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<https://doi.org/10.1111/cobi.14076>

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Association of reproductive traits with captive- versus wild-sourced birds in trade

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Article impact statement: Reproductive traits are associated more with trade in captive-bred birds than with trade in wild-sourced birds.

Funding information

Natural Environment Research Council, Grant/Award Number: Grant NE/R017441/1

Abstract

The wildlife trade is a billion-dollar global business, involving millions of people, thousands of species, and hundreds of millions of individual organisms. Unravelling whether trade targets reproductively distinct species and whether this preference varies between captive- and wild-sourced species is a crucial question. We used a comprehensive list of all bird species traded, trade listings and records kept in compliance with the Convention on International Trade in Endangered Species (CITES), and a suite of avian reproductive parameters to examine whether wildlife trade is associated with particular facets of life history and to examine the association between life-history traits and captive- and wild-sourced traded volumes over time. Across all trade, CITES listing, and CITES trade, large birds were more likely to be traded and listed, but their longevity and age at maturity were not associated with CITES listing or trade. We found species across almost the full range of trait values in both captive and wild trade between 2000 and 2020. Captive trade volumes clearly associated with relatively longer lived and early-maturing species; these associations remained stable and largely unchanged over time. Trait–volume associations in wild-sourced trade were more uncertain. Only body mass had a clear association, and it varied from negative to positive over time. Although reproductive traits were important in captive-sourced trade, species-level variation dominated trade, with even congeneric species varying greatly in volume despite similar traits. The collection and incorporation of trait data into sustainability assessments of captive breeding facilities are crucial to ensure accurate quotas and guard against laundering.

KEYWORDS

captive breeding, CITES, life history, reproductive traits, wildlife trade

Asociación entre los rasgos reproductivos de aves en cautiverio versus las de origen silvestre comercializadas

Resumen: El mercado de fauna es un negocio mundial de miles de millones de dólares que involucra a millares de personas, miles de especies y cientos de millones de organismos individuales. Por ello es necesario resolver la cuestión de si el mercado se enfoca en especies con distinciones reproductivas y si esta preferencia varía entre las especies de origen silvestre y en cautiverio. Usamos una lista completa de todas las especies de aves comercializadas, listados y registros comerciales conforme a la Convención sobre el Comercio Internacional de Especies Amenazadas (CITES) y un conjunto de parámetros de reproducción de aves para analizar si el mercado de fauna está asociado con facetas particulares de la historia de vida. También analizamos la asociación entre los rasgos de la historia de vida y el volumen comercializado de origen silvestre y de cautiverio a lo largo del tiempo.

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En todos los mercados, listas de CITES y mercados CITES, las aves de mayor tamaño tuvieron mayor probabilidad de ser comercializadas y estar enlistadas, pero su longevidad y edad a la madurez no se asoció con el mercado o la lista e CITES. Detectamos especies en casi toda la gama de rasgos tanto en el comercio de cautiverio como el silvestre entre 2000 y 2020. El volumen comercial de cautiverio mostró una asociación clara con las especies relativamente más longevas y de madurez temprana; esta relación fue estable y casi no cambió con el tiempo. La asociación del volumen en las especies de origen silvestre fue más incierta; sólo la masa corporal tuvo una relación clara y ésta varió entre positiva y negativa con el tiempo. Aunque los rasgos reproductivos fueron importantes para el mercado con origen en cautiverio, la variación a nivel de especies dominó el mercado, incluso mostrando una enorme variación del volumen entre las especies congéneres a pesar de tener rasgos similares. La recolección e incorporación de datos sobre los rasgos dentro de los análisis de sustentabilidad de las instalaciones para la cría en cautiverio es crucial para asegurar las cuotas adecuadas y prevenir blanqueo de capitales.

PALABRAS CLAVE

CITES, historia de vida, mercado de fauna, rasgos reproductivos, reproducción en cautiverio

圈养及野生来源鸟类的贸易与繁殖性状的关系

【摘要】 野生动物贸易是一项价值数十亿美元的全球业务, 涉及数百万人、数千个物种和数亿生物个体。了解作为贸易目标的物种是否在繁殖性状上有所不同, 以及贸易上的偏好是否在圈养和野生来源的物种之间存在差异是十分重要的。本研究利用贸易涉及的所有鸟类物种、贸易清单、符合《濒危物种国际贸易公约》(CITES)的贸易记录, 以及一系列鸟类繁殖参数的综合数据, 研究了野生动物贸易是否与特定的生活史性状有关, 并分析了生活史特征与圈养和野生来源鸟类的贸易量之间随时间推移的关系。我们发现在所有贸易、CITES附录和符合CITES的贸易中, 大型鸟类更有可能被贸易和被列入附录, 但它们的寿命和性成熟时间与是否被贸易或被列入CITES附录没有关系。在2000-2020年间, 被贸易的圈养及野生鸟类的性状几乎涵盖了物种性状的所有数值范围。圈养物种的贸易量与相对较长的寿命和较早的性成熟时间显著有关; 这些关联随时间推移保持稳定且基本没有变化。在野生来源鸟类的贸易中, 物种性状与贸易量的关联更不明确。只有体重与贸易量存在明显的关联, 且随时间推移从负相关变为正相关。尽管繁殖性状在圈养鸟类的贸易中很重要, 但物种水平的变异在贸易中仍占主导地位, 即使是同属性状相近的物种在贸易量上也有很大差异。收集性状数据并将其纳入鸟类圈养繁殖的可持续发展评估, 对于确保准确的配额和反洗钱至关重要。**【翻译:胡怡思; 审校:聂永刚】**

《濒危野生动植物种国际贸易公约》, 圈养繁殖, 生殖特征, 生活史

INTRODUCTION

Wildlife trade affects 24% of all terrestrial vertebrates (Scheffers et al., 2019); contributes to elevated extinction risk for many species (Marsh et al., 2022); correlates with declines in species abundances (Morton et al., 2021); is a vast global industry worth billions of dollars (Haken, 2011); and involves the movement of millions of individuals annually (Harfoot et al., 2018). Consequently, trade provides crucial livelihoods and sustenance for millions of people globally (Nielsen et al., 2018). Reconciling the demand and supply of species to meet societal needs and conserve wildlife in a changing world is a key challenge.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) sets regulations for parties to the convention to implement when trading listed

species internationally. Listed species include those threatened by trade (Appendix I), that could become threatened by trade (Appendix II), and those for which parties want specific international assistance in monitoring their trade (Appendix III). The convention makes provisions for wild- and captive-sourced organisms in trade and has advocated captive breeding as a potential conservation tool (CITES, 2010) because captive-bred trade offers an avenue to relieve pressure on wild populations, especially those that are threatened or declining (Tensen, 2016). This is despite criticism that illegal trade and laundering can proliferate under the guise of trade in captive-sourced individuals of certain species (TRAFFIC, 2016). Many heavily commercialized species are predominantly traded from ranched or captive-breeding facilities (Nickum et al., 2018) rather than wild sources. However, the proportion of trade in captive-sourced

organisms varies by taxa, by region, and through time (Harfoot et al., 2018; Nijman, 2010). Trade from wild- or captive-sources varies according to species' suitability for captive breeding (Challender et al., 2019), demand-driven preference for a particular source (Hinsley & 't Sas-Rolfes, 2020), and relative availability and costs of either source. All 3 factors are nuanced and poorly understood for many markets and species. A preference for certain physical traits has been shown for some taxa (e.g., white and multiple flowers in orchids [Hinsley et al., 2015] and color uniqueness in birds [Senior et al., 2022]), but the importance of reproductive traits across taxa has received less attention.

Considering the reproductive traits of traded species is crucial because these traits predispose species to overharvesting (Milner-Gulland & Akçakaya, 2001) and may make a species less economically viable for captive breeding. Combinations of slow traits, including high longevity, late age of maturity, and low reproductive rates, can predispose species to declines from even light collection pressure (Jolly et al., 2021). Conversely, some characteristics, such as early maturation, rapid growth, or large numbers of offspring (often correlated with low adult survival and longevity), typically allow high offtake. Reticulated pythons (*Malayopython reticulatus*) have historically been traded in the tens of thousands without evidence of decline, a result attributed to both their large clutches, ecological flexibility, and cryptic behavior (Shine et al., 1999).

The same reproductive traits that mediate species response to offtake also have a key role in determining species suitability for commercial-scale captive breeding (Phelps et al., 2014). Traits, such as high age of maturity, large size, or various specialized breeding strategies, potentially make captive breeding economically infeasible (Challender et al., 2019), suggesting that relying on captive breeding to offset demand from wild-sourced individuals may not be possible across a large set of species. However, if trade in captive organisms has developed over time to encompass and accommodate species across the spectrum of reproductive traits (e.g., slow to fast maturation, small to large body size), then there is potential for traders to shift between organism sources across the life-history spectrum. However, the diversity of life-history traits in trade has remained largely unquantified beyond highlighting an association between larger body size and global trade presence (Scheffers et al., 2019; Yin et al., 2020). A key knowledge gap therefore remains: whether the trade in captive and wild individuals targets different dimensions of life history and whether this translates from trade presence to trade volumes (e.g., trade in captive-sourced organisms focuses on faster reproducing or smaller species to maximize output or space).

We investigated how reproductive diversity in traded bird species is partitioned between captive- and wild-sourced birds. Birds are an excellent taxon to quantify this because of the relative abundance of trait data, high volumes traded, and broad transition from wild sources to captive sources (Harfoot et al., 2018) and because the interplay of wild and captive sourcing is crucial for resolving the current trade-driven Southeast Asian songbird crisis (Jepson, 2016; Shepherd & Cassey, 2017).

We considered the association between life-history traits and trade via 2 key objectives. First, we sought to identify whether life-history traits associate with a species' probability of being traded or listed under CITES (hereafter CITES listed). Second, we sought to quantify trait–volume dynamics in the international trade of threatened species to determine whether captive- and wild-sourced trade captures distinct facets of reproductive diversity and to determine whether these associations remained constant or shifted through time to encompass an ever-changing diversity of species.

METHODS

Data sources

We used a published data set (Scheffers et al., 2019) of all bird species and their trade status (traded or not) and the full list of all current CITES listings (accessed from <https://checklist.cites.org/#/en>). For data on trade volumes over time, we used the most up-to-date version of the CITES trade database (version 2022.1), which tracks the international legal trade in CITES-listed species and contains 23,680,557 directional trade records. Details of the raw data structure can be found at the point of access (<https://trade.cites.org/>). A recently published database of avian life-history characteristics for all species (Bird et al., 2020) was used for species reproductive traits. Three traits of particular interest were selected and used for subsequent analysis: body mass (small size indicates faster life history and large size correlates with hunting and presence in the bird trade [Keane et al., 2005; Scheffers et al., 2019]); age at first reproduction (low values indicate fast life histories and high reproductive output; other traits held constant); and maximum longevity (low values indicate fast life history, but high longevity relative to size and age of maturity may be of particular interest to pet owners).

For incorporation in models that included species phylogenetic relatedness, we cross-referenced the updated avian taxonomy used by Scheffers et al. (2019) with the avian phylogeny developed by Jetz et al. (2012). The updated avian taxonomy included recently split species that can be resolved to a single species in the phylogeny, which we did. This resulted in a list of 10,254 updated bird species resolving to 9839 species in the phylogeny; thus, there were multiple instances in which a single species in the phylogeny linked to multiple species in the updated Scheffers et al. (2019) data. To this, we matched the avian life-history database. Body mass values were missing for 2.06% of species (203 of 9839 species in the phylogeny). We calculated the phylogenetic signal with Pagel's lambda (Goolsby, 2016) and found that body mass had a significant and strong signal ($\lambda > 0.9$, $p < 0.05$). Therefore, we used phylogenetic imputation with 1 maximum clade credibility tree derived from 1000 possible avian phylogenies (Jetz et al., 2012) to estimate these missing values under Brownian motion and assumed uncorrelated traits. To test for phylogenetic signal and trait imputation, we used the Rphylopars package (Goolsby et al., 2017).

Data preparation

For our first objective, to identify whether life-history traits associate with a species' probability of being traded or listed under CITES, we minimally processed the CITES data to get a list of species traded in any way since 2000 (details in Appendix S1). The CITES species names extracted from the CITES database cover a range of resolutions including subspecies, and sometimes multiple species are listed under a variety of synonyms. This naming diversity was resolved with our processed species lists of traded species. Similarly, we resolved the names of all CITES-listed bird species, where again some species considered synonymous are listed separately and some listed names correspond to more than one recognized species. Thus, to our list of 10,254 bird species (where 4259 were recorded as traded overall), we recorded 1242 species as CITES traded (i.e., is both listed in the CITES Appendices and has been traded internationally while listed) since 2000 and 1473 as currently CITES listed. In the Results, the diversity of species in exporter-reported trade is presented and in Appendices S2 and S3 we report the results with the importer-reported data.

For our second objective, to contrast trait–volume dynamics and trait–temporal dynamics, we focused on the commercial trade in birds from captive and wild sources and used established methods (Harfoot et al., 2018; Morton et al., 2022; Robinson & Sinovas, 2018) (details in Appendix S1). This resulted in a cleaned species-level database of yearly traded commercial volumes of birds from captive and wild sources. Because importation and exportation records differ in the CITES data, we reanalyzed all results with importer-reported values (Appendices S2 & S4–S6). The conclusions remained largely unchanged.

We used the International Union for the Conservation of Nature Red List application programming interface (accessed with `rredlist` R package [Chamberlain, 2020]) to extract historical threat assessments for all traded species. Where species had pre-2000 standard codes (e.g., lr, cd, and nt), these were converted to present standards: lr became least concern; cd and nt became near threatened. We converted all assessments into threatened (T) and nonthreatened (NT) classes for subsequent analyses. Threatened described species classified as vulnerable, endangered, or critically endangered, and nonthreatened described species classified as least concern and near threatened. For each species, we added these time-calibrated threat assessments to their captive and wild time series. We also included the period's species that were not assessed (NE, not evaluated). We considered species assessed as data deficient (DD) as NE because a DD assessment concludes there was inadequate information to make a full assessment and as such the species status cannot be implied. All use of the terms *threatened* and *nonthreatened* and specific statuses, such as vulnerable or endangered, were based on the IUCN Red List assessments, not regional or country-specific terminology.

To this final data set, we added the previously cleaned and imputed life-history trait values. This resulted in a final database of 760 traded bird species, each with 2 series of up to 21 years

each (2000–2020, one for captive and one for wild trade), corresponding threat statuses calibrated through time, annual traded volume, and species-level life-history traits (final data contained 29,514 records).

Statistical analyses

To examine the first set of hypotheses that certain life-history traits correlate with a species' probability of being traded (in all trade generally or through CITES [CITES listed]), we modeled whether a species was traded generally, CITES listed, or CITES traded (since 2000) relative to the species life-history traits. We ran 3 separate models (probability of a species being traded generally, CITES listed, and CITES traded since 2000) assuming a Bernoulli error distribution. The life-history traits modeled were log (base 2) body mass, log age at first breeding, and log maximum longevity; each was mean centered and standardized prior to analysis. All logs were calculated to base 2 to lessen the influence of a very small number of extremely high values. Due to the possible scenario that some of our reproductive traits were perfectly correlated, we assessed this prior to fitting with Pearson's correlation coefficient and found no evidence of perfect correlation (all correlations <0.79). Multicollinearity was assessed after fitting (Appendix S1).

In addition to these 3 population-level effects, we incorporated species phylogenetic nonindependence. From published avian phylogenies (Jetz et al., 2012), we downloaded 1000 complete trees covering 9993 species. As described previously, we resolved our 10,254 species to 9839 distinct species in the phylogenies (resolving instances where species once considered synonymous are now split or where subspecies are now classified as separate species). From the 1000 complete trees, we resolved this to one maximum clade credibility tree and pruned this to our species list. From this, we calculated the phylogenetic variance–covariance matrix. We then fitted our model as a phylogenetic multilevel model. Such a model specifically determines whether species with a high trait (e.g., body mass) for their combination of other traits (e.g., longevity and age at first reproduction) are more likely to be traded or listed. A commonly used alternative method to examine associations between several traits is to fit each separately as the sole predictor. We did not do this because such a method could mask redundant associations (e.g., there is no value in also knowing trait x if trait y is known). Additionally, independent simple models ignore potentially hidden relationships common with correlated reproductive traits (e.g., whether a relatively high body mass for the other trait values is associated with an increased probability of trade).

Priors were specified as weakly regularizing to aid convergence but 0 centered and diffuse because we had little prior certainty of direction or magnitude of effects (normally distributed, mean [SD] = 0 [1]). Each model was run for 1000 iterations, including 500 warm-up iterations, for 4 chains with no thinning. We carried out a number of posterior predictive checks to check model fit, convergence, and the absence of collinearity (Appendix S1).

We assessed the phylogenetic signal of captive- and wild-sourced commercial trade in listed species by appending the lists of commercially traded captive- and wild-sourced species (see “Data preparation”) to the current list of CITES-listed species. In this analysis, we included only traded species listed in 2022 and species that could be resolved to a single species in the phylogeny (hence the reduced number of species compared with the data used to examine trait–volume and trait–temporal dynamics). We quantified the phylogenetic signal of listed species’ presence in the trade in captive- or wild-sourced birds with the D statistic (Fritz & Purvis, 2010).

To examine trait–volume dynamics and trait–temporal dynamics between traded captive and wild birds (second objective), we formulated the simplest theory-driven model of traits in CITES trade through time that respected the structure of the data (namely the time-series nature of observations and the hierarchical structure of repeated observations across non-independent species). The data contained a high proportion of zeroes (years when species that had been traded were not traded) (e.g., a species could have all zeroes for its captive-sourced time series if it was sourced only from the wild). To account for this, we used a hierarchical distributional model that accounted for 2 separate processes, species being traded (reoccurrence) and species volumes when traded. The model used a hurdle negative binomial distribution, in which a Bernoulli distribution was used to model species’ presence and absence in trade, and a truncated negative binomial distribution to model the volumes at which species occur when they are traded. The model parameterization was

$$n \sim \text{hurdle} - \text{NB}(\hat{P}, \mu, \phi), \quad (1)$$

where \hat{P} is the probability of a nonzero value (occurrence in trade), μ is the mean or location parameter of a negative binomial distribution (volume when traded), and ϕ is the over dispersion. This method has particular utility to trade data; separate patterns may associate with species occurrence and volumes (e.g., for a given species, presence may be constant through time, but volumes may be declining).

The minimum model necessary to respect the structure of the data was defined as the fixed effect of time (years 2000–2018, reduced to 0–18, mean centered, and standardized), source (binary variable indicating wild or captive source), and threat category (3-level category: not threatened, threatened, and not evaluated, roughly capturing species rarity). We further included the 3-way interaction (and lower order 2-way interactions) of these variables. This was necessary because previous research on a coarser scale showed diverging trends for captive- and wild-sourced species in trade (Harfoot et al., 2018) and at the species level that threat correlated with differing temporal trends (Morton et al., 2022). Logically, this is also essential because national legislation, and therefore trade, varies depending on whether the source is wild or captive, and less abundant threatened species are less likely to be traded in comparable volumes than more abundant nonthreatened species.

We used a hierarchical structure allowing species intercepts to vary per source and the temporal year trend to vary per source

within species (including the main effect of year). Again, this was essential to capture the many species traded only from one source and allowed species trends to vary freely; assuming the temporal trend for all wild-sourced species only increases or decreases (fixed effect only) is inherently flawed. To incorporate residual temporal fluctuations or shocks (such as large-scale bans [e.g., EU wild bird ban] or novel avian diseases [e.g., H5N1]), we created a categorical year variable (21 levels) and incorporated this as a group effect with varying intercepts per source. Allowing fluctuations to vary per source is logical from a legislative view because trade in wild- or captive-sourced birds will be subject to varying legislative shocks.

To this theory-based minimum model, we added the fixed effects of our life-history traits—body mass, maximum longevity, and age at first reproduction (all converted to log values with base 2 to lessen the influence of extreme values). We allowed these variables to vary by source to examine whether traits associated differently by source. This is logical because certain combinations of traits are potentially less amenable to captive breeding. Similarly, we incorporated trait interaction with time (indexed by source) to probe the temporal stability of trait–volume associations through time. We did not fit the traits independently in separate models for the previously mentioned reasons and because the structure of the data necessitated additional terms. Likewise, we did not use variable selection for the 3 traits because this can produce biased parameter estimates; instead, we presented the full model as outlined above (Forstmeier & Schielzeth, 2011; Freckleton, 2011). We examined whether any traits were perfectly correlated prior to fitting with Pearson’s correlation coefficient and found no such evidence (all correlations <0.75). Multicollinearity was assessed after fitting (Appendix S1). This full model structure was used to parametrize both presence (\hat{P}) and volume when traded (μ) submodels.

We incorporated taxonomic variation dependent on phylogeny via phylogenetic covariance matrices as a separate group effect for both \hat{P} and μ . These covariance matrices were derived using the same method as discussed previously. Zero-centered, diffuse priors (normally distributed mean [SD] = 0 [1]) were specified for model slopes (β), intercepts (α), and standard deviations (σ) (a default Lewandowski–Kurowicka–Joe prior was used for the correlations between grouping factors). Weakly informative zero-centered β priors were used to regularize estimates because they reflect skepticism of large values and shrink posterior estimates toward zero (Winter & Bürkner, 2021). This model was run for 3000 iterations, including 1000 warm-up iterations, for 4 chains with no thinning. See Appendix S7 for a summary of the full model parameter estimates. We carried out extensive posterior checks that are detailed in Appendix S1.

We summarized all posterior values and uncertainties for presentation to the median and 90% highest density interval (HDI). Where we discuss the positive or negative association of parameters, we used the direct probability of direction (pd) to assess the certainty that an effect was positive or negative and 97.50% as a cutoff for a clear evidence of a directional association (Makowski, Ben-Shachar, Chen, et al., 2019). All metrics and summaries are calculated from the full posterior.

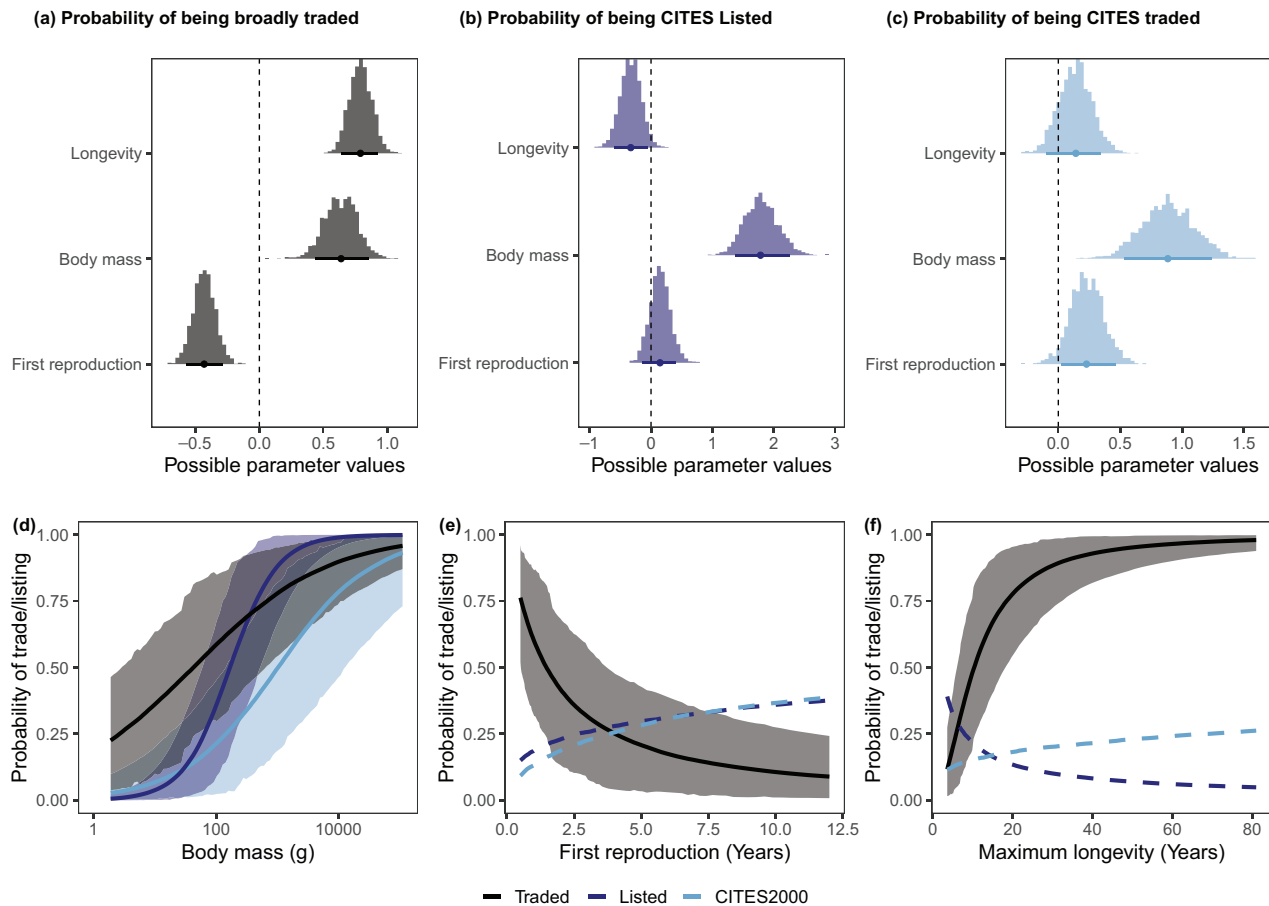


FIGURE 1 Association between life-history traits (longevity, body mass, and age at first reproduction) and species (a) probability of being broadly traded, (b) being listed in the CITES Appendices, and (c) being CITES traded since 2000. All estimates are the direct effect assuming other traits are held constant (points denote the median and horizontal lines the 90% highest density interval). Conditional posterior probability estimates across the full-observed range of that trait with the remaining traits held at their mean for (d) body mass (axis on a log₁₀ scale for clarity), (e) age at first breeding, and (f) maximum longevity (lines, median; dashed lines, coefficient direction uncertain; shading, 90% highest density interval). Conditional estimates are estimated across the full observed range of that trait with the remaining traits held at their mean.

All models were fitted with brms (Bürkner, 2017). For posterior summarizing and testing, we used tidybayes (Kay, 2020) and bayestestR (Makowski, Ben-Shachar, & Lüdtke, 2019). All general data were handled and plotted using tidyverse ecosystem (Wickham et al., 2019), and all phylogenies were handled using ape (Paradis & Schliep, 2019) and plotted with ggtree (Yu et al., 2017). Data and code used for this research are available at github.com/OMorton/Morton_et_al_Traits_in_trade_2023.

RESULTS

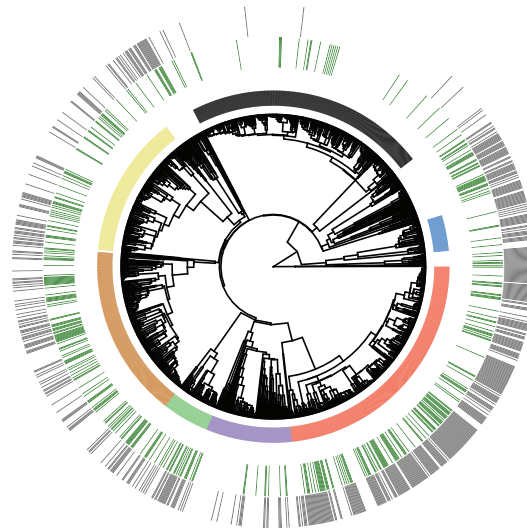
Life-history trait associations with a species' probability of being traded or CITES listed

The association between life-history traits and trade was clearest in the probability of a species being broadly traded (Figure 1a; Appendix S8). As hypothesized, increasing species body mass relative to their other traits had a clear association with increas-

ing probabilities of being broadly traded, CITES listed, and CITES traded (Figure 1a–d). Species with a low age at first reproduction relative to their other trait values also had a clear positive association with their probability of being broadly traded, but no such associations were present for their probability of being listed or CITES traded (Figure 1a–c,e). Increasing species longevity was also associated with a greater probability of being broadly traded (Figure 1a–c,f). No similar pattern was observed in either CITES listing or presence in CITES trade. Although more uncertain, CITES listing displayed the opposite association for birds with a short longevity for their size and age at maturity; they were more likely to be listed ($\beta_{\text{longevity}} = -0.33$, HDI -0.61 to -0.06 , $pd = 97.35\%$).

There was no evidence of phylogenetic clustering in traded captive ($D = 0.32$, $Pr_{\text{random}} = 0$, $Pr_{\text{Brownian}} = 0$) or wild birds ($D = 0.69$, $Pr_{\text{random}} = 0$, $Pr_{\text{Brownian}} = 0$) of CITES-listed species (Figure 2a–c). For certain taxa, wild birds dominated trade over captive-bred birds (e.g., Caprimulgiformes [nightjars, swifts, and hummingbirds]) (Figure 2a), where most trade

(a)



Accipitriformes Caprimulgiformes Falconiformes Galliformes Passeriformes Psittaciformes Strigiformes

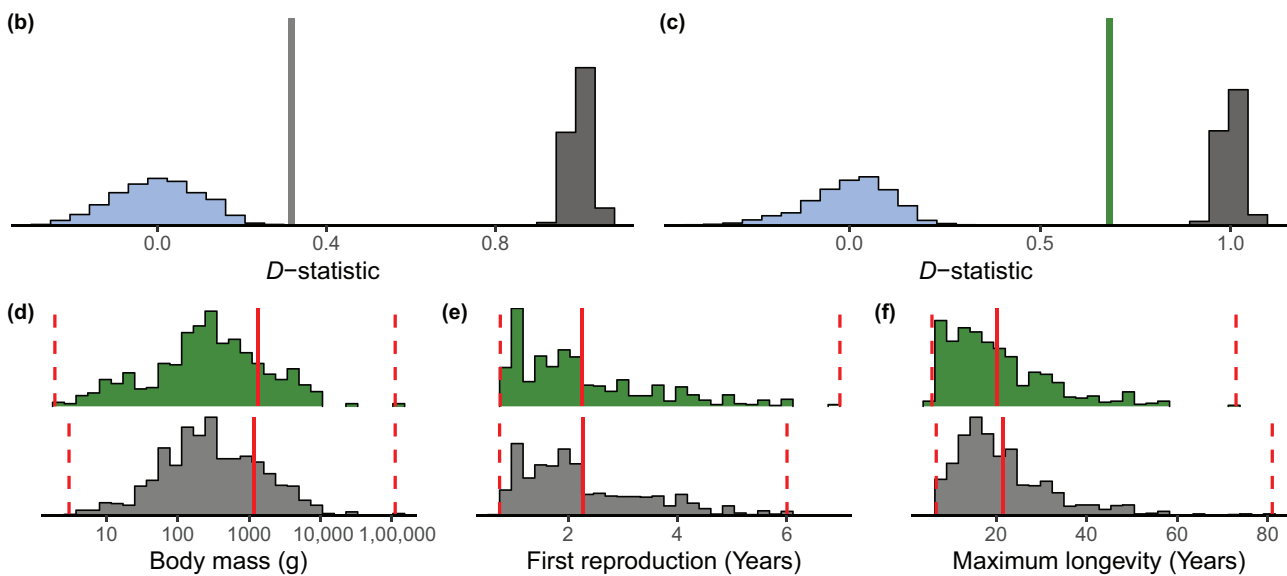


FIGURE 2 Phylogenetic signal of CITES-traded captive- and wild-sourced birds: (a) phylogeny of all currently listed birds (inner ring, taxonomic order of all groups with >25 species listed; outer 2 rings, traded species sourced from captive populations [gray, 628 phylogenetically distinct species] or from wild sources [green, 450 phylogenetically distinct species]; no color in ring, species are listed but have not been commercially traded from either source from 2000 to 2020); (b, c) phylogenetic signal measured by the *D* statistic (blue and gray, random *D* statistic values from null models Brownian motion [blue] and phylogenetic randomness [gray]); vertical lines, observed *D* statistic for captive [gray] and wild [green] traded birds); and (d–f) distribution of body mass, age of first reproduction, and longevity in wild- (green) and captive- (gray) sourced birds in trade (dashed red lines, observed maximum and minimum values traded from each source; solid red line, mean).

diversity came from the hummingbird family, although volumes of wild-sourced species from this group were generally very low. Conversely, captive-sourced trade dominates the trade in Psittaciformes (parrots). Some *Agapornis* (lovebird) species were traded solely from captive sources in volumes over 100,000 whole organism equivalents (WOEs) per year (e.g., Fischer’s lovebird [*Agapornis fischeri*]). High captive-sourced volumes also included much larger species, such as the red-fronted macaw (*Ara rubrogenys*), military macaw (*Ara militaris*), and yellow-

crested cockatoo (*Cacatua sulphurea*) that are traded consistently in the tens and hundreds. Conversely, listed Falconiforme (falcons) and Accipitriforme (other diurnal raptors) species were drawn from a mixture of captive and wild sources over the last 21 years. Many species were traded in relatively low volumes from each source (e.g., golden eagle [*Aquila chrysaetos*], steppe eagle [*Aquila nipalensis*], tawny eagle [*Aquila rapax*]). However, for falcon species highly prevalent in trade, volumes predominantly originated from captive sources. More than 50,000 peregrine

falcons (*Falco peregrinus*), gyrfalcons (*Falco rusticolus*), and saker falcons (*Falco cherrug*) WOE have been traded from captive sources (2000–2020); <10,000 came from wild sources.

Species traded from captive or wild sources spanned nearly the full range of observed species' body mass, age at maturity, and longevity (Figure 2d–f). The very smallest species from wild sources (3 hummingbird species from the *Trochilidae*, each <3 g) were absent from the captive trade. However, for these species, trade in wild-sourced individuals was infrequent and low in volume (Figure 2d). Similarly, the inclusion of slower maturing species in trade from wild sources was driven solely by the inclusion of Rüppell's vulture (*Cypso rüppellii*), which was infrequently traded historically. The also slowly maturing sulfur-crested cockatoo (*Cacatua galerita*), which despite not reproducing until age 6, was consistently traded in the hundreds and thousands from captive sources (Figure 2e). Conversely, the longest lived species in trade, Major Mitchell's cockatoo (*Cacatua leadbeateri*), was only captive sourced (consistently traded between 2000 and 2020). These minor differences at the extreme maximum and minimum trait values were driven by a very small number of species. This suggests that traded birds from across the reproductive spectrum can largely be sourced from both captive and wild sources.

Contrasting trait–volume dynamics and trait–temporal dynamics between captive and wild trade

Trait–volume relationships in the trade of CITES-listed species varied considerably depending on whether birds were captive or wild sourced (Figures 3 & 4a), with the wild-sourced traded birds generally having fewer associations with life-history traits than captive-sourced birds. Similarly, associations between volumes of captive-sourced birds and traits showed stability through time and remained largely consistent from 2000 to 2020 (Figures 3 & 4b).

We found an uncertain association between yearly volumes and increasing mass in the captive-sourced birds (Figure 3a,b; Appendix S9) that did not change through time (Figure 4b). In wild-sourced birds, the association between body mass and trade volume varied through time (Figures 3c & 4b); species presence in trade favored larger individuals more in recent years ($\hat{P} \beta_{\text{body mass} \times \text{year}} = 0.33$, HDI 0.10 to 0.53, $pd = 99.47\%$). No such temporally varying association was found between species mass and volumes when traded (Figure 4b); volumes when traded of wild-sourced birds had a declining yet uncertain association with increasing body mass (Figure 4a) ($\mu \beta_{\text{body mass}} = -0.48$, HDI -0.88 to -0.03 , $pd = 96.58\%$). This indicated that although larger species had a greater probability of reoccurring in trade (particularly in recent years), smaller species were likely present in greater volumes when they were traded.

There was no evidence of associations between age at first reproduction and volumes when traded or trade presence in either captive- or wild-sourced birds or through time (Figure 4b; Appendix S10). For captive-sourced traded species

with greater ages at first reproduction for their longevity and size, species were less likely to be present in yearly trade ($\hat{P} \beta_{\text{first reproduction}} = -0.59$, HDI -0.99 to -0.21 , $pd = 99.40\%$) and if traded only in lower volumes than earlier maturing species ($\mu \beta_{\text{first reproduction}} = -0.54$, HDI -0.80 to -0.29 , $pd = 100.00\%$). However, age at first reproduction had an uncertain association with wild-sourced birds' (Figure 3f) presence in trade and volume when traded (Figure 4a).

Similarly, the association between species longevity and captive-sourced birds in trade remained consistent through time (Figures 3g,h & 4b; Appendix S11). Species with a high longevity for their size and age at first reproduction were associated with an increase in trade volume from captive sources (Figure 3e). Species' probability of occurrence in trade ($\hat{P} \beta_{\text{longevity}} = 2.20$, HDI 1.82 to 2.59, $pd = 100.00\%$) and volumes when traded increased as longevity increased ($\mu \beta_{\text{longevity}} = 0.72$, HDI 0.50 to 0.96, $pd = 100.00\%$) (Figure 4a). However, there was some evidence that the association between longevity and trade in wild-sourced birds shifted through time for the association with volume when traded and to a lesser extent with species' presence in trade. Volume when traded became increasingly more negatively correlated in recent years ($\mu \beta_{\text{longevity} \times \text{year}} = -0.25$, HDI -0.41 to -0.09 , $pd = 99.32\%$), despite remaining generally uncertain. Conversely, the association between longevity and species' presence became more positively correlated with time ($\hat{P} \beta_{\text{longevity} \times \text{year}} = 0.22$, HDI 0.02 to 0.40, $pd = 97.33\%$), although this also remained uncertain ($pd < 97.50\%$).

Overall, species life-history traits explained only a tiny fraction of the variance in trade records, even after accounting for temporally flexible associations (Figure 4c). A variance decomposition analysis highlighted that they recovered <0.001% of the predicted variation when the hierarchical terms were included (Figure 4c). This highlights the importance of incorporating species-level terms independent of trait relationships. For example, Fischer's lovebirds, black-winged lovebirds (*Agapornis taranta*), and gray-headed lovebirds (*Agapornis canus*) are all reproductively similar, small-bodied, colorful, and either least concern or near threatened. However, black-winged and gray-headed lovebirds were traded in yearly volumes only in the hundreds or thousands from captive and wild sources, respectively, whereas Fischer's lovebirds were consistently traded in the hundreds of thousands from exclusively captive sources. This dramatic interspecies variation was poorly explained by life history and likely would not be captured by further morphological nuance (e.g., color), thus highlighting the dominant role interspecies variation had in international trade, independent of phylogeny or function.

DISCUSSION

Our results advance understanding of the role that life-history traits have in species' presence and volume in the wildlife trade. We found clear trait associations with predominantly the captive-sourced trade of CITES-listed birds, and this association

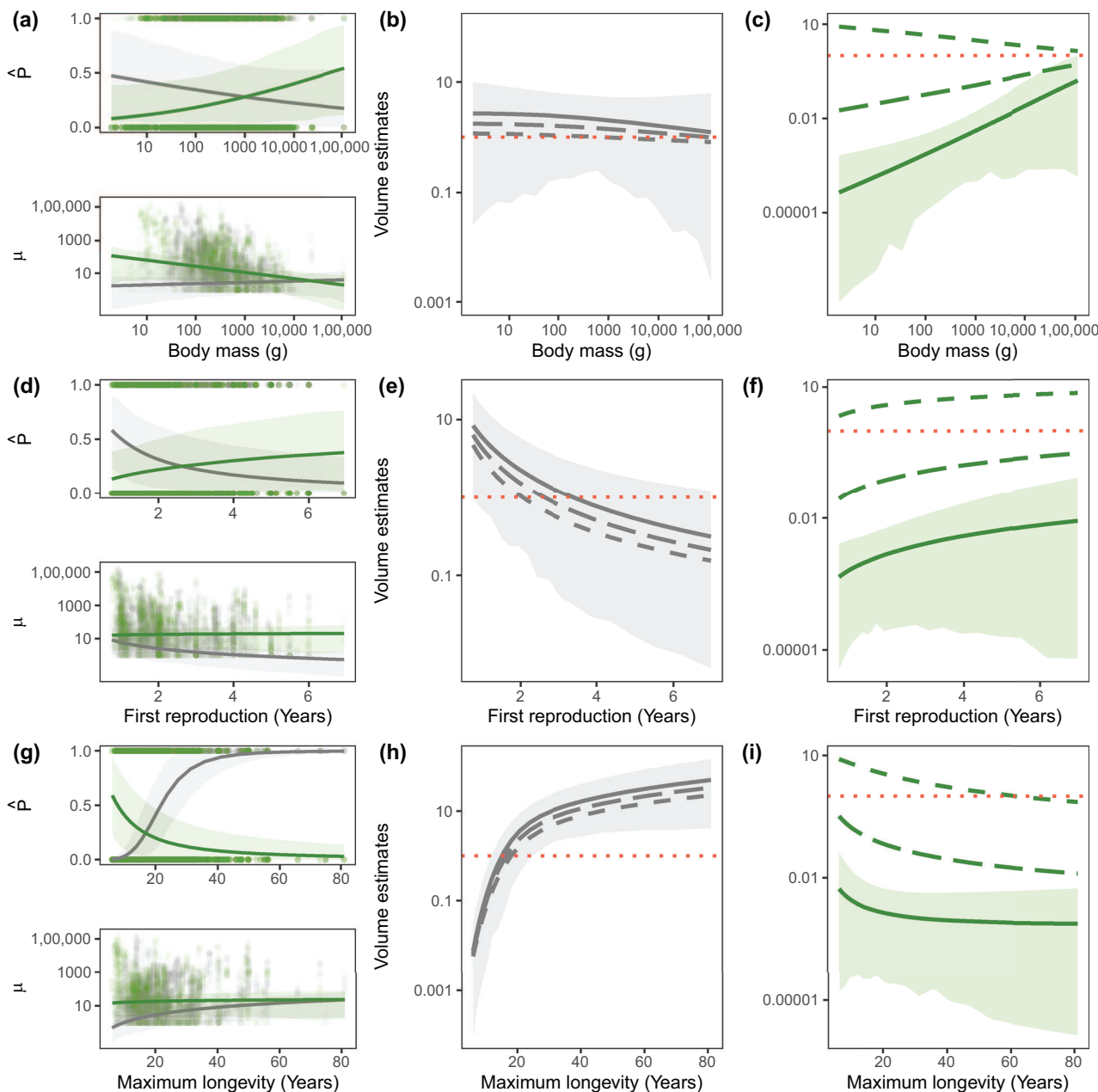


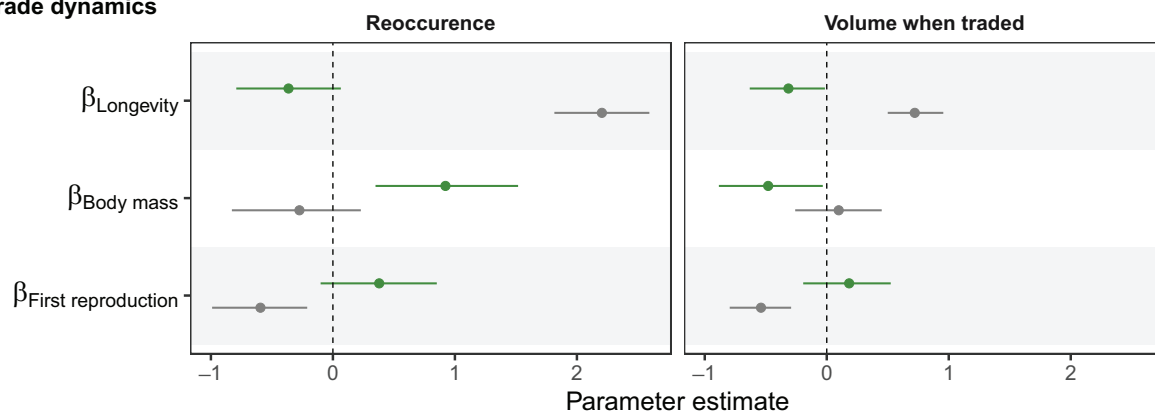
FIGURE 3 Conditional associations of life-history traits on trade volume in captive- and wild-sourced birds for the average species: (columns a, d, g) separate presence in trade (\hat{P}) and volumes when traded ($\hat{\mu}$) model estimates overlaid on all observed data (nonfocal traits held at the mean and year set at 2000) (points, data across years 2000–2020); trends in (columns b, e, h) captive- and (columns c, f, i) wild-sourced birds in trade by life-history trait; focal traits of (rows a, b, c) body mass, (rows d, e, f) age at first reproduction, and (rows, g, h, i) maximum longevity based on the full hurdle negative binomial distribution (solid lines, posterior medians for trait–volume associations in 2020; long-dashed line, associations in 2010; dashed lines, trait–volume associations in 2000; labeled year lines, variation is directional [Figure 4]; shaded ribbon, 90% highest density interval for 2020; red line, shows 1 whole organism equivalent to ease visual comparison across panels). Captive- and wild-sourced estimates of volumes of traded birds are shown in separate panels for clarity due to the low expected volumes of wild-sourced birds traded. Nonfocal traits are held at their mean, and threat status is fixed at nonthreatened.

remained largely stable over the last 20 years despite large-scale shifts in trade dynamics. Conversely, trade in wild-sourced birds showed a generally more uncertain and time-varying association with reproductive traits. Certain traits have been examined previously in the context of species desirability in trade (Hinsley et al., 2015); we examined less-considered reproductive traits and their small association with international trade.

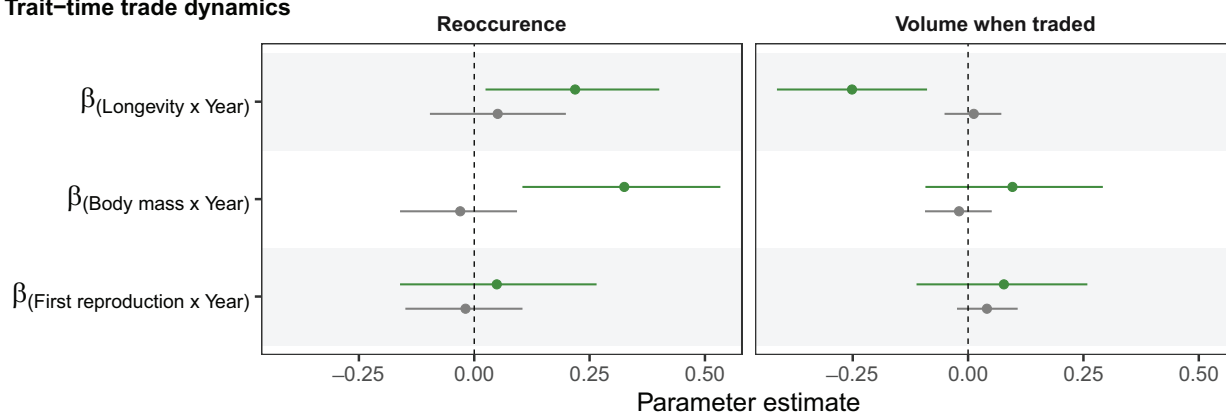
Traits in trade

As in previous studies (Scheffers et al., 2019; Yin et al., 2020), we found that body mass correlated with species’ probability of being generally traded, CITES listed, and CITES traded. Larger bodied individuals have been historically targeted to maximize hunter cost per unit effort (Jerzolimski & Peres, 2003), and

(a) Trait trade dynamics



(b) Trait-time trade dynamics



(c)

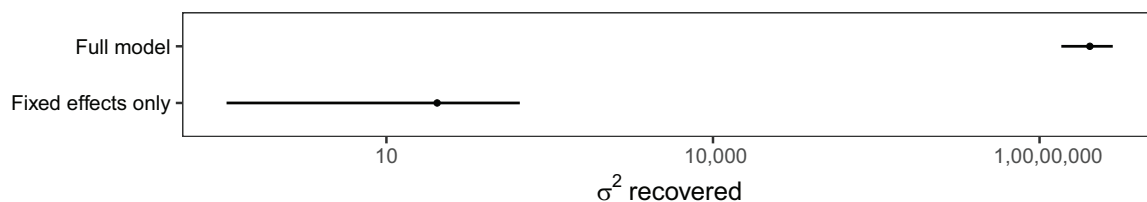


FIGURE 4 (a) Life-history parameter coefficients associations with yearly reoccurrence in trade (\hat{P}) and volumes when traded (μ) for captive- and wild-sourced birds in trade. Because of the higher order interaction with time, these are the associations when the time-varying association is fixed at zero (e.g., 2010 when the year is 0 on the standardized scale). In the presence of a directional trait-time association, (shown in [b]) these should not be interpreted directly except as the association when the standardized year is 0. (b) Life-history parameters varying association over time on trade presence and volume when traded (nonzero, association between a trait and trade changed over the 21-year period). (c) Results of variance decomposition analyses of the posterior predictive distribution (contrasting predictive distribution conditioned on full set of group-level terms [species variation dependent on phylogeny, species variation independent of phylogeny, and global interyear fluctuations] and distribution not conditioned on group-level terms) (points, posterior medians; error bars, 90% highest density interval; green, wild-sourced birds; gray, captive-sourced birds).

globally such species are at increased risk of extinction (Ripple et al., 2017). Although body mass had a clear association with presence in trade (Figure 1), the varying association between body mass and volumes when traded of wild-sourced birds was more nuanced. This likely indicates that much of the diversity originally present has since disappeared from the trade in wild-sourced birds (Morton et al., 2022). Similarly, the lack of association with captive-sourced birds in trade likely comes from the presence of both small (e.g., Fischer's lovebird) and large species (e.g., *Psittacus erithacus*) in relative abundance (Wang et al., 2021).

The increasing volumes of captive-sourced birds in trade with proportionately greater longevity for their size are likely due to the popularity of large, long-lived *Psittacidae* parrots in trade (Sanchez-Mercado et al., 2020), a group commonly traded in large volumes and amenable to captive breeding. The increasing trade volumes of captive-sourced birds with lower ages of first reproduction suggest a complementary trade-off with relatively faster reproducing species for their size or longevity. This potentially reflects the economic necessity of relatively early maturing species for captive breeding facilities. However, the prevalence of thousands (of WOE) of both characteristically faster

breeding (e.g., yellow-fronted Parakeet [*Cyanoramphus auriceps*]; age at maturity: <1 year) and slower breeding (e.g., yellow-crowned Amazon [*Amazona ochrocephala*]; maximum longevity: 56 years) captive species in trade suggests captive breeding can supply species across the reproductive spectrum.

The general lack of clear trait associations in the trade of wild-sourced birds can potentially be attributed to its opportunistic nature and the importance of habitat or range features mediating how accessible species are, rather than specific reproductive traits. Less-quantifiable traits could also be mediating demand and therefore volumes in the trade of CITES-listed species. Such traits could include song beauty or complexity, plumage pattern or color (Senior et al., 2022), or specific utility (e.g., raptors for sport hunting [Panter et al., 2019]). To date, most studies have focused on considering trait associations based on global data sets of traded and untraded species. Such studies provide key insight into global patterns, but mask potential nuance. For example, although larger species are more likely to be present in trade, they may only be traded in smaller volumes. This and the intraspecific temporal diversity in volumes traded highlight that traits alone are not enough to understand preferences and trends in the international trade of listed species. For example, even between the morphologically similar congeneric species, orange-winged amazon (*Amazona amazonica*) and scaly-naped amazon (*Amazona mercenaria*), the former is traded in the thousands from wild sources, whereas the latter has only been infrequently traded in single digits from captive sources.

Although we broadly quantify variation in key avian reproductive traits, we could not incorporate certain factors, such as nesting strategy. Hornbill species, for example, generally require existing tree cavities to reproduce, although there has been some success with artificial nests (Chaiyarat et al., 2012). The presence of species with such specialized strategies from captive sources reflects either the flexibility of captive breeding enterprises or the laundering of wild-sourced species into the captive-sourced trade, as is believed to be the case for many Papuan hornbills (*Rhyticeros plicatus*) exported by the Solomon Islands (Nijman & Shepherd, 2015).

Policy recommendations and conclusions

The Convention has supported the expansion and maintenance of captive breeding to supply the trade in listed species urging parties to provide “incentives to captive-breeding operations... such as faster processing of permit applications ... or possible reduced export fees” (specifically regarding Appendix I species) (CITES, 2010). Given the decline of wild-sourced individuals in trade and the complementary rise of captive-sourced trade (Harfoot et al., 2018), a key issue for ongoing trade sustainability is whether the captive trade can expand to encompass all species in demand. Our conclusions are mixed in this regard. The stability of trait–trade associations through time in the captive trade suggests that traits association with reoccurrence and volume are stable through time and do not appear to be decaying to include species across the diversity of traits. However, the fact that trade from captive and wild sources has encompassed nearly the same

range of reproductive trait values suggests that at some scale, captive breeding across the diversity of species may be possible.

A further question is how commercial traders will balance demand and ease of breeding (e.g., how do costs and benefits balance when producing many, cheap small birds, compared with fewer, expensive large birds). The large-scale transition to captive-sourced species will have considerable implications on individuals involved in trade supply chains at many levels. The generally low barriers to entry often make the commercialization of wild-caught species an attractive income source even in crowded markets (Krishna et al., 2019). Although captive-sourced production of some species for local consumption and sale also has low barriers to entry and high potential earnings (e.g., bamboo rats [Roe & Lee, 2021]), scaling avian captive breeding to supply international demand is unlikely to be possible at the individual and local level without significant investment. Crucial to the wider acceptance and proliferation of captive breeding will be species affordability and public acceptance of their quality. In Brazil, it is estimated that a captive-bred bird can be up to 10 times more expensive than a wild-sourced bird (da Nobrega Alves et al., 2010), thus hampering captive breeding’s role in protecting wild populations. Similarly, in Sumatra captive breeding also has a high cost and is further hampered by the perceived low quality of captive-reared birds relative to wild-sourced birds (Burivalova et al., 2017). Thus, the proliferation of captive breeding must be coupled with effective marketing and price incentives if it is to replace trade in some wild-sourced species.

To trade captive-sourced listed species, CITES currently requires a legal acquisition finding (LAF) for the parental stock and relatively sparse biological information, and only for Appendix I species. The main responsibility falls on the scientific and management authorities of the exporting party to ensure the validity of the LAF. A review of the Indonesian captive-breeding production plan showed that it contained inaccurate or unrealistic biological parameters for 76.7% ($n = 99$ of 129) of amphibian, mammal, and reptile species; 88 species had lower reproductive outputs when corrected parameters were used; and 38 species had quotas set that exceeded the maximum possible output when the inaccurate parameters were used (Janssen & Chng, 2018). This points to the potential for laundering wild-caught individuals so that captive facilities can maintain their output. Future work could extend criminological frameworks, such as CRAVED or CAPTURED (Moreto & Lemieux, 2015; Pires & Clarke, 2012), which are commonly used to assess why certain species or products are poached or illicitly traded, to incorporate why species may be laundered rather than legitimately bred. Such approaches could embed costs, feasibility (e.g., life-history and dietary traits), and market conditions (as in Challender et al. [2019]) in a broader taxonomic and criminological setting to identify species likely to be fraudulently traded as captive bred.

Validating captive-sourced trade records remains a challenge. Global high-resolution data are available for many nuanced geospatial variables of ecological and conservation interest, so the relative paucity and reticence to encourage the collation of data pertaining to trade sustainability must be challenged.

A potentially proactive measure would be the registration of all captive breeding facilities for listed species (not just for Appendix I species). Such a registry containing the year breeding became active and the size of the initial stock could then be cross-referenced with trade and trait data to identify concerning patterns, such as sudden spikes in productivity shortly after establishment in species with high ages of maturity. As international trade continues to pivot to favor trade in captive-sourced individuals, understanding what drives the vast differences in traded volumes of morphologically and reproductively similar species and how this similarity will interact with conservation remains crucially important.

ACKNOWLEDGMENTS

We thank the Sheffield Mynas research group for comments and feedback on earlier versions.

OPEN RESEARCH BADGES



This article has earned Open Data and Open Materials badges. Data and materials are available at https://github.com/OMorton/Morton_et_al_Traits_in_trade_2023 and https://github.com/OMorton/Morton_et_al_Traits_in_trade_2023.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Morton, O., Scheffers, B. R., Haugaasen, T., & Edwards, D. P. (2023). Association of reproductive traits with captive- versus wild-sourced birds in trade. *Conservation Biology*, e14076. <https://doi.org/10.1111/cobi.14076>