (Eastham and Nicholls, 2005). For nocturnal raptors, we predict that smaller-bodied species will be more frequent within the global trade relative to larger-bodied species. This is due to Japan's "Kawaii", i.e., "cute culture", which has dominated mainstream media since the 1980s (Vall-llosera and Su, 2018), and thus favours smaller-bodied, less-imposing species.

2. Material and methods

2.1. CITES Trade Database

Trade data for all CITES-listed raptor species were downloaded from the open-access CITES Trade Database (https://trade.cites.org/) on 21st November 2021, using a compiled Comparative Tabulation Table from UNEP/WCMC. To maximise comparability with previously published studies we only downloaded trade data in comparative tabulation format, i.e., aggregated trade records. The following search terms were used to filter the CITES trade data: "Year Range" was set to include all records between 1975 and 2020, "Source" was set to "ALL", "Purpose" was set to "COMMERCIAL" denoted by the letter (T) and "Trade Terms" was set to "LIVE" which filtered trade records for only live birds. The "Source" variable relates to the original source of the specimens traded (CITES Secretariat and UNEP-WCMC, 2022) and allows the data set to be subset by, but not limited to: specimens bred in captivity (denoted by the letter "C"), specimens bred in captivity for commercial purposes ("D"), specimens taken from the wild ("W") and ranched specimens including those that are reared in a controlled environment, taken as eggs or juveniles from the wild, which would otherwise have a low chance of survival to adulthood ("R") (CITES Secretariat and UNEP-WCMC, 2022). For the purposes of this study, we combined all records where the "Source" was denoted either by: "C" or "D" and hereafter refer to these as 'Captive-bred', and "W" or "R" hereafter 'Wild-caught'. We created subset data sets using these source categories and quantified trade trends for each.

Taxonomic filtering was applied using the "Search by Taxon" function. The taxonomic orders "FALCONIFORMES" and "STRIGIFORMES" were used to obtain trade records for species within these orders. Species within the families *Accipitridae*, *Cathartidae*, *Falconidae*, *Panionidae* and *Sagittariidae* are pooled under the order "FALCONIFORMES" on the CITES Trade Database, and those in the families *Strigidae* and *Tytonidae* are pooled under the order "STRIGIFORMES". For consistency between subgroups, all taxonomies were standardised to species-level, following the Handbook of Birds of the World and BirdLife Taxonomic Checklist v6 (http://datazone.birdlife.org/species/taxonomy). This meant that certain subspecies that are frequent with hobbyists, e.g., the Barbary Falcon (*Falco peregrinus pelegrinoides*), were pooled together with the species-level binomial name within the data set, e.g., the Peregrine Falcon (*Falco peregrinus*). The CITES Trade Database pools together hybrids within species under the alias "hybrid", which does not allow specific hybrid crosses, e.g., Lanner-Lagger Falcons (*Falco biamicus* × *F. jugger*) to be ascertained.

Downloading CITES trade data using comparative tabulations provides data in two aggregated formats: 1) traded quantity for both importer and exporter reported quantities and 2) traded quantity reported by only one of them. As such, it has been recognised that analysing trade data in this way can present challenges (Foster et al., 2014; Berec et al., 2018; Robinson and Sinovas, 2018). Specifically, numerous records have incomplete or missing 'importer quantity' or 'exporter quantity' values (Foster et al., 2014). Often the 'importer quantity' and

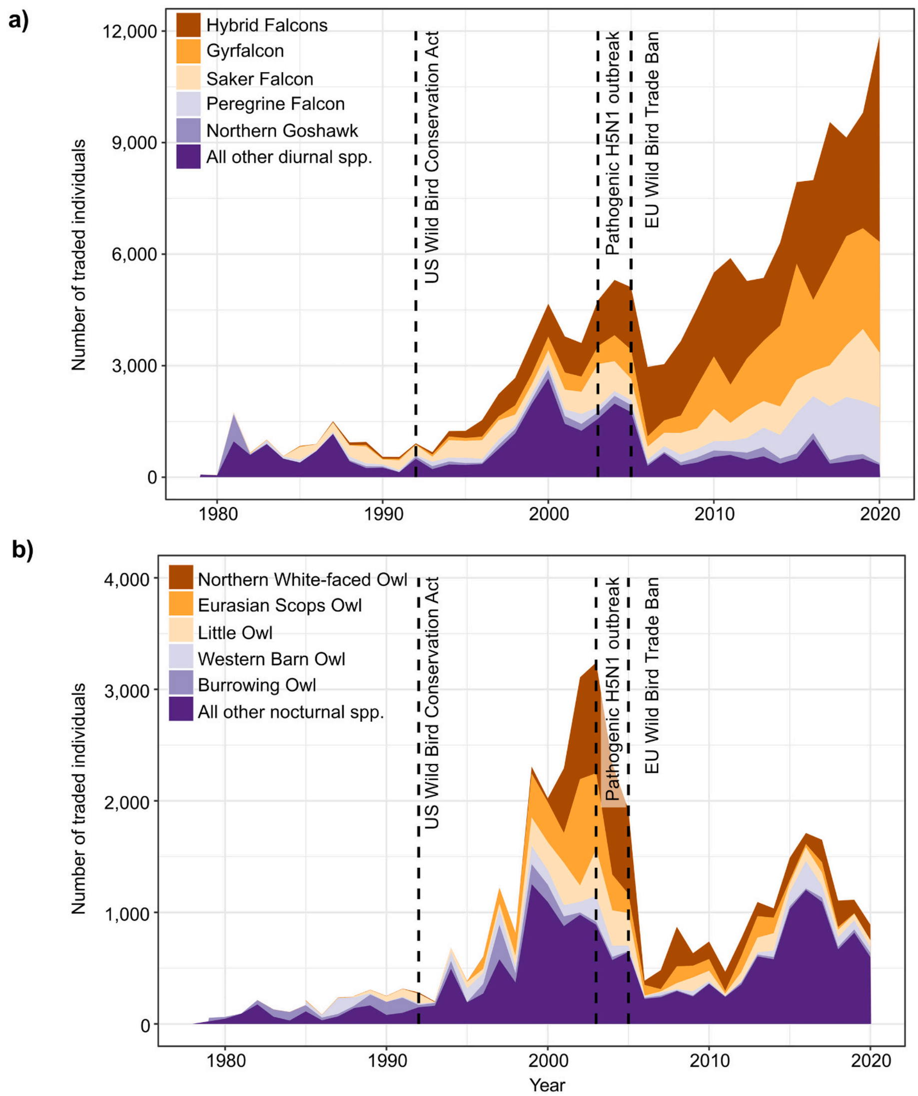

Fig. 2. Number of traded individual a) diurnal and b) nocturnal raptors, by species, listed on the CITES Appendices traded internationally for commercial purposes between 1975 and 2020. Important world events that may impact the international trade of live raptors presented as dashed lines. Note that there were no raptor trade records between 1975 and 1978.

'exporter quantity' values do not match, therefore, reliance on raw importer- and exporter-reported quantities poses challenges to the reliability of actual trade volumes (Chan et al., 2021). This mismatch between importer and exporter values is common in the CITES Trade Database and can occur for several reasons. For example, some countries report data based on permits issued rather than actual traded quantities, and if the true trade quantities fall below the number of permits issued, this can result in under-representation of actual trade volumes (Robinson and Sinovas, 2018). Furthermore, countries are not required to issue import permits for Appendix II species, which means that imports of these species are not always reported. This can lead to inflated trade volumes from exporter-reported quantities relative to importer-reported quantities (Robinson and Sinovas, 2018).

In this study, when trade data for both importer and exporter were available, we used the higher of the two values. Where trade data were only available for one of them, we used the available value. Doing so may reduce the risk of under-representing true trade volumes when making inferences from only exporter-reported data, as in our case, importer-reported quantities were often greater than exporter-reported quantities. A consequence of using this approach is that raptors subjected to re-exports were unable to be distinguished from the resulting data set.

Following geopolitical changes since 1975, we pooled trade records under the former "Serbia and Montenegro" (denoted by ISO Alpha-2 code: CS ex-YU) with records under "Serbia" (RS). Other geopolitical country name changes included "Former Czechoslovakia" (non-ISO code ZC), "Former East Germany" (DD) and "Former Soviet Union" (SU). Trade records under these names were pooled with data for "Czech Republic" (CZ), "Germany" (DE) and "Russian Federation" (RU), respectively.

2.2. Trait, conservation and economic data

Morphological traits and geographical data were obtained from the AVONET database (Tobias et al., 2022) on 17th November 2021. The following morphological traits were extracted from the raw data set and used in subsequent analyses: a) body mass (g), b) beak length (mm; measured as the distance between the tip of the upper mandible to the end of the culmen at an intersection with the cere), c) tarsus length (cm) and d) wing length (cm; from carpal joint to wingtip measured on the unflattened wing). Within the AVONET database, mean trait values are calculated from both male and female individuals, however, the number of samples used to calculate these means varied by species (see Tobias et al., 2022). Geographic range size estimates (km^2) were also retrieved

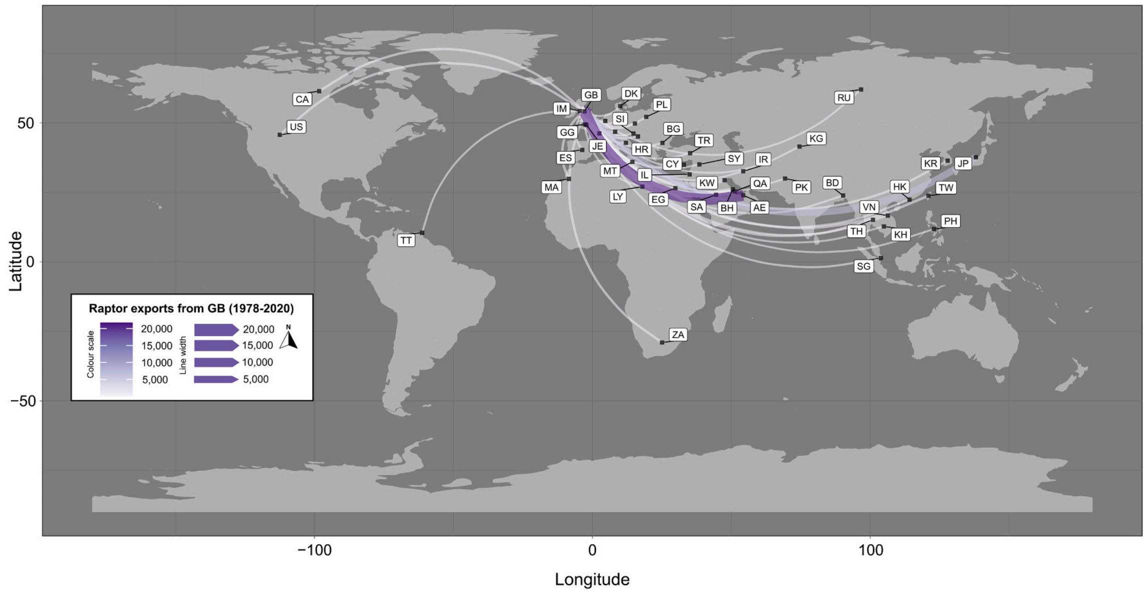

Fig. 3. Global exports of live CITES-listed raptors from the United Kingdom of Great Britain and Northern Ireland (GB) between 1975 and 2020. Values represent estimated trade volumes. Export CITES Party ISO codes included (note that not all export CITES Party codes are shown): AE = United Arab Emirates, BD = Bangladesh, BH = Bahrain, BG = Bulgaria, CA = Canada, CY = Cyprus, DK = Denmark, EG = Egypt, ES = Spain, GG = Guernsey, HK = Hong Kong, HR = Hungry, IL = Israel, IM = Isle of Man, IR = Iran, Islamic Republic of, JE = Jersey, JP = Japan, KG = Kyrgyzstan, KH = Cambodia, KR = Republic of Korea, KW = Kuwait, LY = Libya, MA = Morocco, MT = Malta, PH = Philippines, PK = Pakistan, PL = Poland, QA = Qatar, RU = Russian Federation, SA = Saudi Arabia, SG = Singapore, SI = Slovenia, SY = Syrian Arab Republic, TH = Thailand, TR = Turkey, TT = Trinidad and Tobago, TW = Taiwan, US = United States of America, VN = Viet Nam and ZA = South Africa.

from the AVONET database. These were calculated based on interpolated range polygons which may potentially over-estimate the true extent of occurrence for a given species (Jetz et al., 2008). To examine trends in threatened versus non-threatened species, we also compiled the conservation status (2021 update) for each traded species from the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species (https://www.iucnredlist.org/). In line with the IUCN's guidelines, species listed as either: 'least concern' (LC) or 'near threatened' (NT) were classified as globally non-threatened and those listed as 'vulnerable' (VU), 'endangered' (EN) or 'critically endangered' (CR) were classified as globally threatened. Trade records for species with unresolved taxonomies to species-level, e.g., "*Accipiter* spp.", or hybrid birds, e.g., "Falcon hybrid", were excluded from the threat category analysis. Global economic data was downloaded from The World Bank's World Development Indicators database (https://databank.worldbank.org/source/world-development-indicators) on 2nd March 2022. We downloaded global domestic product (GDP current US$) values for each CITES party and matched the CITES parties with the GDP country names using ISO (3166) Alpha-2 codes. Using these data, we explored the effects of country Gross Domestic Product per capita (GDP; US$) on the number of traded individuals over time. Generally, a growing GDP increases the purchasing power of a population meaning that more people can afford to buy exotic animals for sport and/or entertainment purposes (Ribeiro et al., 2019; Chan et al., 2021). Conversely, human populations in less affluent countries do not have such purchasing power and may therefore sell wildlife and their derivative parts as a source of household income (Brashares et al., 2011). From here onwards, we refer to importers and exporters as "CITES Parties" rather than "countries" as not all CITES Parties hold sovereign nation state status and others are self-governing dependencies of other sovereign states, e.g., the Isle of Man. Trade and species trait data used are available from Panter (2023).

2.3. Statistical analyses

All statistical analyses were performed in R version 4.0.5 (R Core Team, 2022). We explored trends over time in the number of species traded by computing a series of generalized linear models (GLMs) using the R package 'lme4' (Bates et al., 2015). For the first model, we fitted the 'total number of species traded' as the response variable and 'year' fitted as the explanatory variable. We then ran two similar models using subset data sets for diurnal and nocturnal species to explore trends over time by group. These models were fitted with quasi-Poisson error distributions to correct for overdispersion.

To examine the effects of species morphological traits (body mass, beak length, tarsus length and wing length) on trade volume, we used a series of generalized linear mixed models (GLMMs), using the R package 'lme4'. Prior to this, we log-transformed the predictor trait variables due to scaling incompatibilities and tested for multicollinearity via a correlation matrix using the R package 'PerformanceAnalytics' (Fig. S1) (Peterson and Carl, 2020). All morphological traits were positively correlated; therefore, we did not include them within the same model. Instead, we computed four separate GLMMs with the 'number of traded individuals' fitted as the response variable and each continuous log-transformed morphological trait fitted as the explanatory variable. We controlled for species-specific non-independence of data by including 'species' as a random effect. The GLMMs were computed with Poisson error distributions and 'log' link functions. To explore whether a combination of morphological traits, e.g., smaller species with lower body masses (indicative of increased agility) but comparatively larger tarsi (advantageous in hunting-based falconry), may reflect international CITES trade volumes, we calculated the ratio between body mass (g) and tarsus length (cm) by dividing the tarsus length (cm) by body mass (g) for each species, which is also used as a measure of body condition in birds (Yom-Tov, 2001). An additional GLMM was run with 'number of traded individuals' fitted as the response variable, 'body mass to tarsus length ratio' fitted as the explanatory variable and 'species' fitted as a random effect again with a Poisson error distribution and 'log' link function. We then re-ran the GLMMs for each taxonomic group, i.e., diurnal vs. nocturnal raptors, using subset data sets for both diurnal and nocturnal species.

We investigated the effects of GDP (US$) on trade volume via a series

Table 2
Top 10 global exporters and importers of live CITES-listed raptors, traded for commercial purposes, between 1975 and 2020. ISO Alpha-2 Codes provided for each CITES Party with the number of traded diurnal and nocturnal individuals, and total number of traded individuals.

CITES Party	ISO Alpha-2 Code	Number of traded diurnal individuals (% diurnal trade)	Number of traded nocturnal individuals (% nocturnal trade)	Total number of traded individuals (% global trade)
Exporter				
United Kingdom of Great Britain and Northern Ireland	GB	29,659 (19.7)	5055 (13.5)	34,714 (18.5)
Germany	DE	24,390 (16.2)	495 (1.3)	24,885 (13.2)
Spain	ES	18,825 (12.5)	238 (0.6)	19,063 (10.1)
Belgium	BE	5165 (3.4)	5593 (14.9)	10,758 (5.7)
Russian Federation	RU	6767 (4.5)	3011 (8.0)	9778 (5.2)
Uzbekistan	UZ	2437 (1.6)	4797 (12.8)	7234 (3.8)
Peru	PE	3122 (2.1)	3794 (10.1)	6916 (3.7)
Guinea	GN	5279 (3.5)	1630 (4.3)	6909 (3.7)
Togo	TG	773 (0.5)	6107 (16.3)	6880 (3.7)
United States of America	US	6221 (4.1)	219 (0.6)	6440 (3.4)
All other exporters	–	47,987 (31.9)	6585 (17.5)	54,562 (28.9)
Total		150,625 (100)	37,524 (100)	188,149 (100)
Importer				
United Arab Emirates	AE	76,665 (50.9)	128 (0.3)	76,793 (40.8)
Japan	JP	15,731 (10.4)	31,244 (83.3)	46,975 (25)
Qatar	QA	13,765 (9.1)	65 (0.2)	13,830 (7.4)
Saudi Arabia	SA	6944 (4.6)	22 (0.1)	6966 (3.7)
Kuwait	KW	5650 (3.8)	198 (0.5)	5848 (3.1)
United Kingdom of Great Britain and Northern Ireland	GB	3376 (2.2)	401 (1.1)	3777 (2)
Spain	ES	2902 (1.9)	485 (1.3)	3387 (1.8)
Bahrain	BH	3190 (2.1)	0 (0)	3190 (1.7)
Germany	DE	2503 (1.7)	384 (1)	2887 (1.5)
United States of America	US	2449 (1.6)	367 (1)	2816 (1.5)
All other importers	–	17,450 (11.6)	4230 (11.3)	21,680 (11.5)
Total		150,625 (100)	37,524 (100)	188,149 (100)

of Spearman's Rank Correlations. Economic and trade volume data were split into two time periods ('1975–1999' and '2000–2020', respectively). There were gaps in the temporal coverage of the GDP data, therefore, GDP was averaged over these two time periods for each CITES party. The 'number of traded individuals' and 'mean GDP' variables were log-transformed prior to analyses due to scaling incompatibilities. We repeated these correlations using 'number of traded individuals' for both importers and exporters across both time periods, i.e., 1975–1999 and 2000–2020. To explore the effects of geographic range size (km^2) on trade volume, we ran an additional GLM with the log-transformed 'number of traded individuals' fitted as the response variable and 'group' (diurnal vs. nocturnal), log-transformed 'range size' and their interaction (group × range size) as predictor variables. This model was run using a quasi-Poisson error distribution to correct for model overdispersion.

3. Results

3.1. Trade over time and most traded species

Between 1975 and 2020, 13,796 live raptor trade records were reported representing a minimum of 272 species (including records for 15 raptor genera not described to species-level), totalling nearly half of described species, and 188,149 traded raptors. Of these, a minimum of 186 were diurnal species (including nine raptors not described to species-level) comprising 150,625 traded individuals, and a minimum of 86 species were nocturnal raptors (including six raptors not described to species-level) totalling 37,524 traded individuals. Overall, the number of traded species increased over time ($t_{1,41} = 6.82$, $P < 0.0001$; Fig. 1) and was apparent for both diurnal ($t_{1,40} = 3.17$, $P < 0.01$; Fig. 1) and nocturnal species ($t_{1,41} = 11.70$, $P < 0.0001$; Fig. 1).

Hybrid Falcons (50,366 traded individuals) represented a third (33.4 %) of the global diurnal raptor trade and more than a quarter (26.8 %) of the entire global live raptor trade (Table 1; Fig. 2a). Other frequently traded diurnal species included Gyrfalcons (*Falco rusticolus*), Saker Falcons (*F. cherrug*), Peregrine Falcons (*F. peregrinus*) and Northern Goshawk (*Accipter gentilis*) (Table 1; Fig. 2a). The ten most commonly traded diurnal species totalled 69.4 % of the global diurnal raptor trade (Table 1). For nocturnal raptors, Northern White-faced Owls (*Ptilopsis leucotis*; 6725 traded individuals) were the most commonly traded, totalling 17.9 % of the global nocturnal raptor trade and 3.6 % of the entire global live raptor trade (Table 1; Fig. 2b). Other frequently traded nocturnal species included Eurasian Scops-owls (*Otus scops*), Little Owls (*Athene noctua*), Western Barn Owls (*Tyto alba*) and Burrowing Owls (*A. cunicularia*) (Table 1; Fig. 2b). The ten most commonly traded nocturnal species represented 14.2 % of the global nocturnal raptor trade (Table 1).

3.2. Largest exporters and importers of raptors

Across the study period, the largest exporter of live raptors was the United Kingdom (18.5 %; 34,714 traded individuals) (Fig. 3), followed by Germany (13.2 %; 24,885), Spain (10.1 %; 19,063), Belgium (5.7 %; 10,758) and the Russian Federation (5.2 %; 9778) (Table 2). The largest importer of live raptors was the United Arab Emirates (Fig. 4) (40.8 %; 76,793) followed by Japan (25 %; 46,975), Qatar (7.4 %; 13,830), Saudi Arabia (3.7 %; 6966) and Kuwait (3.1 %; 5848) (Table 2). The United Kingdom was the largest global exporter of diurnal raptors (19.7 % of diurnal trade; 29,659) (Table 2; Fig. 3), with the United Arab Emirates being the largest global importer of diurnal raptors (50.9 % of diurnal trade; 76,665) (Table 2; Fig. 4). Conversely, Togo was the largest global exporter of nocturnal raptors (16.3 % of nocturnal trade; 6107), and Japan was the largest global importer of nocturnal raptors (83.3 % of nocturnal trade; 31,244) (Table 2).

For the 1975–1999 period, there was no significant correlation between mean GDP (US$) and the number of exported live raptors ($R^2 = 0.13$, $P = 0.262$; Fig. 5a), however, there was a significant positive correlation for the 2000–2020 period ($R^2 = 0.33$, $P < 0.01$; Fig. 5b). For both time periods (1975–1999 and 2000–2020), there were significant positive correlations between mean GDP (US$) and the number of imported live raptors (1975–1999: $R^2 = 0.45$, $P < 0.001$; Fig. 5c; 2000–2020: $R^2 = 0.59$, $P < 0.0001$; Fig. 5d).

3.3. Species morphological traits

For diurnal raptors, there was a significant positive relationship between body mass (g) and the number of traded individuals indicating a preference for larger bodied diurnal species relative to their smaller-bodied conspecifics (Table 3). Furthermore, there was a significant negative relationship between the ratio between body mass and tarsus length, and the number of traded diurnal species (Table 3). There were no significant trait effects on the number of traded nocturnal species,

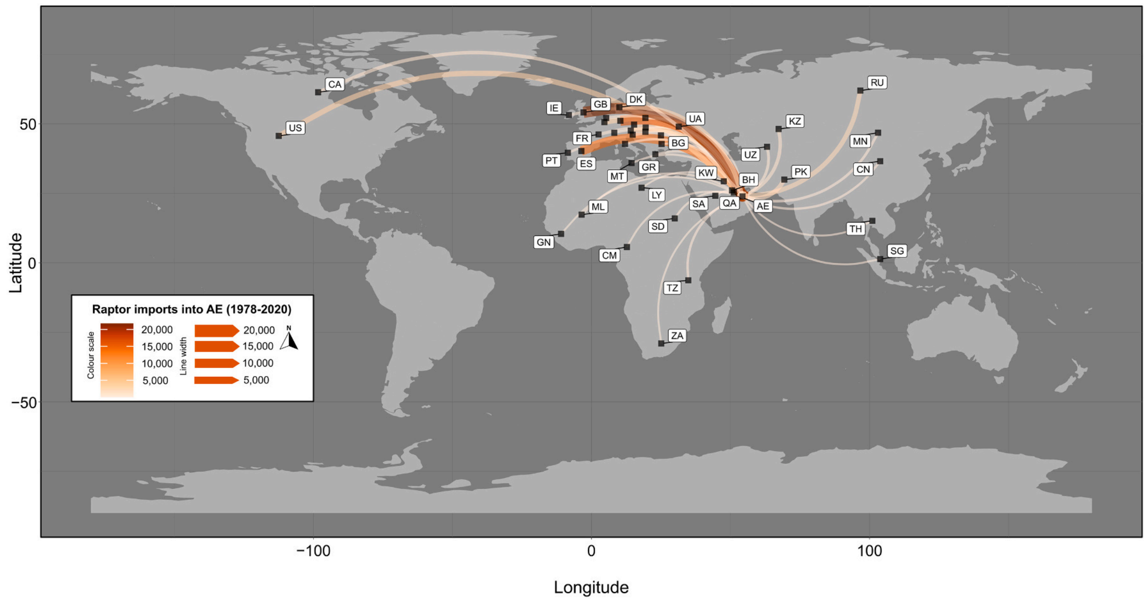

Fig. 4. Global imports of live CITES-listed raptors into the United Arab Emirates (AE) between 1975 and 2020. Values represent estimated trade volumes. Export CITES Party codes included (note that not all export CITES Party codes are shown): BG = Bulgaria, BH = Bahrain, CA = Canada, CM = Cameroon, CN = China, DK = Denmark, ES = Spain, FR = France, GB = United Kingdom of Great Britain and Northern Ireland, GN = Guinea, GR = Greece, IE = Ireland, KW = Kuwait, KZ = Kazakhstan, LY = Libya, ML = Mali, MN = Mongolia, MT = Malta, PK = Pakistan, PT = Portugal, QA = Qatar, RU = Russian Federation, SA = Saudi Arabia, SD = Sudan, SG = Singapore, TH = Thailand, TZ = United Republic of Tanzania, UA = Ukraine, US = United States of America, UZ = Uzbekistan and ZA = South Africa.

which was also found when data for both groups were pooled (Table 3).

3.4. Threat status and range size

There was a notable decline in the number of wild-caught raptors traded globally following the introduction of the European Union's (EU) Wild Bird Trade Ban in 2005 (Figs. 6; S2). Subsequently, the number of captive-bred raptors increased following the EU Wild Bird Trade Ban (Figs. 6; S2). Throughout the study period, 50.9 % of wild-caught diurnal raptors and 0.4 % of wild-caught nocturnal raptors were classified as globally threatened (Fig. S3; Table S1). Comparatively, globally threatened species comprised 25.8 % and 10.8 % of captive-bred diurnal and nocturnal raptors, respectively. Approximately 25.2 % of captive-bred diurnal species, traded internationally for commercial purposes, were classified as globally ‘endangered’. No ‘critically endangered’ captive-bred diurnal species were recorded as being traded internationally throughout the study period (Table S1). Similarly, no ‘endangered’ or ‘critically endangered’ captive-bred nocturnal species were recorded as being traded (Table S1). However, 29.9 % and 16.1 % of wild-caught diurnal raptor species (classified as globally ‘endangered’ and ‘critically endangered’, respectively) were traded internationally for commercial purposes (Table S1). Despite this, 0.1 % of wild-caught nocturnal species that were traded internationally for commercial purposes, were classified as globally ‘endangered’, with no trade records for any ‘critically endangered’ nocturnal species being present within the data set (Table S1). There was a significant positive relationship between global range size and the number of traded individuals, whereby raptor species with larger ranges were more frequently traded (Table 4; Fig. S4).

4. Discussion

4.1. Trends in the global raptor trade

Our study has demonstrated that the legal commercial trade in live CITES-listed raptors fluctuated but largely increased over time in terms of the species traded and the number of traded individuals. This is likely driven by the globalisation of the falconry industry over time (Wakefield, 2012), the intentional purchase of wild-caught birds due to socio-cultural motivations (Ahmed, 2010), and/or changes in species popularity/rarity (Ribeiro et al., 2019). Of the traded raptors, Hybrid Falcons accounted for more than a third of the global trade in live diurnal raptors and nearly a quarter of the entire live raptor trade globally. Northern White-faced Owls were the most commonly traded nocturnal species, comprising approximately 18 % of the global trade in live nocturnal raptors but only ca. 3 % of the entire global live raptor trade. Our findings follow a similar to pattern found in other taxonomic groups. For example, Harfoot et al. (2018) reported that the international trade in CITES-listed species quadruped between 1975 and 2014, with the trade in live birds also increasing over time. The trade of live CITES-listed birds in China peaked during the late 1990s before decreasing to pre-peak volumes after a few years (Li and Jiang, 2014). We also observed an increase in the number of traded raptors towards the end of the 1990s, which may suggest that international trade in CITES-listed birds may be affected by changes in governmental policy in response to external stressors. In 2005 the EU introduced a permanent ban on wild bird imports to counter the spread of the particularly virulent H5N1 avian influenza pandemic (Cardador et al., 2019), which appeared to temporarily reduce global raptor trade volumes as seen in other avian groups (Vall-llosera and Su, 2018; Chan et al., 2021).

4.2. Global exporters and importers of live raptors and effects of GDP

The United Kingdom was the largest global exporter of live raptors for commercial purposes between 1975 and 2020, which may be due to the country's historical relationship with falconry as a recreational sport (Ratcliffe, 1980) and long-term membership of CITES. The length of time that a country has been a signatory of the CITES convention has been shown to influence reported trade volumes (Robinson and Sinovas, 2018) and may partly explain why the United Kingdom was the largest global commercial exporter of live raptors. The United Arab Emirates was the largest global importer of live raptors, which is likely due to the country's long-standing cultural ties to falconry which is still commonly practiced as a traditional pastime (Wakefield, 2012; Bush et al., 2014).

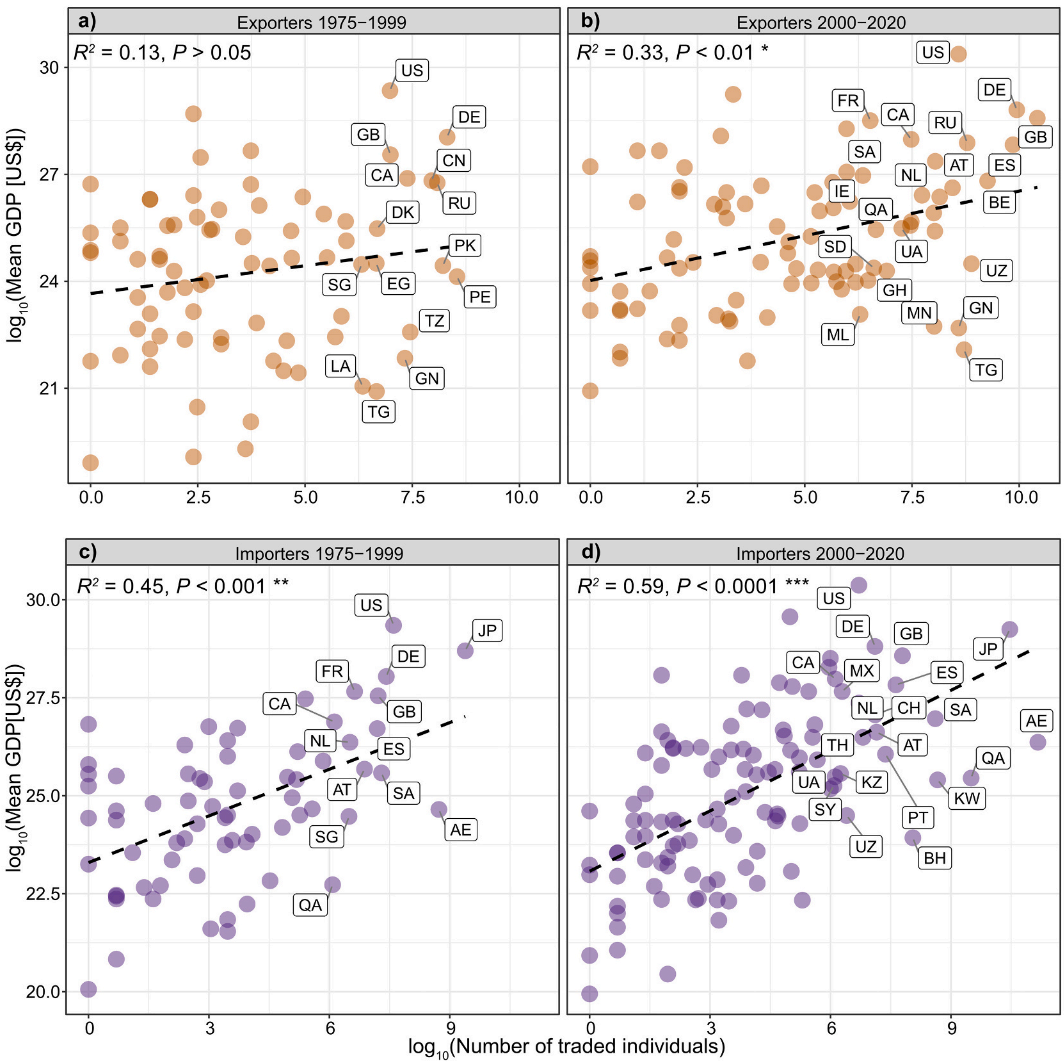

Fig. 5. Correlations between importer and exporter CITES Party mean GDP (US$) and the number of individual live CITES-listed raptors traded for commercial purposes across two time periods. a) Correlation between importer CITES Party mean GDP (US$) and $\log_{10}$(Number of traded individuals) between 1975 and 1999, b) correlation between importer CITES Party mean GDP (US$) and $\log_{10}$(Number of traded individuals) between 2000 and 2020, c) correlation between exporter CITES Party mean GDP (US$) and $\log_{10}$(Number of traded individuals) between 1975 and 199 and d) correlation between exporter CITES Party mean GDP (US$) and $\log_{10}$(Number of traded individuals) between 2000 and 2020. CITES Party labels shown from ≥6 $\log_{10}$(Number of traded individuals) onwards. Spearman Rank Correlation outputs presented for each time period. ISO Alpha-2 CITES Party codes: AE = United Arab Emirates, AT = Austria, BE = Belgium, BH = Bahrain, CA = Canada, CH = Switzerland, CN = China, DE = Germany, EG = Egypt, ES = Spain, FR = France, GB = United Kingdom of Great Britain and Northern Ireland, GH = Ghana, GN = Guinea, IE = Ireland, JP = Japan, KW = Kuwait, KZ = Kazakhstan, LA = Lao People's Democratic Republic, ML = Mali, MN = Mongolia, MX = Mexico, NL = Netherlands, PE = Peru, PK = Pakistan, PT = Portugal, QA = Qatar, RU = Russian Federation, SA = Saudi Arabia, SD = Sudan, SG = Singapore, SY = Syrian Arab Republic, TG = Togo, TH = Thailand, TZ = United Republic of Tanzania, UA = Ukraine, US = United States of America and UZ = Uzbekistan.

As expected, more affluent countries imported more live raptors than less affluent countries, likely due to human populations in countries with growing GDPs (US$) having higher purchasing powers for luxury goods such as exotic pets (Ribeiro et al., 2019). A study on the global trade of CITES-listed parrots also found that countries with higher GDPs, and higher consumer age indices, tended to import larger volumes of birds (Chan et al., 2021). However in our study, less affluent countries did not necessarily contribute the most to the global export of live raptors. Contrary to our findings, an analysis of the seahorse (*Hippocampus* spp.) trade found that trade volumes were significantly higher when the source country had a lower GDP; this may be due to a lack of investment in sustainable production industries (see Kuo and Vincent, 2018).

4.3. Effects of raptor morphology on trade volumes

Larger-bodied diurnal raptors were more frequent within the global live raptor trade than their smaller-bodied conspecifics. Approximately 60 % of the global trade in diurnal raptors comprised of four raptors, namely Hybrid Falcons (26.8 %), Gyrfalcons (16.2 %), Saker Falcons (11.5 %) and Peregrine Falcons (7.1 %), all of which are large-bodied and desired by the falconry community (Eastham and Nicholls, 2005). Falconers often cross falcon species to produce F1, F2 and backcross hybrids of these species' combinations, i.e., Peregrine × Saker, Gyr × Peregrine and Gyr × Saker (Eastham and Nicholls, 2005). Other common hybrid parental lineages include those from Lanner (*Falco biarmicus*) and Lagger Falcons (*F. jugger*). Such combinations result in offspring birds that express selected phenotypic and genotypic characteristics desired for falconry such as increased body size, attractive plumage and increased climate tolerance in regions such as The Middle East (Dixon,

Table 3
Parameter estimates from the Generalized Linear Mixed Models (GLMMs) exploring the effects of species traits a) body mass (g), b) tarsus length (cm), c) beak length (cm), d) wing length (cm) and e) the ratio between body mass (g) and tarsus length (cm) on the number of live CITES-listed raptors traded for commercial purposes between 1975 and 2020. Statistically significant results in bold.

Trait		Estimate ± SE	z	P
All raptors				
Body mass (g)	**Intercept**	**2.595 ± 0.726**	**3.572**	**<0.001**
	$\log_{10}$(body mass)	0.174 ± 0.113	1.533	0.125
Tarsus length (cm)	**Intercept**	**4.060 ± 1.197**	**3.391**	**<0.001**
	$\log_{10}$(tarsus length)	−0.093 ± 0.296	−0.314	0.754
Beak length (cm)	**Intercept**	**2.890 ± 1.129**	**2.561**	**0.010**
	$\log_{10}$(beak length)	0.228 ± 0.321	0.712	0.477
Wing length (cm)	Intercept	2.543 ± 1.698	1.497	0.134
	$\log_{10}$(wing length)	0.201 ± 0.297	0.676	0.499
Body mass (g): Tarsus length (cm)	**Intercept**	**4.026 ± 0.231**	**17.470**	**<0.0001**
	$\log_{10}$(body mass): $\log_{10}$(tarsus length)	−2.383 ± 1.283	−1.857	0.063
Diurnal raptors				
Body mass (g)	Intercept	1.334 ± 0.913	1.461	0.144
	$\log_{10}$(body mass)	**0.321 ± 0.137**	**2.349**	**0.019**
Tarsus length (cm)	Intercept	2.662 ± 1.664	1.600	0.110
	$\log_{10}$(tarsus length)	0.187 ± 0.397	0.470	0.639
Beak length (cm)	Intercept	1.767 ± 1.342	1.317	0.188
	$\log_{10}$(beak length)	0.470 ± 0.374	1.257	0.209
Wing length (cm)	Intercept	−0.349 ± 2.265	−0.154	0.878
	$\log_{10}$(wing length)	0.651 ± 0.388	1.678	0.093
Body mass (g): Tarsus length (cm)	**Intercept**	**3.853 ± 0.260**	**14.831**	**<0.0001**
	$\log_{10}$(body mass): $\log_{10}$(tarsus length)	**−3.186 ± 1.541**	**−2.068**	**0.039**
Nocturnal raptors				
Body mass (g)	**Intercept**	**2.847 ± 1.312**	**2.169**	**0.030**
	$\log_{10}$(body mass)	0.243 ± 0.226	1.076	0.282
Tarsus length (cm)	Intercept	1.927 ± 2.138	0.918	0.359
	$\log_{10}$(tarsus length)	0.614 ± 0.574	1.070	0.285
Beak length (cm)	Intercept	3.012 ± 2.187	1.377	0.169
	$\log_{10}$(beak length)	0.366 ± 0.650	0.562	0.574
Wing length (cm)	Intercept	1.339 ± 3.030	0.442	0.658
	$\log_{10}$(wing length)	0.535 ± 0.557	0.959	0.338
Body mass (g): Tarsus length (cm)	**Intercept**	**4.709 ± 0.463**	**10.179**	**<0.0001**
	$\log_{10}$(body mass): $\log_{10}$(tarsus length)	−2.785 ± 2.296	−1.213	0.225

2012). However important species traits may extend beyond morphology and include temperament, intelligence and agility derived from selective breeding of high performing birds (Parry-Jones, 2012). Therefore, future research should investigate consumer preferences for falconry birds and build upon our current analyses on the drivers of the global commercial trade in live raptors. Conversely, nocturnal raptors are often not used in falconry and the trade in such species is likely driven by entertainment purposes, i.e., owls used as display animals in bird cafes (Vall-llosera and Su, 2018), for religious and ceremonial purposes (Ahmed, 2010), or for human consumption particularly in Asia (Shepherd and Shepherd, 2009). Therefore we expected to find a preference for smaller-bodied nocturnal raptors; however, this was not evident in our data.

4.4. Effects of raptor threat status and range size on trade volumes

Following the permanent EU Wild Bird Trade Ban imports in 2005, there was a notable decline in the number of wild-caught raptors traded globally. Following this, the number of captive-bred raptors increased substantially. Effects of the EU Wild Bird Trade Ban on global trade volumes have also been observed in other bird groups, (e.g., Parrots - Aloysius et al., 2019; Chan et al., 2021; multiple avian taxa – Bush et al., 2014; Vall-llosera and Su, 2018). It is not uncommon for wild-caught individuals to appear as captive-bred on the CITES Trade Database after the introduction of a trade ban, as a result of forged documentation from illegal laundering activities (Eckles, 2010; South and Wyatt, 2011; Shepherd et al., 2012; Poole and Shepherd, 2017). Approximately a quarter of all captive-bred diurnal raptors were categorised as globally ‘endangered’ on the IUCN Red List. The global trade of live Saker Falcons contributed approximately 15 % of the commercial trade of captive-bred diurnal raptors (12,692 birds). Saker Falcons qualify for the ‘endangered’ category due to rapid wild population declines, particularly in Central Asia, which are predominantly caused by excessive trapping for the falconry trade (Dixon, 2012); see also Shobrak (2015) for an example from Saudi Arabia, and Khoury et al. (2020) from Jordan. Attempts to promote a sustainable, “green production” chain of captive-bred Saker Falcons have been reported, for example, Mongolia reportedly generates $3 million in revenue per annum from captive-bred falcon exports (Dixon et al., 2011; Stretesky et al., 2018). Despite this, the majority of raptors in the global commercial trade were categorised as ‘least concern’ on the IUCN Red List, which explains why we found a significant positive range size effect on estimated trade volumes. Overall, it appears that the most sought-after raptor species by the commercial trade are made up of those that are currently not threatened by extinction globally. However, more than half of wild-caught diurnal raptors were globally threatened which warrants further conservation action.

4.5. Conservation implications

Consumer demand and the associated pressures from the legal and illegal wildlife trade, resulting in the overexploitation and unsustainable harvests, remain a challenge for raptors of conservation concern, such as the Saker Falcon. Unrealistic zero trade quotas, and restrictions imposed by governing bodies such as CITES may fail to limit the trade of threatened species and may subsequently force the trade underground via illegal smuggling channels (Challender et al., 2015). The captive-bred raptor trade may help alleviate some of these pressures, however, ongoing trade of live birds must be monitored closely and properly enforced.

Our data showed that Hybrid Falcons constituted a large proportion of the global live raptor trade. Escapee falconry birds and those that are deliberately released are perceived as a considerable threat to wild raptor populations (Eastham and Nicholls, 2005). For example, genetic admixture with escapee falconry birds on the Canary Islands threatens the wild population of Barbary Falcons (*F. peregrinus pelegrinoides*) on

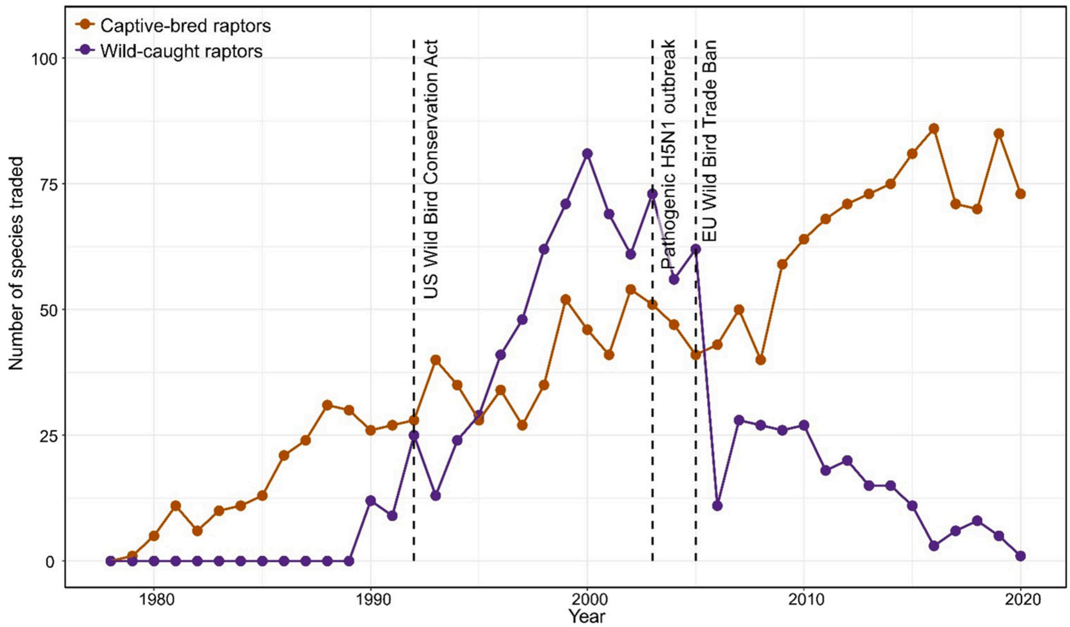

Fig. 6. Number of CITES-listed putatively captive-bred and wild-caught raptor species traded globally for commercial purposes between 1975 and 2020. Important world events that may impact the international trade of live raptors presented as dashed lines.

Table 4
Parameter estimates from the Generalized Linear Model (GLM) exploring the effects of group and range size km^2, and their interaction, on the number of live CITES-listed raptors traded for commercial purposes between 1975 and 2020.

Variable	Estimate ± SE	t	df	P
Intercept	**−2.425 ± 0.547**	**−4.431**	249	**<0.0001**
Group(nocturnal)	0.213 ± 0.809	0.263	–	0.793
$\log_{10}$(Range size km^2)	**0.420 ± 0.080**	**5.232**	–	**<0.0001**
Group(nocturnal) × $\log_{10}$(Range size km^2)	0.008 ± 0.120	0.069	–	0.945

Significant values, i.e., $P < 0.05$ in bold.

Tenerife (Rodríguez et al., 2019). Furthermore, intergeneric hybrids exist within the falconry community, e.g., Harris's Hawks (*Parabuteo unicinctus*) × Cooper's Hawks (*Accipiter cooperi*) and Harris's Hawks × Ferruginous Hawks (*Buteo regalis*) (Fox and Sherrod, 1999), which may extend the risk of genetic admixture beyond wild raptor populations within the subgeneric *Hierofalco* "desert falcon" group (Heidenreich, 1997). The increase in the global trade of hybrid raptors, and improper husbandry by a minority of falconers resulting in the release of hybrid birds into natural populations, may continue to threaten wild raptor populations into the future.

Overexploitation of nocturnal raptors driven by the demand for human consumption and the more recent "Kawaii" media culture in Japan (see Vall-llosera and Su, 2018) may pose a threat to wild owl populations in the future, especially in east Asia (Nijman, 2010; Panter and White, 2020). Japan was the largest global importer of nocturnal raptors in our study and previous research has suggested that this is likely due to the rise in popularity of "bird cafes", i.e., raptors are used as display animals to entice tourists to enter and spend money where they are also sold as pets (Vall-llosera and Su, 2018). The Northern White-faced Owl was the most commonly traded nocturnal species globally. Despite the species being currently listed as least concern on the IUCN Red List, monitoring of wild populations is not performed throughout the species' range and crucial population-level data remains unavailable, such as data on the number of mature individuals and whether the species is experiencing continuing population declines (BirdLife International, 2016). It has been suggested that the increase in popularity of nocturnal raptors within the global wildlife trade may have been influenced by media, e.g., the "Harry Potter" book and film series, however, previous research has failed to find strong support for this (Megias et al., 2017; Siriwat et al., 2020) or has reported a non-conclusive "delayed Harry Potter effect" (Nijman and Nekaris, 2017). The global wildlife trade appears to be moving online (Sung and Fong, 2018; Siriwat and Nijman, 2018; Siriwat and Nijman, 2020; Panter and White, 2020), as social media sites and e-commerce platforms provide sellers with instant access to an increased pool of potential buyers. Therefore, the monitoring and regulation of wildlife and their derivative parts should include online platforms in future policy making decisions and legislative agreements.

4.6. *Challenges associated with the CITES Trade Database*

The CITES Trade Database is an important tool which can be used to inform our understanding of trade volumes and dynamics of the global wildlife trade, however, the database is not without its limitations. A study by Berec et al. (2018) reported discrepancies in the calculated volume of total international trade, when using comparative tabulation reports, especially in the trade of wildlife parts, e.g., teeth and trophies of American Black Bears (*Ursus americanus*). We attempted to overcome these challenges by taking the higher importer- and exporter-reported values from the comparative tabulation report. Our approach may over-represent true quantities of live raptors traded globally, as there were cases where one was substantially lower than the other. Furthermore, raw trade data in comparative tabulation reports are aggregated, i.e., one row could represent more than one trade, meaning that traded individuals cannot be counted for each record. Another by-product of our approach is that we did not make use of the 'origin' column within the data set, therefore, did not account for re-exports. This further highlights potential challenges associated with working from trade records derived from the CITES Trade Database and caution should be taken in data processing. The temporal scale of our study (1975–2020) spanned the entire time series since CITES began recording trade data, though, older trade records are often not complete and inferences made from these may not be as reliable relative to more recent trade data. Our data set also contained trade records for many unresolved taxonomies, e.

g., "Falcon spp.", and may also include identification errors which may not accurately represent true trade volumes. Misidentifications in the trade data are impossible to detect when analysing data from the CITES Trade Database, indicating a potential need for improved identification skills among some enforcement staff. Similarly to Berec et al. (2018), some trade records were incomplete, e.g., "Source" category was blank for 868 trade records, which may have contained important information on the trade of wild-caught raptors.

5. Conclusions

We provide a comprehensive overview of the legal, global commercial trade of live CITES-listed raptors between 1975 and 2020. The trade in CITES-listed raptors increased over time with Hybrid Falcons being the most commonly traded diurnal raptor. An increase in the number of traded individuals reflects the increasing demand for birds over time. Our study provides a valuable baseline resource for analysing the global, legal commercial trade in live CITES-listed raptors. Regulatory bodies and conservation organisations should closely monitor the trade in hybrid raptors, including aforementioned intergeneric hybrids, as improper handling and management of these birds may pose a significant conservation concern for wild raptor populations through genetic admixture. Furthermore, the legal and illegal wildlife trade has already shifted online, therefore, governing authorities should seek to continue monitoring and regulating the sale of wildlife and derivative parts on e-commerce sites and social media platforms. The CITES Trade Database is an important conservation tool and despite its limitations, offers a valuable resource for monitoring the global trade in wildlife and their derivative parts.

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CRediT authorship contribution statement

Connor T. Panter: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft. **Georgia C.A. Jones:** Investigation, Validation, Writing – review & editing. **Rachel L. White:** Conceptualization, Investigation, Methodology, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data used in this study is available via the DRYAD Data Depository doi:https://doi.org/10.5061/dryad.5mkkwh7b9.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110216.

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