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Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Global trade in parrots – Influential factors of trade and implications for conservation

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ARTICLE INFO

Keywords:

CITES
Bird trade
Exotic pet trade
Psittaciformes
Trade regulation
Wildlife conservation

ABSTRACT

Parrots are the most traded birds internationally, mainly to be used as companion pets, which threatens the global biodiversity. Using the large dataset derived from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), we uncovered the spatial-temporal changes in trade volumes and sources of parrots, the topology of the trade network, and the factors behind the global parrot trade in the past 42 years (1975–2016). We found that more than 16 million live CITES-listed parrots in 321 species were traded internationally within that period. There were large changes in the temporal trend of global parrot trade volumes and spatial patterns of trade hubs. These changes appeared to be influenced by the trade restrictions in some of the leading traders and the occurrence of pandemic zoonosis, such as the H5N1 avian influenza. Developing states in Western and Southeast Asia have emerged as the most recently developed parrot trade hubs, with South Africa and Europe being some of the major suppliers. The sources of parrots being supplied internationally has also gradually shifted from wild-caught to captive-sourced. Wild-caught individuals of some parrot species, currently classified as Endangered, were traded substantially until 2013. We demonstrated that parrot species with larger wild population sizes, more color morphs, and those in the Least Concern category of the IUCN Red List, were being traded internationally in higher quantities. The GDP per capita and the aging index of states were also correlated with the net import quantities of parrots. Based on our findings, we suggested that greater scrutiny of parrots traded in large volumes, many of which are not monitored in the wild, should be considered. We advocate the uplisting of a few endangered species from Appendix II to I, using an accreditation system to prevent the laundering of wild-caught parrots into captive-bred ones, and conducting more research on newly emerged importers to protect wild parrot populations.

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<https://doi.org/10.1016/j.gecco.2021.e01784>

Received 1 December 2020; Received in revised form 26 August 2021; Accepted 26 August 2021

Available online 27 August 2021

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1. Introduction

Global wildlife trade is a lucrative economic activity amounting to hundreds of billions of US dollars to date, with millions of organisms or their derivatives being legally and illegally traded worldwide every year (Chan et al., 2019; Harfoot et al., 2018; Rosen and Smith, 2010). The wildlife trade is primarily driven by the demand for the animals to be used as food, pets, entertainment, luxury goods, commodity goods, and traditional medicine. In particular, the use of wildlife as pets and for entertainment is a substantial component of the wildlife trade, which has been documented by 82 out of 374 (22%) reports analyzing the drivers of the global wildlife trade (Baker et al., 2013). The most popular taxonomic class of terrestrial vertebrates in the exotic pet trade is class Aves (birds) (Bush et al., 2014), which has the highest number of traded species among the classes being traded (Scheffers et al., 2019). During the 2010s, birds were heavily traded worldwide, and approximately half a million of birds were exported globally per year (CITES, 2020). More recent studies have shown that 2 345 species, accounting for almost one-fourth of all bird species, were involved in the wildlife trade (Scheffers et al., 2019) and at least 585 species of birds have been reported to be in the exotic pet trade (Bush et al., 2014).

Among avian orders, order Psittaciformes (parrots) is the most traded group, mainly for live companion pets, followed by Passeriformes (passerines), Falconiformes (falcons) and Columbiformes (pigeons and doves) (Bush et al., 2014; Furnell, 2019). A recent analysis of live bird trade records in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), has indicated that almost 90% of all live birds traded were from the order Psittaciformes (Furnell, 2019). One of the three families of true parrots, Psittacidae, was among the twenty most heavily traded families in the global bird trade (Scheffers et al., 2019). However, despite the significance and scale of the global parrot trade having both welfare (Baker et al., 2013) and conservation implications (Tella and Hiraldo, 2014), there is no study that has explicitly focused on analyzing all the CITES data concerning live parrots. It is unclear what the species of these parrots were and the respective abundances that are being traded in internationally. It is also unclear which states are considered the key traders constituting the trade network over the years.

Parrots are widely distributed in tropical and subtropical habitats of the Southern Hemisphere, with the highest species richness being in Southeastern Australia, Papua New Guinea, Amazonia, and northeastern South America (Kosman et al., 2019). They have been sought after as household and companion pets throughout human history, probably owing to their colorful and complex plumage (Berg and Bennett, 2010), remarkably high intelligence levels (Cussen, 2017), and impressive ability to mimic different sounds including the human voice (Bradbury and Balsby, 2016). Captive breeding has proven possible for many species (Mench et al., 2018). However, a number of popular parrot species are not able to be bred in captivity (e.g., species that are rare or are very difficult/impossible to be bred in captivity). Furthermore, the permitting quota or holding capacity of the breeding or trading of various captive parrot species, have limited the supply of certain desired species from captive breeding (Collar and Butchart, 2014). Parrots in the wild are also used as a source of stock for captive breeding. Moreover, captive-bred parrots can be unavailable or unaffordable to consumers in some states (UNODC, 2020). In addition, due to socio-economic and cultural variations, laws regulating the international and domestic parrot trade are not being enforced effectively by government agencies in some regions (Pires et al., 2016). For instance, wild parrot poaching and smuggling have been found to be concealed under the auspices of legal breeding and trading systems. These complicated and intertwining conditions have led to certain parrot species being disproportionately captured from the wild over many years, both legally and illegally (Pires, 2012). It has been reiterated in the literature that detailed information on the wild population sizes, and statuses of many parrot species over time, is insufficient because conducting field studies on parrots has been very challenging. Furthermore, it is not impossible but very difficult to obtain quantitative data on the abundance of individuals existing in and taken from the wild over time (Martin, 2018b), and these data are lacking for the vast majority of species. Without the concrete body of knowledge on the spatial and temporal changes of wild parrot populations and the activity of trappers, the unsustainable trapping of parrots from the wild driven by demands from the pet trade has rendered many parrot species at risk of population reductions or even extinction in some areas of their native range (Forshaw, 2017).

Psittaciformes are now considered to be one of the most threatened taxa of birds, with 29% (117 of 402) of extant species categorized as globally threatened and 58% (233 of 402) as having a decreasing trend in their population sizes (IUCN, 2020). Although, once abundant, several parrot species are now facing extinction (Berkunsky et al., 2017). For example, wild populations of the gray parrot (*Psittacus erithacus*, endemic to Africa) have shrunk by over 50% in many areas due to overharvesting and forest loss (Annorbah et al., 2016). Spix's macaw (*Cyanopsitta spixii*, native to Brazil) is classified as Critically Endangered (probably Extinct in the wild), and its population collapse was attributed to both the deforestation and exploitation of wild populations (BirdLife International, 2020b). The potential threats to wild parrot populations posed by the exotic pet trade warrant the early listing of the entire order Psittaciformes in the Appendices of CITES, except for four relatively common species that are not currently listed (CITES, 2020). Moreover, the international parrot trade also brought about a number of threats that could have adverse consequences on biodiversity conservation (Kitzes et al., 2017), economics, and public health (Can et al., 2019). An example of this is the spread of invasive alien species (Menchetti and Mori, 2014) and diseases to both humans and other animals (Hogerwerf et al., 2020) across countries, through the escape or release of exotic parrots, and their associated pathogens and parasites (Ortiz-Catedral et al., 2019). Alarmingly, recent research has found that the global parrot trade likely resulted in the transmission of the beak and feather disease virus (BFDV) to eight countries where there were previously no known record of BFDV occurrence (Fogell et al., 2018; Morinha et al., 2020). BFDV is the causative agent of psittacine beak and feather disease, which is incurable once infected, and considered detrimental to the health of parrots or lethal to them (Massaro et al., 2012). It is, therefore, crucial to better understand the dynamics of the international parrot trade, so as to formulate effective conservation measures and management plans for protecting biodiversity from depletion and to prevent the invasion of alien species within all global regions (Reino et al., 2017).

Currently, the principle multilateral agreement for regulating international wildlife trade is CITES, which subjects the trade in species of conservation concern to certain controls through a system of appendices and permits/certificates. There are 183 signatories, that are national authorities (known as Parties), who implement CITES through national laws; however, laws and regulations may differ among parties. CITES maintains a long-term database (which began in 1975) of the legal trade of restricted species (CITES, 2020; Harfoot et al., 2018). This publicly available database on legal wildlife trade has facilitated research on the trends of the international parrot trade of certain flagship species for conservation or major trading parties. For instance, some of the more recent studies have focused on *Psittacus* spp. (the gray parrot and the Timneh parrot) (Martin, 2018b; Poole and Shepherd, 2017), while other studies have analyzed important transshipment hubs like Singapore (Aloysius et al., 2020), key importers like Japan (Vall-Ilosera and Su, 2019), and countries with endemic parrots like Australia (Vall-Ilosera and Cassey, 2017). They have also hypothesized and tested different combinations of variables that could be correlated with the volumes of the parrot trade. Examples of the main factors used by these studies include demographics, life history, morphological and behavioral factors of traded parrot species, as well as the demographic, socio-economic and cultural factors of trading countries (Vall-Ilosera and Cassey, 2017; Vall-Ilosera and Su, 2019; Ye et al., 2020; Yin et al., 2020). However, it is uncertain how these important variables are associated with the volume of the parrot trade on a global scale.

Considering the importance and deficiency of knowledge on the global parrot trade, in this study we aimed to investigate the dynamics of the international parrot trade and the multidimensional and synergistic factors underlying it. This was done using long-term data spanning more than 40 years (1975–2016) from CITES. We first demonstrated, temporally, the trends of parrot trade quantity by genera, continents and IUCN Red List status. We then determined the association between international trade quantity and consumer-level factors by investigating a number of parrot variables, including ecological (IUCN Red List status and the wild population size), biological (main body color, number of color morphs, body mass, brain-body mass ratio, and lifespan), and economic (price per bird) factors. These are important factors that were hypothesized to be associated with consumer preference for the quantity and species of pet parrots. We also visualized the geographical patterns and shifts of international parrot trade routes in detail, to identify the major exporters and importers in three time periods between 1978 and 2016 (39 years). Finally, we tested if the national-level demographic-economic factors, such as population aging and gross domestic product (GDP) per capita, can be predictors of the trade quantities of states or regions (both are referred as ‘states’ hereafter). Based on our findings of the global parrot trade, we highlighted issues of concern that needed more attention and discussed the conservation implications.

2. Materials and Methods

2.1. Data collection and analysis of the global parrot trade

We downloaded the comparative tabulation reports of Psittaciformes trade records for the period of 1975–2016 from the CITES trade database (<http://www.unep-wcmc-apps.org/citestrade/trade.cfm>, accessed on June 2018). We included only transaction records of all live CITES-listed parrots (in Appendix I, II and III) that were legally traded for all sorts of purposes (e.g., commercial, scientific, or personal, unless otherwise specified; Bush et al., 2014; Can et al., 2019; Vall-Ilosera and Cassey, 2017; Vall-Ilosera and Su, 2019) among all reporting CITES or non-CITES states. Detailed data on transactions in the downloaded reports were used in our analyses, including the ‘year of trade occurred’, ‘species name of specimen’, ‘CITES appendix of the species’, ‘importer’, ‘exporter’, ‘importer quantity’, ‘(re-)exporter quantity’, ‘origin’, ‘purpose of the transaction’, and ‘source of the specimen’. In the reports, the ‘quantity’ data in one transaction is not the trade quantity of one shipment, it is the sum of all the quantities reported in all shipment records where the following details are the same: ‘species name of specimen’, ‘term’, ‘importer’, ‘exporter’, ‘origin’, ‘purpose of the transaction’, ‘source of specimen’, and ‘year of trade occurred’ (CITES, 2013).

Because the names and/or borders of some states were altered between 1975 and 2016, we renamed those states (for example, ‘South Yemen’ as ‘Yemen’) and followed Vall-Ilosera and Cassey (2017) for the changes in political divisions of states, so as to track the trade quantities of the same geographical regions in that period. Furthermore, we either lumped or split the trade quantities according to the changes in parrot taxonomy. We referred to the checklist of BirdLife International for the species names (<http://datazone.birdlife.org/species/search>, accessed on June 2020) (BirdLife International, 2020a). Traded parrots identified as genus/family or as hybrids were also included for all analyses (except the analysis using phylogenetic generalized least squares (PGLS), see ‘Data analysis of factors correlating with the global parrot trade’ in Section 2.2). Based on the checklist, 40 species names, used in the original CITES data, were updated (Table S1).

During data handling, we observed that discrepancies in reported quantities occurred in the raw data. Many transactions had data either on ‘importer quantity’ or ‘exporter quantity’ only (Table S2), so if we only use these importer/exporter-reported quantities for analyzing imports/exports, we will underestimate the sum of quantities being traded for a given period, species, or region. Unlike many other wildlife trade studies that directly presented or used the importer/exporter-reported statistics, we ‘corrected’ these discrepancies in the raw data for our analyses. We obtained the ‘corrected import quantity’ (refer to as ‘import quantity’ hereafter) of a transaction by substituting ‘exporter quantity’ for ‘importer quantity’ when there was no data on the ‘importer quantity’ in that transaction. The same rule was also applied to obtain the ‘corrected export quantity’ (refer to as ‘export quantity’ hereafter) (Fig. S1). If the ‘importer quantity’ and ‘exporter quantity’ reported were not consistent, the CITES system would, in most cases, split this transaction into two records (‘importer quantity’ in one record and ‘exporter quantity’ in another record), so this transaction would be duplicated in the raw data. In these cases, we used the larger quantity when ‘exporter quantity’ and ‘importer quantity’ are not consistent in the same transaction (Martin, 2018a; Vall-Ilosera and Cassey, 2017) (Fig. S1). We also excluded all records of re-exports and seizures.

We removed 36 888 re-exports and 9 616 duplicates out of 177 695 transactions. After data processing and filtering, the temporal trade trends in export and import quantities were analyzed. All data analyses were performed using R software environment version 4.0.2 (R, 2020). For the comparison of temporal shifts on the trade routes, three 13 year-period route maps (1978–1990, 1991–2003, and 2004–2016) were plotted using ArcGIS version 10.7 (ArcGIS, 2020).

The ‘source of the specimen’ of each transaction was categorized by letter codes under CITES (CITES, 2013). In order to analyze the temporal trade trends in the sources of traded parrots, according to the 2016 IUCN Red List status, we grouped relevant source codes into three types: ‘Wild-Caught’ for W (specimen from the wild), F (animals born in captivity that do not fulfill the definition of ‘bred in captivity’) (Bush et al., 2014; Foster et al., 2016; Lyons et al., 2017), and R (ranch-d specimens taken as eggs or juveniles from the wild); ‘Captive-Bred’ for C (animals bred in captivity) and D (Appendix I animals bred in captivity for commercial purposes); and ‘Unknown’ for U (source unknown), O (pre-Convention specimens), as well as miscoded and uncoded specimens. We then assigned our ‘type’ to each transaction based on the ‘source of the specimen’ for analysis. The results were plotted using the R packages ‘ggplot2’ (Wickham, 2016) and ‘ggpubr’ (Kassambara, 2017).

2.2. Data analysis of factors correlating with the global parrot trade

2.2.1. Factors of parrot species

We gathered data on eight factors of traded parrot species that might be associated with the consumer preference on parrots and which may also be correlated with the trade quantities (Carpenter et al., 2014; Dieter, 2009; Vall-Ilosera and Su, 2019). When export and import quantities disagree in a transaction, we used import quantities to maintain consistency (Bush et al., 2014). We followed the approach of Vall-Ilosera and Cassey (2017), with modifications, and selected variables that fit the context of our study (Pires and Clarke, 2012; Vall-Ilosera and Cassey, 2017). These variables included (1) population size in the wild, (2) IUCN Red List status, (3) main body coloration, (4) number of color morphs, (5) body mass, (6) brain to body mass ratio, (7) lifespan, and (8) price per bird. Because body mass and population size in the wild were positively correlated with body length ($r(254) = 0.871, p < 0.001$) and distributional range ($r(121) = 0.478, p < 0.001$), respectively (Table S3), only body mass and wild population size were included in the analysis. These eight variables could be relevant to one or more of the following three aspects: (i) *availability*, (ii) *attractiveness*, and (iii) *value*. (i) *Availability*: parrot species with small wild population sizes, large body sizes, and great longevity are predicted to be less common in the wild and, hence, traded in fewer numbers. (ii) *Attractiveness*: species with large body sizes, brightly-colored plumage, and high intelligence levels are predicted to be more sought after by pet owners and traded in larger quantities. Here, we used a large ratio of brain to body mass as a proxy for high intelligence levels, which may facilitate behaviors such as learning tricks and mimicking the human voice (Chappell, 2017). We also predicted that species with more color morphs would be more attractive to pet owners, especially breeders (Van den Abeele, 2016), thus, they would be traded in larger quantities. (iii) *Value*: species that are officially classified as threatened, or those that have higher market prices, might be correlated with the trade volume.

We collected data on the eight factors of each species in the following manner. We obtained the estimates of (1) the population size in the wild (number of individuals) and (2) the IUCN Red List status from the IUCN Red List (<https://www.iucnredlist.org>, accessed in December 2018) (IUCN, 2020). We defined (3) the main body coloration of the parrot as a human-perceived color that covers 50% or more of the body (Billerman, 2020). Information on the (4) number of color morphs (both natural and captive color varieties) was also extracted from literature (Martin, 2002). In addition to this, we obtained data on (5) body mass (g) and brain volume (g) from Kinkaid (2015), Dunning (2007) and Tsuboi et al. (2018), and used it to calculate the (6) brain to body mass ratio. Furthermore, data on the (7) the lifespan in years were obtained from Young et al. (2012). Lastly, we referred to the data from Vall-Ilosera and Cassey (2017) for (8) the price per bird (AUD) (Dunning, 2007; Kinkaid, 2015; Tsuboi et al., 2018; Vall-Ilosera and Cassey, 2017; Young et al., 2012).

We tested the correlation between import quantities (under purpose codes T (commercial) and P (personal) only) and the eight factors using PGLS with the R package, *caper* (Orme et al., 2012). Import quantities and the factor data (except the IUCN Red List status and main body coloration) were \log_{10} transformed for analysis. We used PGLS to control for the phylogenetic relationships among the species. We used the parrot phylogeny from Kosman et al. (2019) to fit the PGLS model (Kosman et al., 2019) and we used the Akaike information criterion, corrected for small sample sizes, (AICc) to choose the best explanatory model. A phylogenetic tree and the data for the eight factors were plotted using the R package, *ggree* (Yu et al., 2017).

2.2.2. Factors of states

We hypothesized that states with high GDP per capita would purchase more exotic pets, such as parrots (Olah et al., 2016). Further, because parrots are mostly traded as live companion pets, we further hypothesized that states with an aging population should have higher demands for ‘companions’; consequently, pet parrots should be traded in larger quantities in these areas (Mugford, 1975; Olbivich, 1989). We tested the correlation of GDP per capita and aging index with net import quantities (calculated by subtracting exports from imports, ≥ 0) under purpose codes T (commercial) and P (personal) only (CITES, 2013). The aging index is defined as ‘the number of elderly (≥ 65 years old) per 100 young persons (≤ 15 years old) in a specific population (per year)’ (Preedy, 2010). In other words, the aging index increases when the population ages. We focused on the period of 1980–2016, which had the complete datasets of all variables available. We downloaded the yearly data on the GDP per capita (USD) and the percentages of the population at ages 0–14 and ≥ 65 of states from the World Bank Open Data (<https://data.worldbank.org>, accessed December 2018) (The World Bank, 2020). The net import quantities and the data for the factors were \log_{10} transformed for analysis. The effects of GDP per capita and the aging index were analyzed by performing a generalized linear mixed model using the R packages, *lme4* and *MuMIn* (Barton, 2019; Bates et al., 2015) with the states and year set as the random effects.

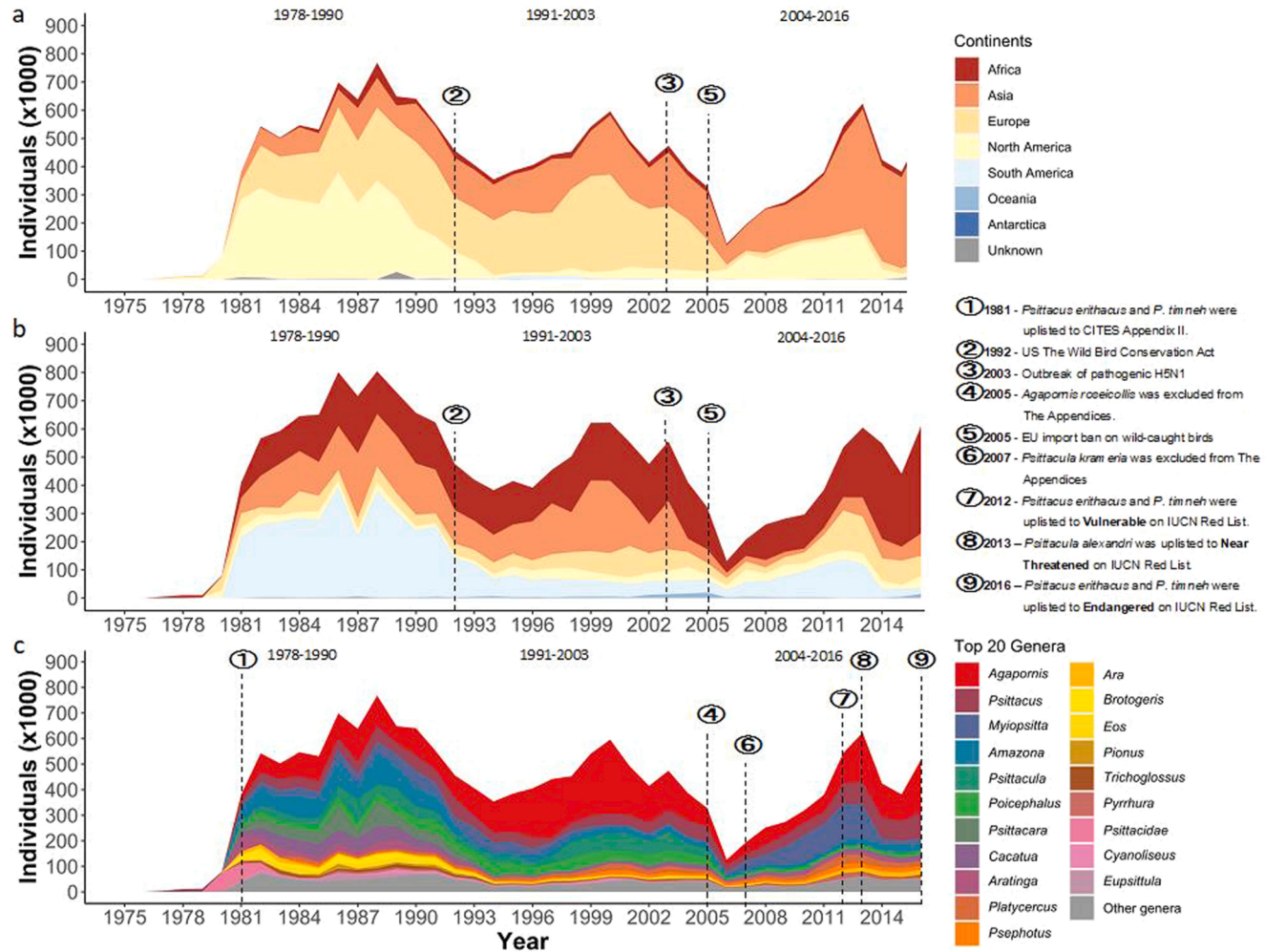
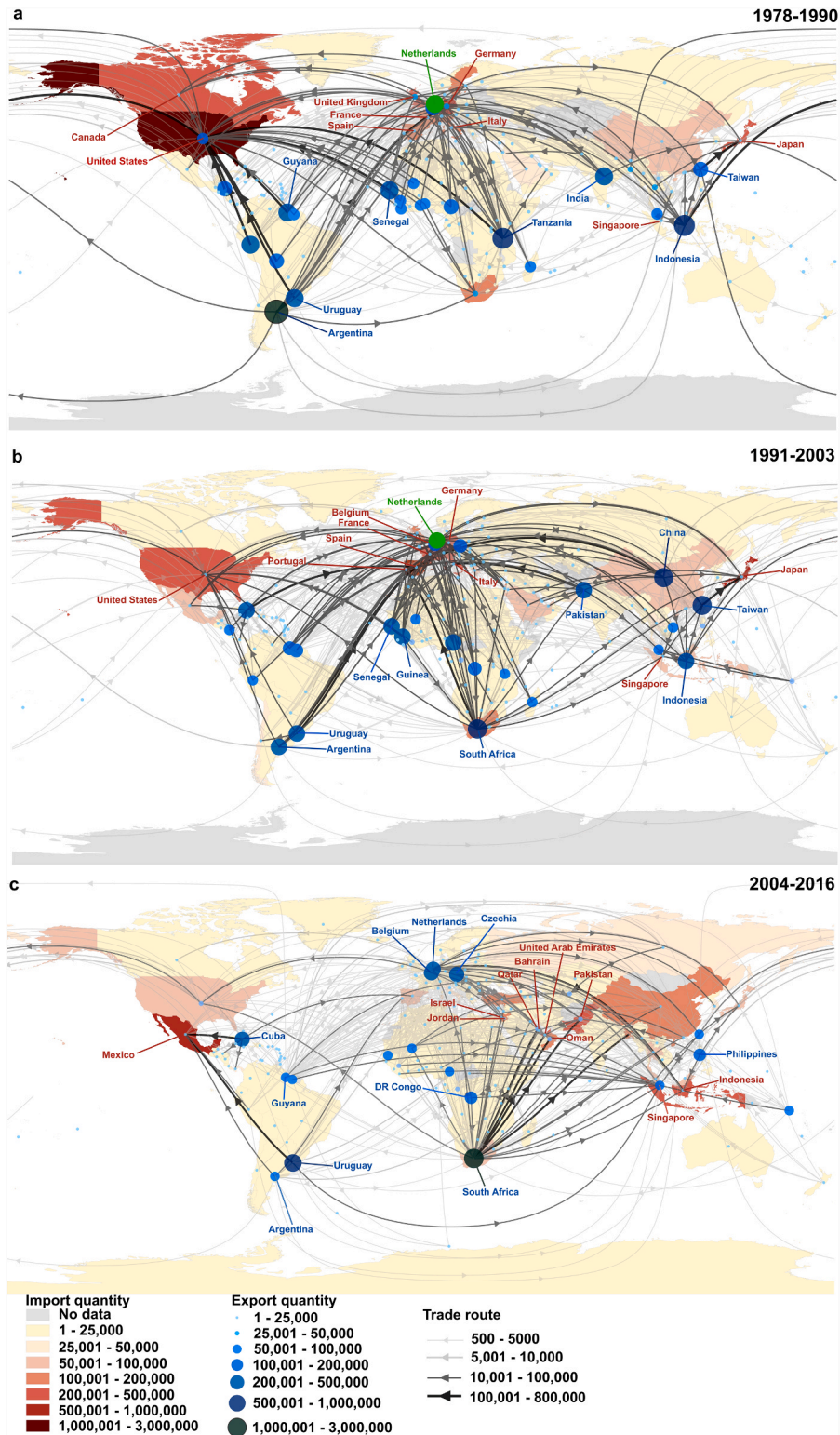


Fig. 1. Temporal pattern of the trade quantity by (a, b) continents and (c) genera under CITES between 1975 and 2016. Stacked (a) import and (b) export quantities of the seven continents ('Unknown' represents the data without information on location) and (c) import quantities of the twenty most traded genera of parrots are color-coded. A selection of events with their respective time points, which are relevant to the global parrot trade, are indicated by dashed lines and are labeled with circled numbers. The three time periods (1978–1991, 1992–2003 and 2004–2016) are marked by solid lines in light blue for better illustration. (For the colored version of this figure, please refer to the online version of this article.)



(caption on next page)

Fig. 2. Parrot trade routes under CITES between (a) 1978 and 1990, (b) 1991 and 2003, and (c) 2004 and 2016. Sizes of the blue colored dots and intensity of the red colored areas/polygons are proportional to the export and import quantities, respectively. Transparency level and thickness of the lines and arrows are proportional the import/export quantity of the trade routes. Trade flows are indicated with arrows. Names of the top ten importers and exporters are shown in red and blue colors, respectively. Traders qualified as top ten importers, as well as top ten exporters, are indicated by green dots and names. Transactions reported to CITES between 1975 and 1977 are excluded here because the trade quantity was relatively low in the early days of CITES (signed by only 21 Parties, see Fig. 1). Trade routes for less than 500 individuals of parrots being transported are not displayed. States that are not the CITES members were also included here to illustrate their trade flows. (For the colored version of this figure, please refer to the online version of this article.)

3. Results

3.1. Temporal trends and geographical patterns of the global parrot trade

Based on our analyses on the 1975–2016 data from CITES, a total number of 16 738 512 individual parrots were imported worldwide (quantity/year on average = 398 536). To provide a more recent number, 556 525 individuals were imported globally in 2016. In total, 321 out of 402 (80%) parrot species in 85 genera were found in the CITES trade records between 1975 and 2016. Our results on the temporal trends of the parrot trade show that the import quantity increased sharply from 1979 to 1981 (Fig. 1a). Afterwards, the quantity steadily increased and reached its first peak in 1988 ($n = 829\ 173$). After this first peak, the import quantity gradually decreased until 1994 and recovered to arrive at its second peak in 2000 ($n = 615\ 676$; Fig. 1a). Since 2000, the international parrot trade experienced a rapid decline and had low import quantities in the following 10 years to come, with the quantity in 2006 ($n = 149\ 748$) being the lowest among the years. The import quantity then rebounded rapidly from 2010 to the third peak in 2013 ($n = 655\ 280$). The quantity then dropped slightly but regained the upward trend until 2016. When we compared the import quantities of three consecutive time periods (13-year periods with different trade patterns; Fig. 1 and Table S4), that is, 1st period: 1978–1991, 2nd period: 1992–2003, and 3rd period: 2004–2016, the import quantity of the 3rd period was the lowest among them (1st period, $n = 6\ 005\ 277$; 2nd period, $n = 5\ 975\ 552$; and 3rd period, $n = 4\ 753\ 116$). We also showed that the temporal change in export quantity between 1975 and 2016 followed a very similar trend in import quantity (Fig. 1b and Table S4).

Trade quantities of different continents varied greatly over the years and, in general, the export quantity was larger than the import quantity (Figs. 1a and b, and S2-S3). Africa, Asia, Europe, and South America were the key continents exporting parrots to the market during the 39-year period. Africa has been consistently exporting parrots to other continents over these periods, and is currently the largest exporting continent (Africa in the 3rd period: $n = 2\ 358\ 205$, 46.8%). South America was the largest exporting continent in the 1st period, but the export quantity declined sharply since 1992. South America and Europe are currently the second and third largest exporters (South America in the 3rd period, $n = 864\ 791$, 17.2%; Europe in the 3rd period: $n = 809\ 334$, 16.0%). Asia was the second largest exporting continent during the 1st and 2nd periods, but this role diminished in the 3rd period (3rd period, $n = 532\ 361$, 10.6%). North America was found to regularly exported a very small quantity throughout the years (3rd period, $n = 396\ 702$, 7.9%) (Fig. 1b and Table S4).

Nevertheless, our results demonstrate that Asia, Europe, and North America were the three main continents importing most of the traded parrots over the above-mentioned periods. North America and Europe were the first and second largest importing continents, in the 1st period, respectively, but the import quantity of North America collapsed in the 2nd period since 1992 and grew slightly during the 3rd period (3rd period, $n = 992\ 424$, 20.9%). Europe replaced North America to become the largest importing continent in the 2nd period, but the import quantity of Europe also plummeted to a very low level after 2005, and this low level was maintained thereafter (3rd period, $n = 492\ 949$, 10.4%). Although Asia imported the least among the three continents in the 1st period, Asia gradually imported more and more as time progressed, and now is recognized as the largest and most dominant importing continent of parrots in the world (3rd period, $n = 3\ 041\ 402$, 64.0%). It is important to note that, Africa regularly imported a very small quantity relative to the three continents throughout the periods investigated (Fig. 1a).

As indicated by the trade among continents, the global trade routes of parrots show that the geographical distribution, scale, and trader composition of the parrot trade changed drastically between 1975 and 2016 (Fig. 2). In total, there were 199 export states and 223 import states during this period. Within the 1st period, the network of the parrot trade was more intensely centered around the Americas, Western Europe, and Africa in the Western Hemisphere (Fig. 2a). Top importers included the United States, Canada, the United Kingdom, Germany, France, Spain, Italy, the Netherlands, Japan, and Singapore. Meanwhile, the top exporters were Argentina, Peru, Uruguay, Guyana, Tanzania, Senegal, the Netherlands, India, Indonesia, and Taiwan. After transitioning to the 2nd period, the center of the network shifted eastward towards the prime meridian, and the trade routes became more widely spread (Fig. 2b). Regions in Eastern Europe, South Africa, and Asia began to engage more frequently in the trade. Portugal and Belgium replaced Canada and the United Kingdom as the top importers; while South Africa, Guinea, Pakistan, and China replaced Peru, Guyana, Tanzania, and India as the top exporters. During the 3rd period, the network shifted further eastward, and more regions in the Middle East and Southeast Asia in the Eastern Hemisphere appeared to be active in the trade (Fig. 2c). Mexico, Bahrain, Jordan, the United Arab Emirates, Oman, Qatar, Israel, Pakistan, and Indonesia replaced the United States, Portugal, Spain, Germany, France, Belgium, Italy, the Netherlands, and Japan to become the top importers. Meanwhile, Cuba, Guyana, the Democratic Republic of the Congo (DRC), Belgium, the Czech Republic, and the Philippines replaced Guinea, Senegal, China, Pakistan, and Indonesia as the top exporters. Throughout the periods, Singapore and the Netherlands were always the top importers and exporters, respectively (Fig. 2).

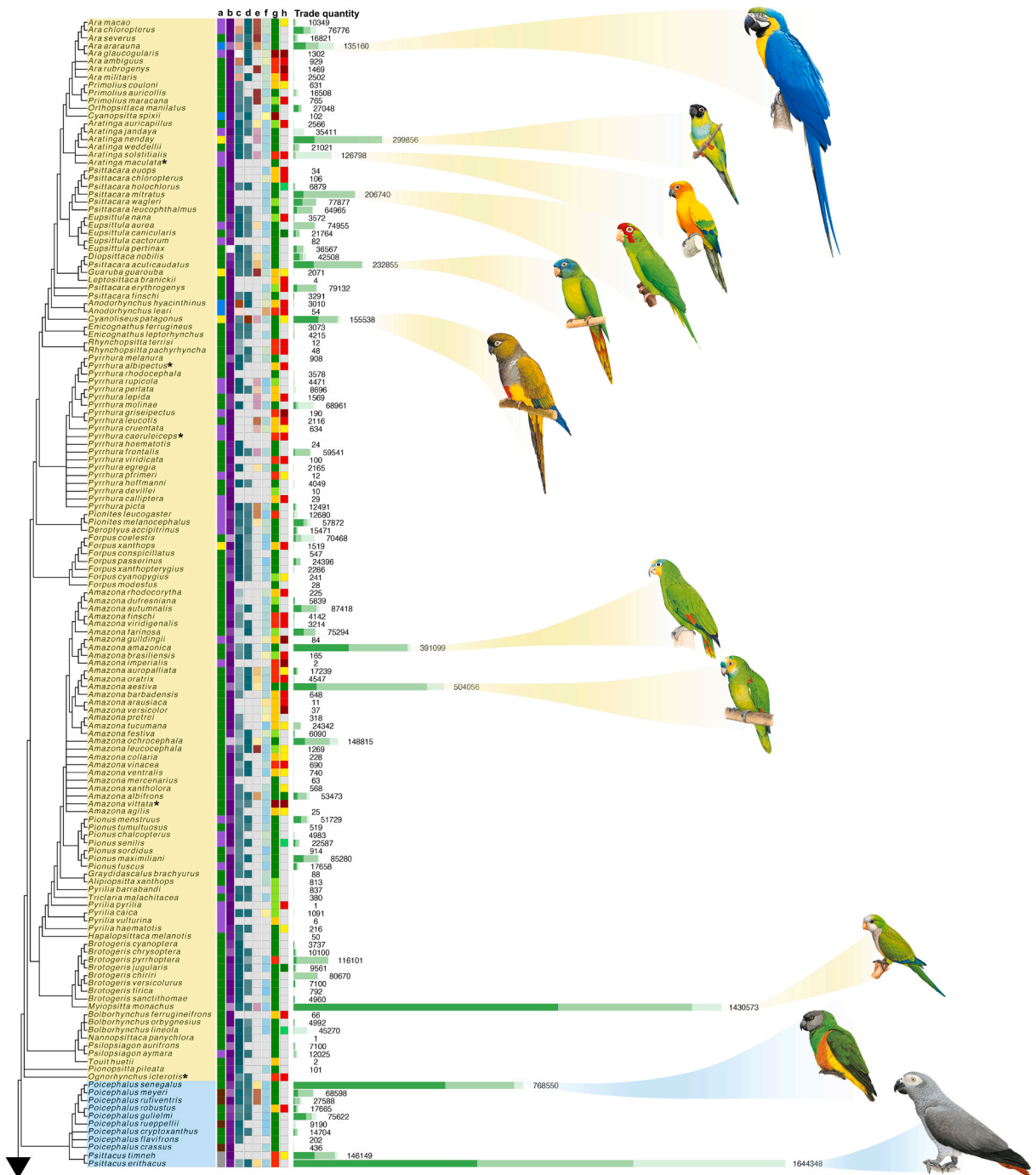


Fig. 3. Phylogenetic tree of the CITES-listed parrot species traded between 1975 and 2016 (n = 320). The tree is color-coded by the biogeographic realms (BirdLife International 2020a). Values/categories of the eight variables (a to h) and the trade quantity of each parrot species are displayed by colored squares/bars next to the tree. Light gray squares represent no data (NA). Lengths of stacked green bars next to the column h correspond to the trade quantities (number of individuals). *Agapornis roseicollis*, *Melopsittacus undulatus*, *Nymphicus hollandicus*, and *Psittacula krameri* (all labelled with #) were included for comparison despite not being listed by CITES at the time of this study; consequently, their respective trade quantities might be underestimated because of their earlier exclusion in the CITES dataset. *Poicephalus fuscicollis* was not included here because it was not available in the phylogeny tree by Kosman et al. (2019). The trade quantities of species (names labelled with *) only documented in re-exports or seizures were not showed here. Illustrations reproduced with permission of Lynx Edicions. (For the colored version of this figure, please refer to the online version of this article.)

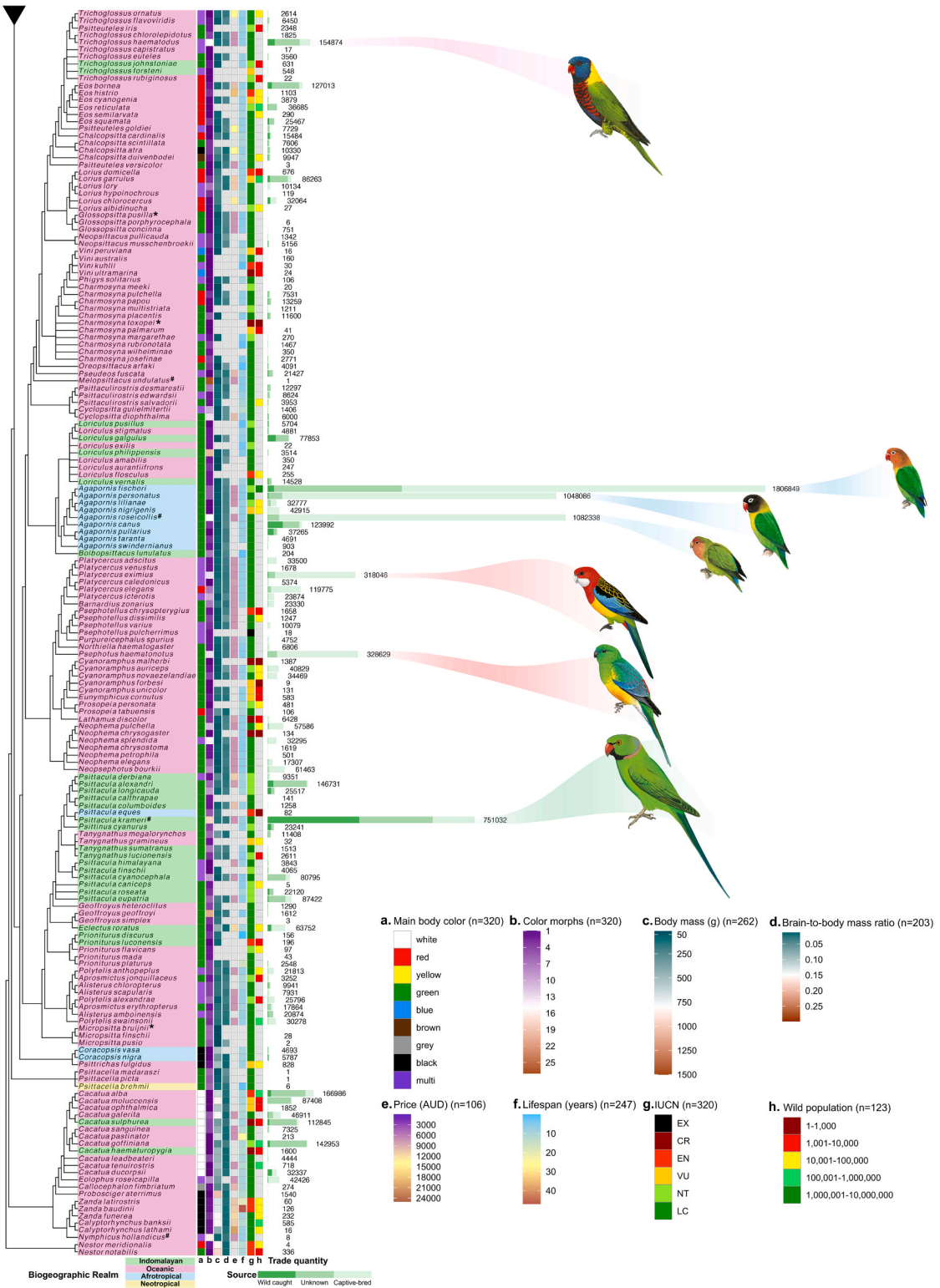


Fig. 3. (continued).

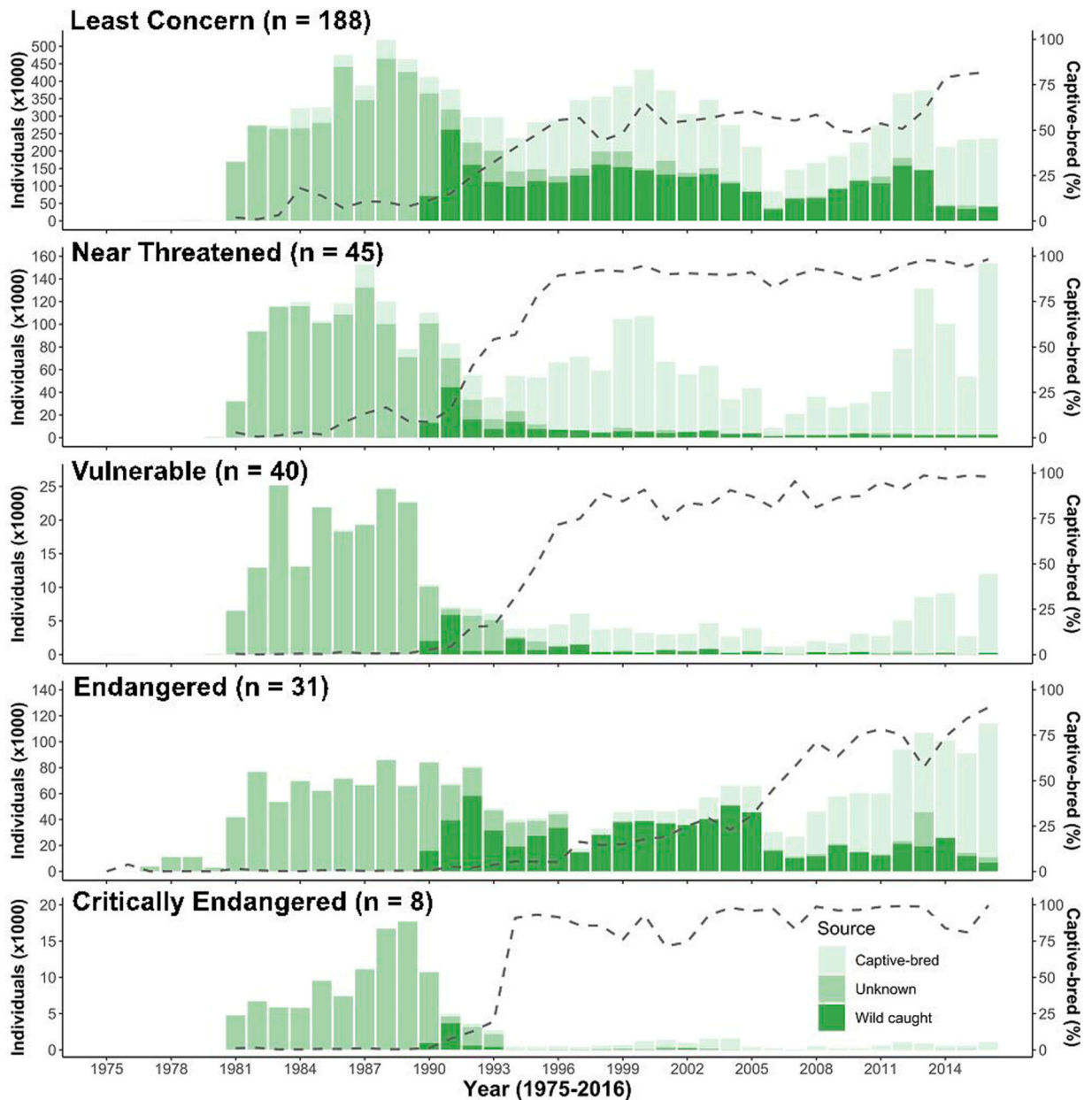


Fig. 4. Temporal trends in import quantities of parrots from different sources by the five IUCN Red List Status between 1975 and 2016. Stacked bars in each graph are color-coded by the three different types of sources. Each dashed line represents the proportions (%) of captive-bred parrots traded per year over the 42 years. For a similar graph using the export quantities, please refer to the [Supplementary Fig. S2](#).

3.2. Temporal trends on the taxa and sources of traded parrots

The ten most traded genera of parrots under CITES between 1975 and 2016 were *Agapornis* (lovebirds, $n = 4\,287\,540$, 25.6%), *Psittacus* (the gray parrot and the Timneh parrot, $n = 1\,790\,740$, 10.6%), *Myiopsitta* (the monk parakeet and the cliff parakeet, $n = 1\,430\,574$, 8.5%), (Amazon parrots, $n = 1\,334\,143$, 8.0%), *Psittacula* (Afro-Asian ring-necked parakeets, $n = 1\,136\,843$, 6.8%), *Poicephalus* (*Poicephalus* parrots, $n = 985\,399$, 5.9%), *Psittacara* (South and Middle American parakeets, $n = 688\,448$, 4.1%), *Cacatua* (cockatoos, $n = 610\,672$, 3.6%), *Aratinga* (South American conures, $n = 532\,453$, 3.2%) and *Platyercus* (rosellas, $n = 504\,098$, 3.0%) (Fig. 1c). We found that there are eight parrot species from which more than half a million individuals were traded under CITES during

the 42-year period. The most traded species of all within the period studied was *Agapornis fischeri* (Fischer's lovebird, Near Threatened, $n = 1\,806\,849$, 10.8%) (IUCN, 2020) followed by *Psittacus erithacus* (the gray parrot, Endangered, $n = 1\,644\,348$, 9.8%), *Myiopsitta monachus* (the monk parakeet, $n = 1\,430\,573$, 8.5%), *Agapornis roseicollis* (rosy-faced lovebird, $n = 1\,082\,338$, 6.5%, excluded from the Appendices in 2005), *Agapornis personatus* (yellow-collared lovebird, $n = 1\,048\,086$, 6.3%), *Poicephalus senegalus* (Senegal parrot, $n = 768\,550$, 4.6%), *Psittacula krameri* (rose-ringed parakeet, $n = 751\,032$, 4.5%, excluded from the Appendices in 2007), and *Amazona aestiva* (turquoise-fronted amazon, $n = 504\,056$, 3.0%) (Fig. 3).

Regarding the temporal trends in the sources of traded parrots analyzed based on their conservation status in 2018 IUCN Red List, the proportions of the import quantity of wild-caught, unknown, and captive-bred individuals during the entire period were 23.5%, 37.6%, and 38.9%, respectively. Least Concern (LC) species comprised a major proportion (totaling 65.3%) of the import quantity (Fig. 4) and the trade trends of LC species generally followed the trends of the international import quantity (Fig. 1a). The majority of traded parrots in the 1st period came from the unknown sources. Captive-bred parrots were gradually traded in larger proportions after the 1st period, except for those species that are now considered Endangered (EN). Wild-caught individuals of species that are currently listed as EN were predominantly traded during the 2nd period and continuously contributed a smaller but notable proportion of import quantity in the 3rd period. Moreover, by trading substantially more captive-bred individuals, the trade trends of Near Threatened (NT) and EN species generally increased over the periods. Species currently listed as Critically Endangered (CR) were mainly traded in the 1st period, but after this the import quantity dropped and afterwards remained at a low level (Fig. 4). The temporal trade trends of the CITES Appendix I- and II-listed species qualitatively followed those of EN and LC, respectively (Figs. S2-S3). Moreover, we found a general pattern which showed the more populated the parrot species were in the wild, the higher the numbers of wild individuals of the species being caught for legal trade, regardless of their current IUCN conservation status (Fig. S4).

3.3. Factors correlating with the global parrot trade

We tested eight factors concerning parrot species (Fig. 3), as well as two factors of states, for their correlations with the quantity of the global trade of parrots. Our results indicated that three of the factors concerning parrots were positively correlated with the import quantity (Table S5). These factors are the population size in the wild (adjusted R^2 : 0.328, $F_{1116} = 58.1$, $SE = 0.10$, $p < 0.001$, $\lambda = 0.741$, λ 95% confidence interval (CI) = 0.298, 0.943), the number of color morphs (adjusted R^2 : 0.146, $F_{1305} = 53.41$, $SE = 0.22$, $p < 0.001$, $\lambda = 0.683$, λ 95% CI = 0.482, 0.825) and the Least Concern IUCN status (estimate = 1.06, $SE = 0.40$, $p < 0.001$; IUCN status full model: adjusted R^2 : 0.131, $F_{4302} = 12.54$, $\lambda = 0.657$, λ 95% CI = 0.46, 0.80). The best model to explain the quantity of each traded species is the population size in the wild (AICc: 350.4; Table S5).

Our results show that the net import quantities of states between 1980 and 2016 depended on the interaction between GDP per capita and the aging index of the states (Tables S6 and S7, $R^2_m = 0.19$; $R^2_c = 0.74$, $p < 0.001$). Among states with a high aging index, the majority also had a high GDP per capita at the same time. These were the states that had high net import quantities of parrots (Figs. 5 and S4). Among states with a low aging index, it was found that those with a low GDP per capita imported a smaller number of parrots (Figs. 5 and S5), when compared to the wealthier states that had high net import quantities. These wealthy states were mostly Middle Eastern and included the United Arab Emirates (UAE), Bahrain, Oman, Qatar, Saudi Arabia, and Kuwait (Figs. 5 and S5).

4. Discussion

4.1. Shifts among the global parrot trade hubs in the last four decades

Our study shows that there is a profound change in the spatial and temporal trends in the international trade of CITES-listed parrots

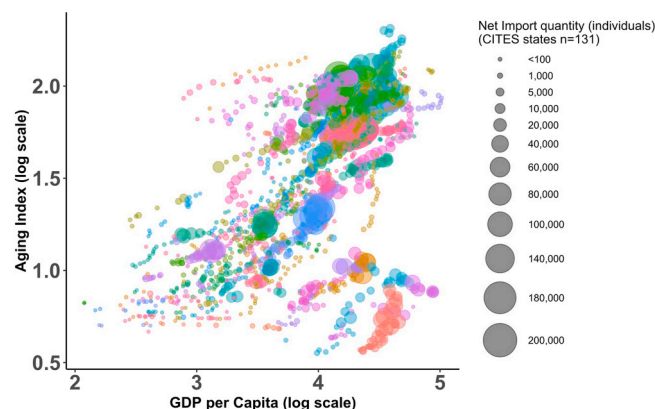


Fig. 5. Scatter plot on the aging index (log), GDP per Capita (log) and net import quantities of parrots (1980–2016). Dots coded in the same color represent data points of the same state from different years. Please refer to Fig. S5 for the state identities and years.

in the last 42 years. Large fluctuations were observed in the temporal trend of the global parrot trade, with several troughs in the trade volumes apparently coinciding with two impactful events in the exotic bird trade: the changes in regulations among leading traders and the occurrence of pandemic zoonosis (UNODC, 2020; Vall-Iloera and Cassey, 2017). Prior to 1992, the United States (US) was the largest importer of parrots. The first substantial drop in parrot trade quantity in the early 1990s occurred around the enactment of the Wild Bird Conservation Act (WBCA) in the US in 1992. This WBCA was the first legislative act focused on limiting the import of exotic bird species, which were listed by CITES, to the US (Pires, 2012; Fish and Wildlife Service International Affairs, 2020). This restriction led to an immediate reduction in the number of wild-sourced parrots being legally imported to North America, as well as being exported from South America. This had a long-lasting impact, and Europe later emerged as the leading importer of parrots. In 1997, the highly pathogenic avian influenza virus, H5N1, caused flu outbreaks among birds and humans in Asia, which has spread significantly worldwide since 2003 (Lai et al., 2016), eventually resulting in the implementation of trade restrictions in many importing countries (Martin, 2018a). Since 2002, the European Union (EU) began to assess the animal health and welfare risks associated with the import of wild birds into the EU (European Food Safety Authority, 2006). A few years later, the EU imposed a permanent ban on wild bird imports to Europe in 2007 (Cardador et al., 2019). Similarly to what occurred in North America, this control led to a drastic decline in parrot imports to Europe, and Asia shortly became the largest parrot importer thereafter. These marked declines in trade volumes from 1975 to 2016 have also been documented in other pieces of research on the exotic animal trade (Cardador et al., 2017; Harfoot et al., 2018; Reino et al., 2017).

By comparing the three consecutive periods of 1978–1990, 1991–2003, and 2004–2016, the international trade quantities of exotic parrots has been maintained as alternative consumer markets periodically emerged, despite the implementation of these unilateral regulations. After the trade bans, the previous large consumer markets in the developed states of North America, Western Europe, and East Asia were gradually redirected towards developing states in Western and Southeast Asia. The increased imports of exotic parrots in these developing states might be attributed to their recent economic development, human population growth, expansion in international travel routes, improved internet connectivity, and cultural shifts (Bush et al., 2014; Ding et al., 2008; Martin, 2018a; McNeely et al., 2009). The Middle East in Western Asia emerged as one of the main destinations of exported parrots after the trade bans. From 2004–2016, this region imported approximately 1.57 million (33.1%) live parrots, and as much as 85% of the imported parrots were reported to be captive-bred. Top importers in the Middle East included the UAE, Bahrain, Oman, Qatar, Jordan, and Israel. These six states imported parrots from a large number of states (84 states) and each of the six states imported 118–161 parrot species in the same period. It was previously reported that neighboring states within the Arabian Peninsula had a complex network of trade in which re-exports within the Peninsula were substantial (Martin, 2018a). A few studies on the wildlife trade, some focusing on illegal ones, in Jordan, Lebanon, the UAE, and Saudi Arabia, similarly documented that birds constituted a high proportion of species found in their pet markets (Abi-Said et al., 2018; Ehab and Handal, 2018; Eid et al., 2011; Giangaspero and Ghafri, 2014). The Middle East is also known to be the main importer of other exotic birds such as falcons from Europe for use in falconry, which is a traditional pastime (Bush et al., 2014). Although the Middle East was heavily involved in exotic pet businesses, about 44% of the states in the Middle East were not CITES Parties until 2001 or later. For instance, top importing states such as Bahrain and Oman joined CITES after 2008 (CITES, 2020). Thus, it is important to note that the actual quantity of the international parrot trade that preceded the bans in this part of the region was unclear or underestimated because data or information on parrots or other traded birds was unavailable.

Other states in the rest of the Asia, such as Bangladesh, Pakistan, and Nepal in South Asia; Indonesia in Southeast Asia; and China and South Korea in East Asia, were regions where parrot imports increased by at least two-fold between 2004 and 2016 compared to their respective volumes between 1991 and 2003; with Bangladesh, Pakistan, and Indonesia also being the most recent top importers. We also observed another state, Mexico in Latin America, has an increase in the imports of parrots overseas over the years. In order to protect the 22 native Mexican parrot species, almost half of which are threatened by trade and habitat loss, the Mexican government permanently outlawed the capture, export, and import of their native parrots in 2008 (Cantú and Saldaña, 2018). Nevertheless, despite being homes for highly diverse parrots, Indonesia and Mexico have gradually changed to become prominent importers.

In terms of parrot supplies, South Africa is gaining a prominent role as a supplier in the global parrot trade. After the implementation of the WBCA in the US, South Africa became one of the major exporters and importers of parrots between 1991 and 2003. Despite exporting over 70 000 parrots per year during 1991–2003, early captive-breeding facilities in South Africa have been importing more readily available wild-sourced parrots as captive breeding stock mainly from Guinea, Madagascar, Cameroon, DRC, and Congo (Martin, 2018a). With the continuous investment in captive facilities, South Africa has built an enormous aviculture operation over the past two decades. By 2015, it was estimated that there were over 1 600 breeding facilities in South Africa (Martin, 2018a). South Africa exported more than 1.8 million (37.1%) parrots of 209 species to 118 destinations in the period of 2004–2016, mainly to expanding consumer markets in Western and Southeast Asia.

Another significant change is the role of the European states, which changed from being parrot importers to prominent exporters after the trade bans. Although Europe is not in the native range of wild parrots, the Netherlands, Belgium, and the Czech Republic exported 750 thousand (14.9%) parrots from 213 species to 99 destinations between 2004 and 2016. The Netherlands had been very active in the international parrot trade business as the top importer from 1978 to 2003, as well as a top exporter from 1978 to 2016. Given the large parrot export quantity from Europe after the EU ban, it is likely that the number of parrot breeding farms in European states had expanded considerably with the imported parrots serving as the breeding stock in earlier years. In addition, Uruguay remained the top exporter over the 42 years. Remarkably, it exported more than 650 000 parrots from 2004 to 2016, nearly all of which were *Myiopsitta monachus*. Ninety-five percent of the *M. monachus* individuals were exported to Mexico and the rest to a number of destinations in Asia and Europe. The Philippines and the Solomon Islands were also emerging as more important exporters in the previous decade, but the Solomon Islands became a CITES Party in 2007.

4.2. Impacts of trade to threatened species in the wild

The temporal trends of the sources of parrots reported in the international trade across the study period indicate that the parrots being supplied internationally has shifted from being wild-caught to being captive-sourced, especially after 1992. This trend was observed for all species, regardless of their IUCN status. Based on our data, some of the parrot species, which are currently classified as Endangered, were heavily traded and transported to more than 150 destinations worldwide before 2005. These included *Psittacus erithacus*, *Psittacus timneh*, *Cacatua alba* (white cockatoo in Indonesia), and *Amazona auropalliata* (yellow-naped amazon in Mexico and Costa Rica). *Psittacus* spp. accounted for 95% of the wild-caught parrots of the Endangered group in the 42 year period, representing more than half a million individuals. Our data indicate that during the recent period from 2004 to 2016, more than 280 000 wild- and unknown-sourced (W/U) *Psittacus* parrots were mostly exported from the DRC, Congo, and Cameroon in Central Africa to a number of key destinations, including Turkey, the Netherlands, South Africa, Singapore, Hong Kong, and Serbia. To avoid overexploitation of *Psittacus* parrots (Valle et al., 2020), CITES transferred *P. erithacus* from Appendix II to I in 2017 (CITES, 2020). *Aratinga solstitialis* (sun parakeet in northeastern South America), *Pionites leucogaster* (green-thighed parrot in western South America), and *C. alba* are other examples of Appendix II species that were uplisted to EN status during 2013–2014. Notably, at least a thousand W/U individuals of each of the species were traded in the same period. Substantial quantities of LC parrots were also captured from the wild for trade. *Myiopsitta monachus* (>635 000 W/U individuals), *Pocephalus senegalus* (>100 000), *Amazona amazonica* (orange-winged amazon in tropical South America, >50 000), and *Psittacula krameri* (>40 000) were some of the most traded parrots between 2004 and 2016. They are currently listed in Appendix II (except for *P. krameri*). *Myiopsitta monachus* originates from Argentina and the surrounding states of South America. This species, as well as *P. krameri*, are known to be highly invasive in many states outside of their native range. The Mexican wildlife authorities did not officially list *M. monachus* as an invasive species until 2016 and allowed the massive import of this species before 2015 (Cantú and Saldaña, 2018). International trade involving these invasive species is expected to continue and the trade could be an issue for the protection of native biodiversity in many importing regions (Menchetti and Mori, 2014).

Although captive-bred parrots have been frequently regarded as a sustainable source to meet the global parrot demands and lessen the overexploitation pressure of wild populations, some studies show that illegally harvested parrots could be laundered through captive breeding operations, particularly in those that are large scale (Martin, 2018a; Vall-Ilosera and Cassey, 2017). This laundering could have been made possible by the deliberate misuse of CITES source codes so that wild-caught specimens became exported as captive-bred ones, which might not have otherwise been allowed to be exported (Aloysius et al., 2020). Fertilized eggs illegally collected from the wild could also be smuggled to the breeding centers where hatchlings are ringed and mislabeled as captive-bred (Furnell, 2019). Some experts worried that the increased supply of captive-bred parrots might have fueled the global demands and, in turn, threatened the wild populations (Martin, 2018a). Moreover, careful planning is required for exchanging parrots between captive breeding colonies; otherwise, continuous inbreeding in overseas colonies could result in a loss of genetic diversity and alterations of wild-type phenotypes, possibly leading to the viability of these inbred parrots not being maintained in the future (Vall-Ilosera and Cassey, 2017). Therefore, studies are needed to determine the sustainability of captive-bred populations, and more national-level monitoring and intervention efforts are required to increase the welfare of captive parrots. We have shown that parrot species that are more abundant in the wild tend to have higher numbers of wild-caught individuals being reported in legal trade, regardless of their IUCN conservation status. This implies that an increase in captive-bred populations will not decrease the number of parrots sourced from the recovering wild populations. This could be because of the relative ease and lower costs of sourcing from the wild for many parrot species, particularly the larger ones with longer lifespans. As a result, capture bans and effective law enforcement at both local and international levels are still critical in minimizing the number of threatened parrots sourced from the wild.

4.3. Influential factors of parrot trade volumes

Despite the temporal variation in the trade volumes of parrots, our study found that both the availability and attractiveness of parrot species are linked to the species trade quantities. Parrot species that have a larger population size in the wild, higher number of color morphs, and those that are currently listed as Least Concern in their IUCN status, had a larger trade volume. This is in line with our finding that parrot species that were more widely abundant were more likely to be caught and made available in the exotic pet markets or for captive breeding to further supply the markets. Recent studies in states including Mexico, Peru, and Bolivia, have demonstrated that parrot catching was done most often without much organization and opportunistically by villagers or peasants. These individuals see nestlings in nearby areas during the breeding season and they take advantage of this for additional income (Cantú et al., 2007; Dauphine, 2008; Pires, 2012). Species that were more widely abundant and accessible were more likely to be caught (Pires, 2012; Pires et al., 2016; Vall-Ilosera and Cassey, 2017). The majority of consumers may have no knowledge of the sizes of the wild populations or the conservation status of different parrots and simply buy those species that they often encounter in the market. A higher number of color morphs of a parrot species provide more choices and more individuals from the same species in different color morphs may be displayed in the market. This leads to a higher chance of a species fulfilling the color preference of the consumers and, thus, being purchased more. Alternatively, the number of color morphs might not be a direct driver of trade. Because some parrot species have been kept and captive-bred for a longer time in history, there is a higher chance for their relatively larger domesticated populations to have new color mutants arise. Similar to our findings, studies on the bird trade in Japan (Vall-Ilosera and Su, 2019), or on parrots endemic to Australia, found that species with larger native distributions were traded more frequently than the other parrot species. However, cheaper species in the domestic markets of Australia (Vall-Ilosera and Cassey, 2017) and in internal online sales in China (Yin et al., 2020), were traded in higher volumes than expensive species, which contrasts with our results on global trade. These studies that focused on a particular group of parrots or on a region also found that traits of parrot species, such as the black main body

color or generation length and body mass, correlated with trade volumes. However, there was no association between trade volume and any of the biological traits of parrots, except for the number of color morphs, when we consider trade on a global scale. This suggests that the factors influencing the domestic trade of a state are different from those of international trade.

While the internal sales of parrots are likely to be affected by regional economic factors (Ye et al., 2020), our results show that the global parrot trade is influenced by both the economy (i.e., GDP per capita) and the demography (i.e., aging index) of the states. In general, a growing GDP increases the purchasing power of a human population; consequently, more people can afford to buy exotic pets for entertainment (Ribeiro et al., 2019). Being some of the most long-lived, social, and intelligent animals, parrots are in higher demand in aging communities because aged groups are usually more in need of companions and they have more spare time to take care of animals after retirement. To the best of our knowledge, there is no investigation on GDP or the aging index as the drivers behind the global legal trade of parrots. However, a recent study using CITES data demonstrated that GDP can be a common driver in the legal trade of mammalian, avian, and reptilian products between 2004 and 2013 based on gravity modeling (Symes et al., 2018). Some Middle Eastern states appear as a distinct group in our analysis, as they have a relatively young population but also had high quantities of net imports of exotic parrots. These Middle Eastern states, including the United Arab Emirates, Bahrain, Oman, Qatar, Saudi Arabia, and Kuwait, are very wealthy and, together with the cultural reasons discussed earlier, these regions overall had a high import level on exotic wildlife in the past decades.

4.4. Conclusions

Using the CITES dataset, we showed that developing regions in Western and Southeast Asia have emerged as prominent importers of exotic pet parrots between 1975 and 2016, including regions such as the Middle East and Indonesia. However, numerous knowledge gaps currently exist in these regions, which should be the focus of future research. For instance, to understand 1) the state-related and consumer-related drivers behind the recent imports of exotic pet parrots, 2) patterns and trends of the parrot trade in these regions, and 3) the supply chains in their internal trade. This information will be crucial in informing national and international laws and policies, finding target groups of consumers to raise awareness of biodiversity loss, and to reduce the demand for exotic parrots through conservation campaigns. In terms of species conservation, *Psittacus* parrots were being heavily traded while they were considered Least Concern by the IUCN, with actions by CITES taken after dramatic population collapses. Therefore, greater scrutiny of parrots traded in large volumes, many of which are not monitored in the wild currently, should be considered. With reference to the case of *P. erithacus*, consideration should be given to uplist more EN species, such as *Aratinga solstitialis*, *Pionites leucogaster*, and *Cacatua alba*, from Appendix II to I because their current population statuses in the wild are highly uncertain (IUCN, 2020). In addition, because more captive-bred parrots than wild-caught parrots are being traded worldwide, more monitoring and intervention efforts are needed to prohibit captive facilities from acting as a cover for wild-caught trade. One way to accomplish this is through the use of an accreditation system that, for example, requires breeding farm owners to keep detailed records on the sources and pedigree of their captive parrots, and the use of an individual identification system (e.g., leg ring or microchip) for information tracing. As part of the accreditation system, regular parentage tests on captive parrots can be performed to confirm pedigree information. Stable isotope analysis can also be used to reveal the source of traded parrots and prevent laundering (Alexander et al., 2019; Jiguet et al., 2019). Lastly, it is necessary to note that the international parrot trade records documented by the CITES are only part of the total parrot trade activities of the world. Therefore, it is equally important to conduct more studies on the domestic and illegal trades of parrots, and to determine the links between them and international trade, as these are also essential pieces that constitute the global picture of the exotic pet parrot trade.

CRedit authorship contribution statement

DTCC: Investigation, Formal analysis, Visualization, Writing – original draft. **ESKP:** Conceptualization, Investigation, Writing – original draft. **ATCW:** Formal analysis, Visualization. **SYWS:** Conceptualization, Supervision, Writing – review & editing.

Declarations

Funding

This research did not receive any grant from funding agencies in the public, commercial, or not-for-profit sectors.

Ethics approval

Not applicable.

Consent to participate

All authors consent to participate in this study.

Consent for publication

All authors consent to publish this manuscript.

Code availability

Not applicable.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01784](https://doi.org/10.1016/j.gecco.2021.e01784).

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