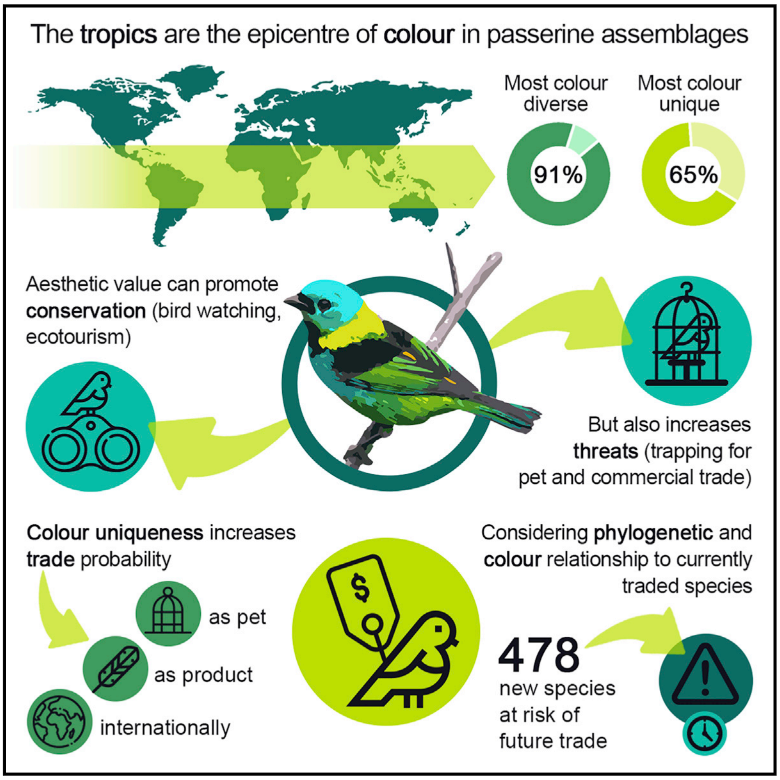
Report

Current Biology

Wildlife trade targets colorful birds and threatens the aesthetic value of nature

Graphical abstract



Highlights

- Color is associated with threat and trade in passerines globally
- Hotspots of color diversity and uniqueness are concentrated in the tropics
- Based on their traits, 478 additional species are likely targets for future trade
- The loss of threatened and traded species could erode nature's aesthetic value

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In brief

Senior et al. combine data on passerine plumage color with bird trade data, finding that unique coloration—prized by birdwatchers and typical of flagship species—is also associated with trade and extinction risk. The tropics are an epicentre of color, but loss of desirable species would erode aesthetic value and mute nature's color palette.

Senior et al., 2022, Current Biology *32*, 4299–4305
October 10, 2022
https://doi.org/10.1016/j.cub.2022.07.066

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Report

Wildlife trade targets colorful birds and threatens the aesthetic value of nature

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https://doi.org/10.1016/j.cub.2022.07.066

SUMMARY

A key component of nature's contribution to people is aesthetic value.[1,2] Charismatic species rally public support and bolster conservation efforts.[3,4] However, an insidious aspect to humanity's valuation of nature is that high value also drives wildlife trade,[5,6] which can spearhead the demise of prized species.[7–9] Here, we explore the antagonistic roles of aesthetic value in biodiversity conservation by using novel metrics of color to evaluate the aesthetics of the most speciose radiation of birds: passerines (i.e., the perching birds). We identify global color hotspots for passerines and highlight the breadth of color in the global bird trade. The tropics emerge as an epicentre of color, encompassing 91% and 65% of the world's most diverse and most uniquely colored passerine assemblages, respectively. We show that the pet trade, which currently affects 30% of passerines (1,408/5,266), traverses the avian phylogeny and targets clusters of related species that are uniquely colored. We identify an additional 478 species at risk of future trade based on their coloration and phylogenetic relationship to currently traded species—together totaling 1,886 species traded, a 34% increase. By modeling future extinctions based on species' current threat status, we predict localized losses of color diversity and uniqueness in many avian communities, undermining their aesthetic value and muting nature's color palette. Given the distribution of color and the association of unique colors with threat and trade, proactive regulation of the bird trade is crucial to conserving charismatic biodiversity, alongside recognition and celebration of color hotspots.

RESULTS & DISCUSSION

Geography and taxonomy of color

For better or worse, aesthetics can determine both necessity and opportunity for wildlife protection. It is therefore critical to understand the diversity of aesthetic value from a biogeographic perspective. A long-standing assumption, dating back to Darwin and Wallace,[10,11] is that the tropics are dominated by colorful species. Here, to identify the most color-diverse and colorful locations for passerines globally, we provide maps of passerine plumage coloration. Our maps are based on human-centred metrics of color (red, green, and blue [RGB] values; Figure 1) for six anatomical plumage patches of most known species of passerines (order: Passeriformes; n = 5,358 species[12]). Although birds see color differently than humans (in particular, birds can detect ultraviolet light), human-based color vision models are appropriate here, because human-centred measures of color are the most relevant to quantifying species' aesthetic value to people.

Recent studies have expanded on Darwin's observation of the "gaudy colouring of the intertropical productions,"[10] documenting latitudinal gradients of color in eggshells[14] and sexual dichromatism.[12] Our results confirm Wallace's famous observation that "the number of brilliantly-coloured birds in almost every part of the tropics is very great."[11] We quantified color using various metrics. In the simplest, we summed the number of species representing each of 15 color categories, defined based on the hue-saturation-brightness colorspace (Table S1). Color diversity was defined as the volume of the minimum convex hull uniting species in three-dimensional RGB space, while color uniqueness is the average distance of each species in RGB space from its nearest neighbors. Each metric—color richness (Figure S1), color diversity (Figures 2A and 2B), and community average color uniqueness (Figures 2C and 2D)—was found to peak in the tropics.

Globally, the tropics contain 81% of the most species-rich communities, compared to 91% and 65% of the most color-diverse and uniquely colored passerine assemblages, respectively. Latitudinal patterns of color are further highlighted by the marginal density plots to the right of maps in Figure 2 and persist when accounting for the greater number of passerine species in the tropics (Figures 2B and 2D). Of the 15 broad color categories (Table S1), colors like azure, cyan, and chartreuse green are more commonly observed in species traded as pets

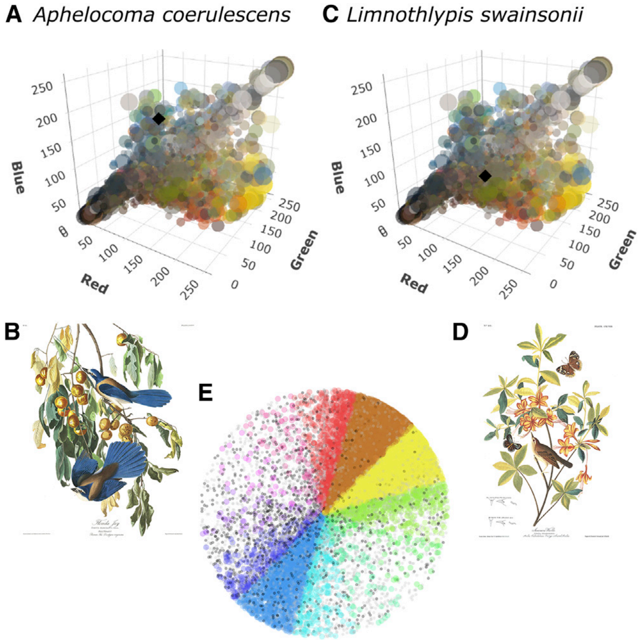

Figure 1. The distribution of color in the passerines of the world

(A–E) Two example species are given for comparison: the Florida scrub jay (*Aphelocoma coerulescens*) (A and B), with a blue crown, and Swainson's warbler (*Limnothlypis swainsonii*) (C and D), with a brown crown. (A) and (C) plot the crown color of all passerines globally in RGB space, with the example species represented by a black diamond in their respective panels. Illustrations are from plate 87 (B) and plate 198 (D) of Birds of America,[13] courtesy of the John James Audubon Center at Mill Grove, Montgomery County Audubon Collection, and Zebra Publishing. (E) depicts the distribution of hues for all anatomical locations of all species across the color wheel (Table S1). Dark and light datapoints are also plotted according to hue but appear dark or light because of low saturation and/or low brightness.

than in non-traded species ($p < 0.05$; Figure S2A) and are geographically skewed towards tropical latitudes (Figure S1). Light- and brown-colored plumage, conversely, was more common in non-traded species than in traded species. Pure white, however, is a relatively unique plumage color (Figure 1) within the broader "light" color category, such that average color uniqueness was high in snow-camouflaged but depauperate Arctic communities,[15] contrasting with the low color diversity of these same communities (Figure 2). Color uniqueness showed a strong phylogenetic signal ($\lambda = 0.59$, $p < 0.001$; Figure 3), with some of the most striking, diverse, and uniquely colored passerine families (Data S1 A)—such as birds of paradise (Paradisaeidae), cotingas (Cotingidae), and tanagers (Thraupidae)—largely restricted to the tropics. Other tropical families are dominated by brown species (e.g., antbirds [Thamnophilidae]), while some extratropical families, such as tits (Paridae), also include several uniquely colored species.

Color in trade

Close to 3,000 bird species globally—approximately 30% of all extant birds[9]—are traded as pets or products (e.g., as feathers, bills, or eggs). This trade is, in large part, driven by humanity's passion for beauty and aesthetics, based on attributes like color, pattern, shape, and texture. While legitimate beauty industries, such as cosmetics, fashion, and art, gross over US$500 billion annually, aesthetics also drive one of the world's largest illegitimate businesses: the illegal wildlife trade, which reaps from US$5 billion to US$23 billion annually.[16] Unsustainable legal trade can be similarly devastating and driven by aesthetics. For example, the plumage trade of the mid-1800 and early 1900s was linked to drastic declines in bird species like the white-colored great egret (*Ardea alba*), the maroon-brown *augustavictoriae* subspecies of Raggiana bird of paradise (*Paradisaea raggiana*), and pink-colored roseate spoonbills (*Platalea ajaja*). Colorful species also tend to sell for more in the pet trade than dull-colored species.[5] The plum-headed finch (*Neochmia modesta*), for example, sold for around AU$52.50 in Australia between 2003 and 2014, while the congeneric crimson finch (*Neochmia phaeton*) sold for four times more, at AU$225.[5]

Using the recently published Songbirds in Trade Database (SiTDB),[17] we find that the exploitation of songbirds by trade is closely linked to their coloration. In total, pet trade impacts 1,408 passerine species ($\sim$30%), and trade status was non-random with respect to phylogeny ($D = 0.62$, $p < 0.001$; Figure 3). Species with more unique coloration were both more likely to be traded as pets ($p < 0.001$; Figure 4) and more likely to be classed as threatened ($p < 0.001$), and this was also the case when tested with an alternative trade database from Scheffers et al. (2019).[9] Although we cannot rule out other potential disturbances as primary drivers of threat in colorful and traded birds, we believe the relationship between aesthetic value and pet trade is the most logical explanation and is supported by similar studies on parrots.[18–20] Pet trade was notably intense in colorful families such as the birds of paradise (Paradisaeidae) and weavers (Ploceidae). The slope of the relationship between trade probability and color uniqueness varied across families, with some—such as estrildid finches (Estrildidae)—demonstrating a higher intercept, indicative of a high probability of trade even at relatively low values of color uniqueness. An alternative metric of color, contrast ratio, was not a strong predictor of pet trade in passerines ($p > 0.05$).

Comparing among trade types based on data from Scheffers et al. (2019),[9] color uniqueness was a stronger driver of the pet trade than the trade of birds as products (Figures 4A and 4B). This is intuitive, since the trade of birds as products includes many items that are for medicinal uses or comprise aesthetically valuable parts other than plumage (e.g., bills), compared to relatively few products for which market value is expected to be influenced by the aesthetic value of plumage (e.g., taxidermied birds and fly-fishing lures). Conversely, the importance of color as a predictor of the pet trade confirms that color is indeed a component of aesthetic value that humans desire in their pets.

Within the pet trade, data from the SiTDB[17] revealed that increasing color uniqueness is correlated with an increasing probability of international trade ($p < 0.001$; Figure 4D), but not of domestic trade ($p > 0.05$; Figure 4C). The latter may instead be primarily driven by characteristics such as song,[21] availability, or affordability.[6] There is also evidence of regional variation (Figure S3B), with several zoogeographic realms,[22] such as the Neotropical and Oriental realms, demonstrating generally higher color uniqueness in species that are traded domestically

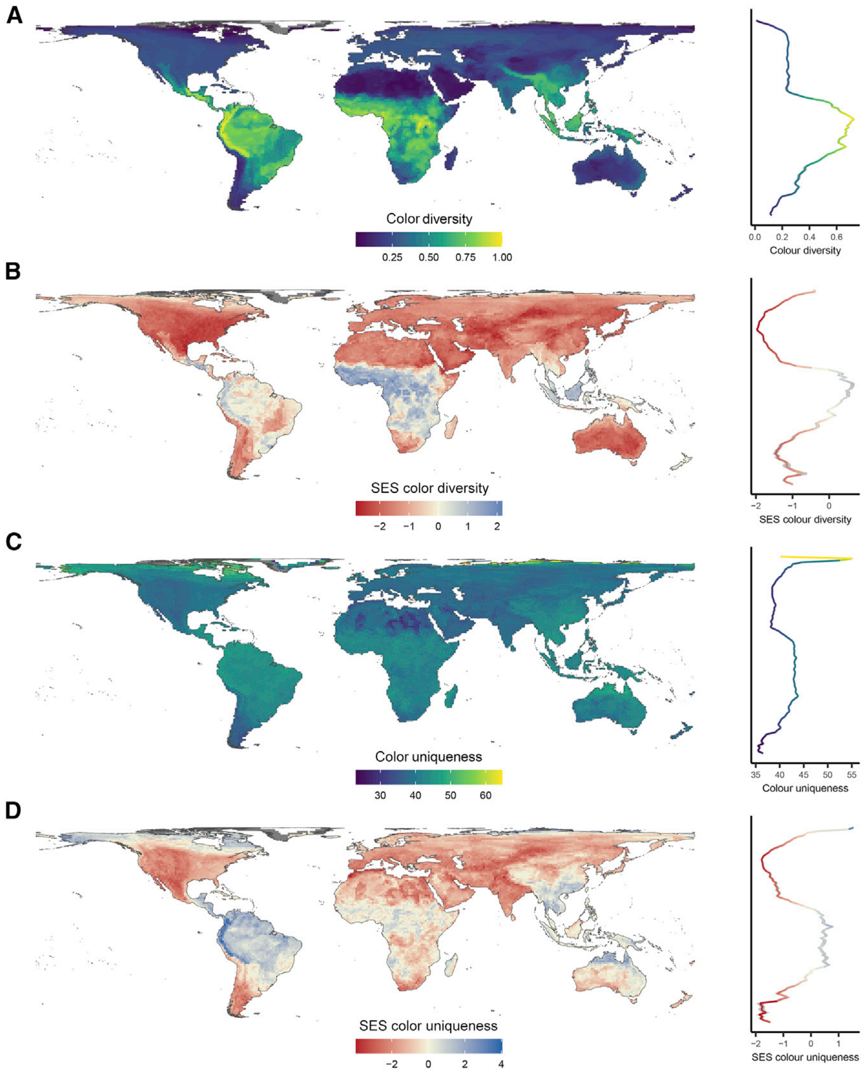

Figure 2. Spatial distribution of color in passerines

(A–D) Color is captured by various metrics: color diversity (A) and its standardized effect size (SES; B), plus color uniqueness (C) and its SES (D). Negative SES values (red) indicate lower color diversity or color uniqueness than expected, while positive values (blue) indicate greater color diversity or color uniqueness than expected. Marginal plots on the right-hand side represent the mean latitudinal value (with 95% confidence intervals in grey).

See also Figure S1.

compared to species that are not traded domestically, while the opposite is true elsewhere, including the Nearctic. As color uniqueness increases, the probability that species are traded internationally increases most rapidly for Critically Endangered species, which underscores important interactions between aesthetic value, trade, and extinction risk. More colorful species trade at higher prices,[5,6] and increasing rarity feeds back to make trade more profitable, which may deplete wild populations.[23]

The impact of trade on wild populations can be mitigated if individuals are sourced from captivity. However, the relationship between color and trade was generally stronger where individuals were primarily sourced from the wild rather than from captivity (Figures 4E and 4F), which could suggest that if there is a general demand for colorful pet birds, it is not currently supplied by captive breeding. The exception was uniquely colored and Critically Endangered species, which had a high probability of being traded only if individuals were primarily sourced from captivity. This may be because rarity and law enforcement make Critically Endangered species both harder to find and harder to trade, combined with possible laundering of wild-caught individuals as captive bred.[24] At a global scale, our study quantifies how species' coloration influences susceptibility to enter the wildlife trade, which is, in turn, associated with increased risk of extinction.[7]

The future of color

As the abundance of targeted species declines, trade shifts to congenerics with similarly desirable features.[9,25] Since pet trade non-randomly targets specific colorful clades (Figure 4), we can predict which species not yet (or not yet known to be) traded are at high risk of future trade when currently traded congeneric species become rare or go extinct. Of the 3,858 passerine species not currently present in the pet trade, we estimate that between 95 to 478 species are at risk of future trade based on >75% and >50% probabilities, respectively (Data S1B). Given the considerable time lags associated with establishing trade restrictions,[26] it would be prudent to proactively monitor those species at higher risk of being targeted by trade in the future, particularly where we suspect that such trade would negatively impact wild populations.

The association of colorfulness with trade and threat status paints a potentially drabber future for passerines. Based on simulated scenarios in which currently threatened and traded species go extinct, we predict loss of absolute avian community color diversity most notably in the tropics, including Southeast Asia and Brazilian Atlantic Forest (Figure S4). Relative to the number of species removed, however, North Africa, Australia, and New Zealand are the places predicted to experience disproportionate loss of community color diversity (Figure S4). Similarly, greater than expected declines in community-level color uniqueness, driven by the loss of individual unique species, were predicted for Australia and New Zealand, as well as the Andes, the Caribbean, and parts of North America (Figure S4). As scenarios become more extreme (i.e., greater loss of currently traded species), they become more uncertain. Without conservation, extinctions could contract avian colorspace, with a shift away from blue hues and towards orange and brown (Video S1).

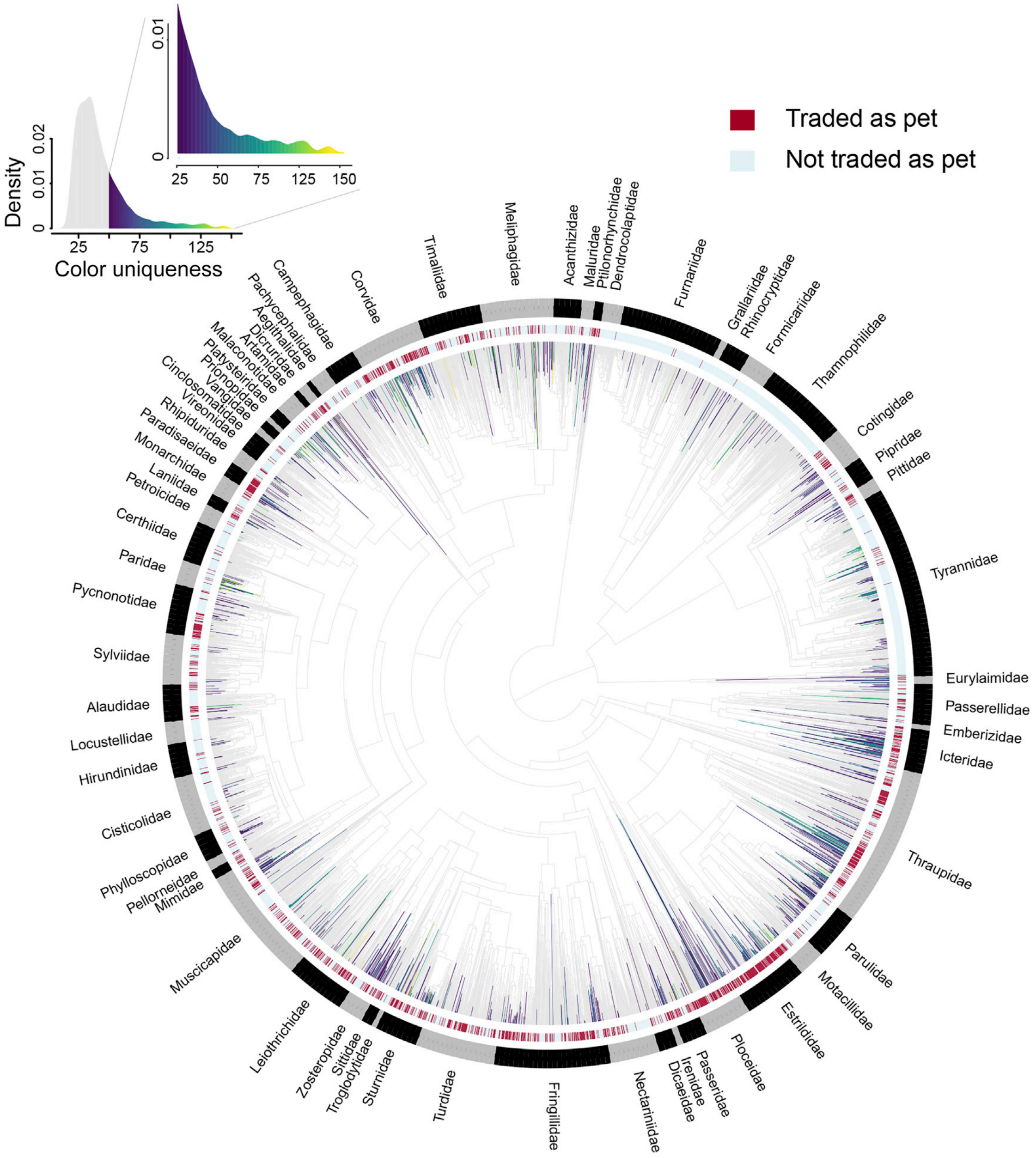

Figure 3. Phylogeny of color in passerines traded as pets

Branch colors depict color uniqueness from low values (<50) in grey, to medium (purple) and high (yellow). The same color scheme is used in the inset, which displays the density distribution of color uniqueness. The outermost ring identifies passerine families, and the inner ring identifies whether species are traded as pets (red) or not (blue). Note that this phylogeny depicts only species with threat and trade information. For visual simplicity, we also exclude families with fewer than ten species.

See Figure S3A for a simplified phylogeny of the top 20 most uniquely colored families.

The conservation of color

The same factors that make colorful birds suitable flagship species to promote conservation[18,27,28] could also make their protection more acutely necessary, because color drives their global trade (Figure 4)—an irony that complicates the conservation of birds. The uniquely colored Bali myna (*Leucopsar rothschildi*), for example, is an important flagship species that is also critically endangered, in large part because of its high desirability in the pet trade.[29] Similarly, the endangered Sumatran laughingthrush (*Garrulax bicolor*) is prized for its attractive song and is valuable in both the pet trade[21] and as a flagship species for zoos. Both of these species also score among the top 20 most uniquely colored passerines. Our study celebrates the astonishing color spectrum that exists in nature but also critically identifies where proactive conservation efforts might need to focus—towards colorful

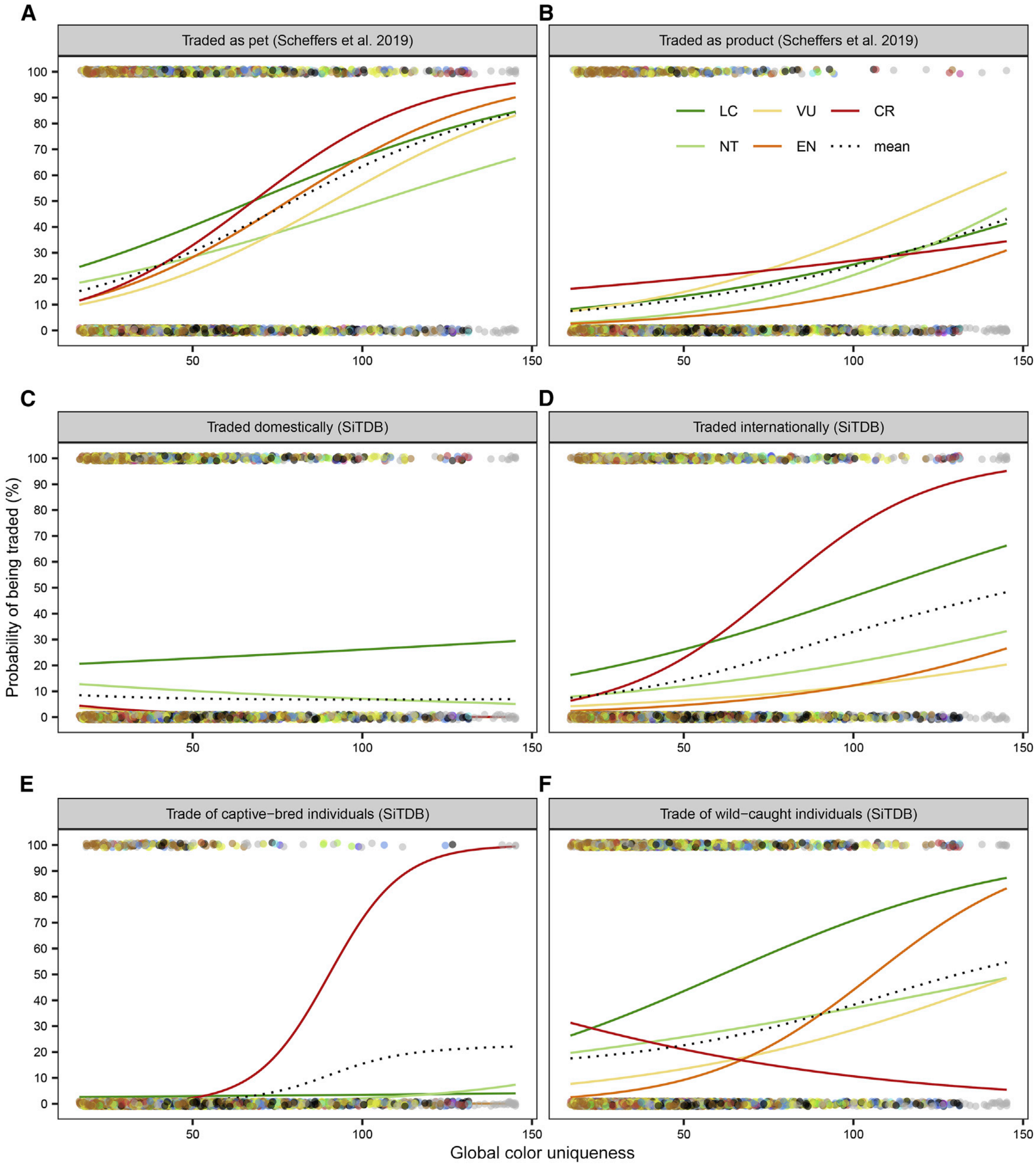

Figure 4. Relationship between species-level color uniqueness and the probability of a species being traded

Colored lines differentiate between Red List categories (Least Concern, dark green; Near Threatened, pale green; Vulnerable, yellow; Endangered, orange; and Critically Endangered, red), with a black dotted line for the mean across all categories.

(A and B) The top row is based on data from Scheffers et al. (2019)[9] and separates trade into pet trade (A) and trade of products (B).

(C–F) The middle and bottom rows are based on data from the SiTDB[17] and compare domestic (C) versus international pet trade (D) and the pet trade of captive-bred (E) versus wild-caught individuals (F). Semi-transparent background points indicate raw values, shaded according to the color category to which the species' crown was assigned.

See also Figures S2–S4.

species with a high probability of being targeted by trade in the future (Data S1B).

As we focused on passerine coloration, we did not assess the relationships between color, threat, and trade for other notably colorful and highly traded bird groups, such as parrots and hornbills.[18] The relationship between color and trade is much better studied in these groups, particularly parrots,[19,20] whereas songbirds have typically been considered to be traded largely for their song, especially in Southeast Asia[21,30] (but see Vall-llosera and Casey[5]). Here, we argue that color is also an important component of songbird trade. Combining the different facets of species' aesthetic and cultural value to identify their additive and interactive influence on the wildlife trade would be a fruitful avenue for future research.

Conserving nature's aesthetic value through protection of the most colorful places on Earth will be broadly beneficial to global biodiversity, because most of these areas are located in the tropics, where most terrestrial biodiversity remains[31] and is under threat.[32] Safeguarding color diversity particularly requires protecting at-risk species and places against unsustainable exploitation, while respecting cultural values of traditional communities. For select passerine families, such as Australasian wrens (Maluridae), species that are more uniquely colored are also more evolutionarily distinctive ($p = 0.0025$; Data S1C), such that the loss of these species would disproportionately erode community phylogenetic diversity.[33] For other families, there is no evidence of a correlation between evolutionary distinctiveness and color uniqueness, though we do not yet know the contribution of uniquely colored species to functional and acoustic diversity.

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services explicitly recognizes aesthetic value under the "physical and psychological experiences" category of "nature's contributions to people."[1] Our study empirically assesses that value through the lens of plumage coloration. People care about conserving aesthetically appealing species,[4] and birdwatching generates income for local communities and finances avian conservation.[3] Yet, what appeals to the public and birdwatchers also appeals to traders. We show that color diversity and uniqueness in passerines is exceptionally high in the tropics, but uniquely colored bird species are both vulnerable and traded. Colorful species can play the part of both icon and victim in the conservation of color, and the balance between roles depends on society's ability to sufficiently value and protect nature's aesthetics.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.07.066.

ACKNOWLEDGMENTS

Thanks to IUCN, CITES, and BirdLife International for collating and maintaining the threat, trade, and range data used in this study. Funding was provided by a Royal Society of New Zealand Marsden grant (15-MAU-136; J.D.), and the Alfred P. Sloan Research Fellowship (B.R.S). Thanks also to the two anonymous reviewers, whose comments greatly improved this manuscript.

AUTHOR CONTRIBUTIONS

R.A.S., B.F.O., and B.R.S. conceived the study. J.D. and B.F.O. collected data. R.A.S. and B.F.O. analyzed the data. R.A.S. wrote the manuscript with input from all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: July 23, 2021
Revised: December 7, 2021
Accepted: July 25, 2022
Published: September 15, 2022

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Colour data for passerines.	Dale et al.[12]	Zenodo: https://doi.org/10.5281/zenodo.6577805
Original code used in this analysis.	This manuscript	Zenodo: https://doi.org/10.5281/zenodo.6577817
Additional supplementary material (2 figures, 1 table)	This manuscript	Zenodo: https://doi.org/10.5281/zenodo.6822621
Software and algorithms		
R version 3.6.3, on platform: x86_64 Windows 10 (64-bit)	The R Foundation for Statistical Computing	https://cran.r-project.org/
RStudio version 2021.09.1+372 "Ghost Orchid"	RStudio	https://www.rstudio.com/products/rstudio/download/
Other		
Songbirds in Trade Database (SiTDB)	Juergens et al.[17]	https://doi.org/10.1016/j.dib.2021.107093
Alternative trade database	Scheffers et al.[9]	https://doi.org/10.1126/science.aav5327
IUCN Red List species categories	IUCN Red List	https://www.iucnredlist.org/
Species range maps	BirdLife International	http://datazone.birdlife.org/species/requestdis
Avian phylogeny	Jetz et al.[34]	https://doi.org/10.1038/nature11631
Zoogeographic realm polygons	Holt et al.[22]	https://macroecology.ku.dk/resources/wallace

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Rebecca Senior (rebecca.a.senior@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data have been deposited at Zenodo and are publicly available as of the date of publication. Accession numbers are listed in the key resources table. Summary data are included in Data S1.
- All original code has been deposited at Zenodo and GitHub (https://github.com/rasenior/colour-trade), and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This study builds on existing, publicly available datasets. All data sources are listed in the key resources table.

METHOD DETAILS

RGB data

Colour data were taken from Dale et al. 2015,[12] comprising RGB (red, green, blue) values for males and females of all 5983 passerine species (Order: Passeriformes). We provide a brief summary of these methods, noting that an in-depth description is included in the original publication.[12] Passerine images were scanned from plates in the Handbook of the Birds of the World,[35] and RGB values extracted for six anatomical patches (nape, crown, forehead, throat, upper breast and lower breast) using the R package 'colorZapper'.[36] By quantifying plumage colour from images drawn by humans, using a colourspace tailored to human vision, our metrics are particularly suited to capturing colour as it is perceived and valued by humans.

The colour at a given anatomical patch was defined as the mean R, G and B values across 400 pixels randomly drawn from within each patch. Both sexes of each species were assigned a 'plumage score', based on the percentage of males in the nearest 1% of data points in RGB space.[12] We were primarily interested in colours that are aesthetically appealing to humans, which in sexually dichromatic passerines tends to be males. For each species we therefore selected the sex with the higher plumage score to capture the more colourful sex of that species.

Threat and trade data

Data on species' risk of extinction were derived from the IUCN Red List.[37] We consider as threatened those species under the categories of Vulnerable, Endangered, or Critically Endangered. Non-threatened species are those in the categories Near Threatened or Least Concern. Data used to determine species' trade status originate from two studies. Unless otherwise stated, results are based on trade data from the 'Songbirds in Trade Database' (SiTDB).[17] The SiTDB is the most comprehensive database documenting the trade of live songbirds (commercialised as pets, for expositions, circus, or zoological gardens), combining information from the IUCN Red List and the CITES Appendices, with trade records from several additional sources, such as the USA's Law Enforcement Management Information System (LEMIS), and the TRAFFIC Wildlife Trade Information System (TRAFFIC International). The SiTDB does not, however, include comprehensive information on the trade of birds as dead products (commercial bushmeat, trophy hunting, clothing, medicine, or religion), which can instead be obtained from Scheffers et al. 2019.[9] Scheffers et al. used string matching algorithms and manual verification to collate trade data, again from the IUCN Red List and the CITES Appendices. After verifying that the two datasets produced comparable results for the trade of live passerines (see 'Statistical analyses'), we used data from Scheffers et al. 2019 in one analysis only: to compare trends between colour uniqueness and the trade of live versus dead passerines (i.e. pet versus product).

Distribution and phylogeny

We obtained species range maps from BirdLife International, from which we created a global 110 x 110 km presence/absence grid projected onto a cylindrical equal-area projection. We determined species presence in a cell if its range intersects with that cell. We excluded all grid cells with less than 30% land cover from our analyses. We define a community as the set of species present in a grid cell. We explored biogeographic patterns in colour and trade using boundaries of zoogeographic realms.[22]

We used the phylogenetic tree from Jetz et al.[34] overlaid on the Hackett family-level backbone, which represents the most recent high-level avian topology available.[38] This phylogeny is available in a set of 10000 trees, from which we obtained a single Maximum Clade Credibility (MCC) tree for use in downstream analyses. The MCC was obtained using the maxCladeCred function from the R package 'phangorn', version 2.4.[39] All analyses were restricted to the 5831 passerine species included in the avian phylogeny and, where relevant, the species with range data (n = 5358) and with information on both threat and trade status (n = 5266).

Colour metrics

To qualitatively describe global patterns of colour in passerines we converted colour values from RGB colour space to the hue-saturation-brightness (HSB) colour space, which more closely resembles how humans perceive colour attributes.[28] Hue refers to the pure colour of interest, with values across the colour wheel ranging from 0-360° (Figure 1C). Saturation and brightness (also known as 'value') describe colour intensity and darkness, respectively, ranging from 0-100%.

To categorise colours we divided hue into twelve 30° bins, with the central value corresponding to recognised primary, secondary and tertiary colours: red, orange, yellow, chartreuse green, green, spring green, cyan, azure, blue, violet, magenta, and rose (Table S1). Humans perceive very little colour when saturation or brightness are low, hence we included the additional categories 'dark' for colours with a low brightness and which appear more black, and 'light' for colours with both a low brightness and low saturation, which appear more white (Table S1)[28]). At the most extreme minima of brightness and/or saturation, the categories 'dark' and 'light' include the colours black and white, respectively. We also distinguish the colours 'brown' and 'orange' based on saturation and brightness (Table S1), to reflect the negative feelings that people have towards the colour brown.[40] We mapped the richness of each colour category (15 in total) by summing the total number of species in each grid cell with that colour represented by at least one anatomical patch (Figure S1; Data S1A).

To quantify colour diversity within passerine communities (defined as the species present in a grid cell), we calculated the volume of the smallest convex hull that unites all species in RGB space.[41] This approach is analogous to that used for calculating functional richness.[42] Community-wide colour diversity was calculated for each anatomical patch separately, and combined into a single metric of colour diversity by taking the mean across all anatomical patches. To enable comparison of colour diversity across communities with different species richness, we calculated standardised effect sizes (SES). For each community, we randomly resampled the same number of species from the global species pool to create 100 null communities. We re-calculated colour diversity for each null community, and then calculated SES colour diversity as the difference between the observed and mean null colour diversity, divided by the standard deviation of null colour diversity. Positive SES represents higher colour diversity than expected by random chance, whereas negative SES represents lower colour diversity than expected.

From a conservation perspective, species with unique plumage colouration are of interest both because they are irreplaceable, and because they might be attractive to traders. We quantified the colour uniqueness of each species as its mean Euclidean distance in RGB space to the nearest 10% of neighbours (cf. Dale et al. 2015[12]). Colour uniqueness was calculated for each anatomical patch separately, and we use the maximum uniqueness value across the six anatomical patches in downstream analyses. To aggregate colour uniqueness at the community level, we took the mean of species-level colour uniqueness across all species occurring in a grid cell. SES colour uniqueness was calculated for each grid cell in an analogous way to SES colour diversity. Here, a positive SES represents more colour uniqueness than expected by random chance, whereas a negative SES represents less colour uniqueness than expected.

An additional metric that is frequently associated with aesthetic value is colour contrast, which we measured using contrast ratio. We converted RGB scores to relative luminance, which quantifies the relative brightness of a given colour between 0 (black) and 1 (white).[43] Contrast ratio is then given by the maximum luminance across all six anatomical patches (plus 0.05), divided by the minimum luminance across all six anatomical patches (plus 0.05).[43] Values range from a minimum contrast of 1 (the two colours are the same), up to a maximum of 22 (white versus black).

As colour is desired in both the bird trade and in non-exploitative activities, such as bird watching, the relationship between colour, trade, and threat suggests that future species extinctions could erode the aesthetic value of passerine communities over time. To simulate future communities we created 20 scenarios spanning a range of global extinction possibilities, starting with the loss of 5% of currently traded species, incrementally increasing the loss of traded species by 5% each time up to the most severe scenario: loss of 100% of species currently traded as pets. The process of selecting traded species to remove was repeated 100 times for each scenario, and the probability that a given traded species would be selected for removal was always weighted by its probability of extinction (determined by its Red List category).[44] Thus, traded species that are Critically Endangered were effectively removed first, followed by Endangered, Vulnerable, Near Threatened and Least Concern species. The probabilistic nature of our simulations ensured that traded species that are at lower risk of extinction always retained a possibility of being selected (i.e. going extinct), but this was less likely than for more threatened species. Although we acknowledge that multiple disturbances will ultimately drive extinction for most species, our approach here reflects the dynamic nature of real-world trade. Target species can switch rapidly in response to market fluctuations, with the potential to deplete previously stable populations.

In each iteration of each extinction scenario, we recalculated community colour diversity and uniqueness after removal of the target species, and subtracted these values from current colour diversity and uniqueness, to quantify change. At the same time, we created 100 null communities for comparison, removing the same number of species as in the simulated future scenario, but where the species selected for removal were chosen at random from the community species pool (i.e., irrespective of extinction risk or trade status). SES colour loss was calculated as the difference between colour loss under the trade-based scenarios and mean colour loss for the null scenarios, divided by the standard deviation of the null scenarios (Figure S4). A positive SES indicates greater loss of community colourfulness than expected by random extinctions, whereas a negative SES indicates lower loss of community colourfulness than expected.

To visualise changes in the colour of potential future passerine communities we plotted various attributes of community colourfulness. To detect overall shifts of the convex hull in RGB space we calculated the central point ('centroid') of each convex hull for each simulated future community, by taking the mean across all R, G and B values for all hull vertices. Predicted changes in the overall hull shape and location within RGB space are shown in the online animation of Video S1.

QUANTIFICATION AND STATISTICAL ANALYSIS

All analyses were performed in R version 3.6.3,[45] using the packages 'phylolm' version 2.6,[46] 'phytools' version 0.6[47] and 'lme4' version 1.1-27.1.[48] To investigate whether species-level colour uniqueness was associated with trade status and threat status we used phylogenetic generalised linear models (GLMs), because all response variables showed strong phylogenetic signal based on either the D statistic (for binary variables[49]) or Pagel's lambda (for continuous variables[47,50]). Colour, trade and threat status could interact in a variety of ways (e.g. rarity itself drives trade[23]), and trade patterns might be different depending on the nature of trade.

To characterise all components of trade (live and dead birds) we used data from Scheffers et al. 2019.[9] We first verified that this database produced comparable results to the SiTDB for pet trade only, by running two analogous phylogenetic GLMs for whether species were traded as pets (1) or not (0) as a function of species-level colour uniqueness. In one model, whether or not species are traded as pets was determined based on Scheffers et al. 2019, the other based on the SiTDB. Trends were similar regardless of the database used (Figure S2B). We therefore used data from Scheffers et al. 2019 to test separately whether pet trade and trade for products (binary response variables) were associated with colour uniqueness and threat status, and the interaction between them.

It is possible for trade to be sustainable and not a significant threat to wild populations if, for example, trade volumes are low relative to population size, or if most traded individuals are bred in captivity. We also know that the international bird trade changed substantially when the USA and EU banned the import of wild-caught birds.[51] Data availability can make it difficult to account for these factors, because we frequently lack information on when, where and to what extent trade threatens species in the wild. The SiTDB allowed us to unpack some of the nuances by comparing domestic versus international trade of passerines as pets, and by comparing the pet trade of species primarily sourced from captivity versus wild-caught. We again used phylogenetic GLMs to test whether the probability of species being traded as pets was associated with colour uniqueness and threat status, changing only the type of trade that was assessed. In the first comparison, we ran separate models for domestic trade and for international trade. In the second comparison, we ran separate models for trade of individuals primarily sourced from captivity, and then considering only trade of individuals primarily sourced from the wild.

To predict the probability that species will be traded alive in the future, we extracted the fitted values from the phylogenetic generalised linear model of pet trade probability against colour uniqueness. This is equivalent to a phylogenetic logistic regression, where the fitted values represent probabilities of being traded (1) or not (0), and where that probability is influenced by the parameters that are input to the model: colour uniqueness and phylogenetic relatedness to currently traded species. We removed from the list species that are already currently traded as pets (Data S1B).

As we observed a phylogenetic signal for both trade and colour uniqueness, we were additionally interested in the extent to which the relationship between pet trade probability and colour uniqueness varied between taxonomic families. This we assessed using an analogous binomial generalised linear model[48] for the number of traded (versus non-traded) species as a function of colour uniqueness, but with a standard (non-phylogenetic) model framework that instead included a random slope and intercept for taxonomic family. Additionally, the phylogenetic tree (Figure 3) suggested that uniquely coloured species evolved more recently. We tested this hypothesis using a phylogenetic linear model of species' evolutionary distinctiveness (ED)[52] as a function of colour uniqueness and its interaction with pet trade. ED values derive from Jetz et al. 2014.[33] Species with higher ED tend to be more phylogenetically isolated, and therefore have usually arisen further back in evolutionary time, and contribute disproportionately to community phylogenetic diversity.[52]

Finally, we explored whether contrast ratio and particular colour categories were associated with trade. For the former, we used a phylogenetic generalised linear model to test whether contrast ratio and threat status, and the interaction between them, predicted species' probability of being traded alive. For the latter, we note that the definition of colour categories is somewhat subjective (Table S1), but named colours are also intuitive and tangible. Here, we used phylogenetic binomial generalised linear models to model the presence or absence of each of the 15 colour categories as a function of whether or not the species is traded alive.